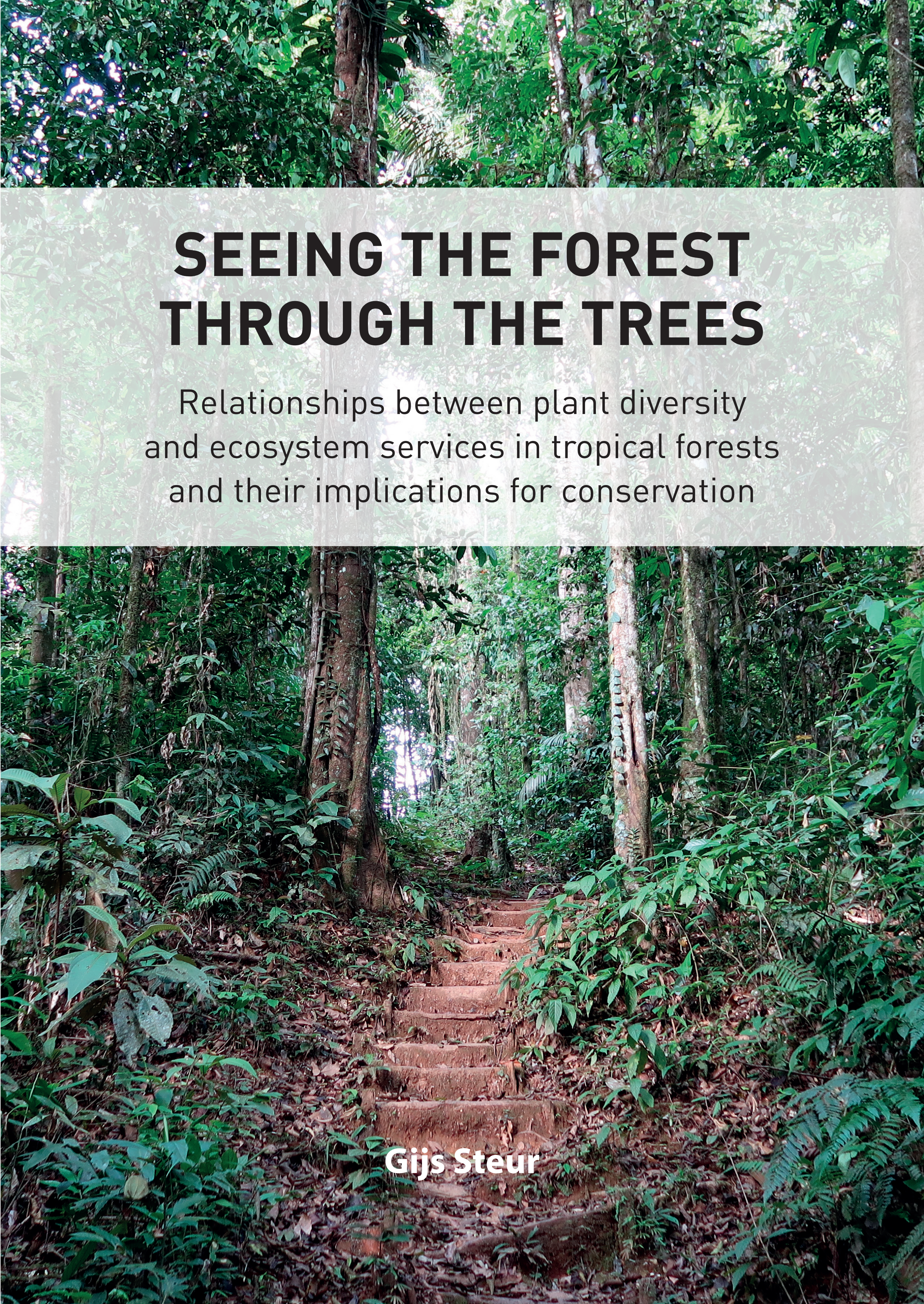

SEEING THE FOREST THROUGH THE TREES

Relationships between plant diversity and ecosystem services in tropical forests and their implications for conservation

Gijs Steur

Seeing the forest through the trees

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Seeing the forest through the trees

Relationships between plant diversity and ecosystem services in tropical forests and their implications for conservation

Door de bomen het bos zien

Relaties tussen plantendiversiteit en ecosysteemdiensten in tropische bossen en hun implicaties voor natuurbehoud

(met een samenvatting in het Nederlands)

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LAY SUMMARY

Tropical forests are rich in plant diversity while also delivering essential 'ecosystem services': goods and services that benefit our well-being. However, tropical forests are under increasing pressure of deforestation and degradation, threatening our well-being and life on Earth in general. New conservation measures are increasingly focussing on protecting ecosystem services under the assumption that biodiversity and ecosystem services are positively linked. If this assumption is true, then protecting ecosystem services would help to protect biodiversity as well. Yet, for tropical forests, relationships between plant diversity and ecosystem services are unclear. This thesis identified three important knowledge gaps. First, it is unclear how plant diversity in a broad sense (including taxonomic, functional and structural diversity) is related to the 'stock' (which represents potential use) and the 'flow' (representing actual use) components of ecosystem services. Second, questions have been raised on how using a different 'plot size' (the geographical area of the vegetation measurement) or 'geographical extent' (the geographical area from which plots were sampled) can affect the outcome of tested relationships. Third and last, it is unknown how the combination of ecological factors, such as the distribution and production of plant species, and socio-economic factors, such as the cost of harvest and the price on the market, related to the delivery of ecosystem services can influence relationships.

Therefore, this thesis aimed to explore the relationships between plant diversity and three important ecosystem services in old-growth tropical forests: carbon storage, timber provisioning and the provisioning of non-timber forest products ('NTFPs'; products such as medicines, food and cultural totems). As there were many potential relationships to consider, this thesis specifically intended to "see the forest through the trees" and to come to general implications for tropical forest conservation.

A systematic review of studies from across the tropics found many relationships between plant diversity and carbon storage, but also identified that relationships concerning timber and NTFP provisioning had been poorly studied. For carbon storage, plant diversity in a broad sense showed mainly positive relationships, regardless of the stock or flow. Although the reported positive relationships were in line with predictions, the discovered mix of positive and negative relationships was surprising. Plot size was found to moderate relationships, where relationships were more often significant when smaller plots (< 1 ha) were used. This moderating effect likely reflects sampling artefacts. For timber and NTFP provisioning, the preliminary findings in the literature suggest that plant diversity might show different relationships to these services than to carbon storage.

As follow-up, this thesis also analysed the relationships between tree species richness (the richness of tree and tree-like palm species) and the stock component of the three ecosystem services, directly. The analyses showed that that tree species richness was consistently positively related to carbon stock in tropical forests, both within and across Amazonia. Evidence was found suggesting that previously reported zero to negative relationships between tree species richness and carbon stock were probably due to moderating effects of sampling a large amount of environmental heterogeneity (the amount of variation in environmental variables such as precipitation or species composition). Such moderating effects can be brought about by including a large geographical extent. The positive relationship between tree species richness and carbon stock suggests that protecting carbon-rich tropical forests in the Amazon is likely to protect concentrations in tree species diversity as well.

By contrast, timber stock and NTFP stock were not consistently related to tree species richness, at least not in the tropical forests of the Guiana Shield (a region within Amazonia). Instead, the stocks of these services are more likely related to the floristic compositions of the different subregions and forest types. Specifically for NTFP stocks in Suriname, it was found that across floristic compositions a very small number of plant species were responsible for half of the NTFP stock, which were named 'NTFP oligarchs'. These findings suggest that forests with high timber and NTFP stocks require additional conservation measures other than those focused on high carbon stocks or high tree species richness.

For NTFP provisioning in Suriname, socio-economic factors such as the demand, costs related to harvest, transport and processing, and harvest rules, proved to be very important. These socio-economic factors determined which forest stocks were harvested, regardless of how much NTFP stock or plant diversity was present. Instead, forests with important NTFP stocks were often located near forest-dwelling communities. As evidence was found that the harvest of such NTFP stocks can be ecologically and socially sustainable, NTFP stocks could be protected by allowing community management of forests. For example, in the form of multiple use protected areas or indigenous territories.

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A white-faced saki (*Pithecia pithecia*) on a *Cecropia peltata* tree on Brownsberg, Suriname, viewing the Brokopondo lake.
Photo by Lieke Guinée.

1

General Introduction

1.1 Ecosystem services as focal point for conservation efforts

Under the ever-increasing human pressure that marks the Anthropocene, natural ecosystems are being degraded and lost at an alarming rate, and this is threatening the world's biodiversity and our quality of life (Cardinale et al., 2012; Díaz et al., 2019; Rockström et al., 2009). A recent assessment of the state of the world's ecosystems by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) illustrated the ongoing decline of natural ecosystems and their biodiversity. According to IPBES, indicators for the extent and condition of natural ecosystems have been showing an average decline of 47% since the 1970s (IPBES, 2019). This has been coupled to large losses of local biodiversity, of 20% on average (S. L. L. Hill et al., 2018). More specifically, since 1500 CE, at least 1,200 unique plant and animal species have gone extinct, and currently, around one million animal and plant species are being threatened with extinction (Díaz et al., 2019). However, during the last 50 years, it has also become increasingly clear that beneficial goods and services that we as humanity derive from natural ecosystems have been sharply declining as well (Costanza et al., 2017; Díaz et al., 2019). As shown by the same IPBES assessment, 78% of assessed ecosystem goods and services that benefit human wellbeing have been declining since the 1970s (Díaz et al., 2019).

In response, policy makers, the academic world and non-governmental organisations are increasingly putting ecosystem services forward as the focal point of conservation efforts (Bennett et al., 2015; Guerry et al., 2015; Mace, 2014; Schröter et al., 2014; Watson et al., 2014). Ecosystem services are an anthropocentric concept that denotes the benefits that humanity derives from ecosystems, including both goods and services (Costanza et al., 2017). It is widely assumed that ecosystem services and biodiversity are positively linked (Mace, 2014). Either biodiversity underpins ecosystem services or biodiversity is an ecosystem service in itself and shows positive covariation with other ecosystem services (Díaz et al., 2006; Mace et al., 2012; Schröter et al., 2014). Such linkages suggest synergies in protecting ecosystem services and biodiversity (Watson et al., 2018). For instance, if biodiversity drives ecosystem services, then safeguarding ecosystem services would support the conservation of biodiversity as well. However, if a limited number or no positive relationships can be found between ecosystem services and biodiversity, then ecosystem service-based conservation measures cannot be expected to consistently contribute to biodiversity conservation.

During the last few decades, multiple meta-analyses have found support for positive relationships between biodiversity and ecosystem services in general (Balvanera et al., 2006; Cardinale et al., 2012; Harrison et al., 2014; Quijas et al., 2010). However, questions remain regarding the relationships between biodiversity and ecosystem services for specific ecosystems. These arise owing to three important general gaps in knowledge, which can be briefly summarised as follows. First, current evidence is fragmented and incomplete as studies use different methods and address limited parts of the wide range of biodiversity-ecosystem service relationships (Balvanera et al., 2014; Bennett et al., 2015; Duncan et al., 2015; Harrison et al., 2014; Ricketts et al., 2016). This obscures the evidence for specific relationships between biodiversity and ecosystem services. Second, it is unclear how spatial scale and its related aspects such as plot size and geographical extent can affect the relationship between biodiversity and ecosystem services (Bennett et al., 2015; Cardinale et al., 2012; Isbell et al., 2017; McGill, 2010; Scheiner et al., 2011). This makes it difficult to infer what are generally valid relationships between biodiversity and ecosystem services. Third, there is a lack of understanding as to how ecosystem services are delivered under the interplay of both ecological and socio-economic factors (Bennett et al., 2015; Costanza et al., 2017; Guerry et al., 2015; Mace et al., 2012; Reyers et al., 2013). This hampers the quantification of ecosystem service and consequently, the identification and prediction of the relationships between biodiversity and ecosystem services (Duncan et al., 2015).

In this doctoral thesis, these gaps in knowledge will be addressed in four studies that focus on the relationship between plant diversity and ecosystem services in old-growth tropical forests. Tropical forests are among the most biodiverse biomes in terms of plant diversity, and they provide many important goods and services that contribute to human wellbeing (Bonan, 2008; Brandon, 2014; Corlett & Primack, 2011; Myers et al., 2000). For instance, it has been estimated that 96% of the worlds tree species and about 66% of all flowering plant species occur in tropical forests (Corlett, 2016; Fine et al., 2008 in Poorter et al., 2015). In addition, global species diversity of ferns, fern-allies and liverworts peak in tropical forests (Corlett, 2016). At the same time, tropical forests provide timber, supply non-timber forest products (NTFPs) such as food, medicines and cultural ornaments (Baraloto et al., 2014; Putz et al., 2012; Ros-Tonen & Wiersum, 2005), store an estimated 54% of the global aboveground carbon stock (Liu et al., 2015), and regulate local and global precipitation patterns (Bonan, 2008; Brandon, 2014; Watson et al., 2018). However, tropical forests are under increasing pressure of deforestation and degradation (Mitchard, 2018), driving species extinction and the loss of ecosystem services (Barlow et al., 2018; Corlett, 2016). For instance, climate models have shown that converting tropical forests to pastureland creates a warmer and drier local climate, thus not only negatively affecting human wellbeing but also accelerating the degeneration of the remaining tropical forest (Bonan, 2008).

This thesis focuses on three important ecosystem services of tropical forests: carbon storage, timber provisioning and NTFP provisioning. There are several reasons to expect relationships between plant diversity and these three ecosystem services. Plant species are the primary producers and the habitat engineers of tropical forests, forming the main component of aboveground biomass (Chave et al., 2006; Corlett, 2016). As the three ecosystem services are derived from aboveground biomass, it can be expected that plant diversity would show relationships to these ecosystem services. In particular, there are three popular hypotheses in the literature on biodiversity-ecosystem service relationships that suggest that there are positive relationships between plant species diversity and carbon storage, timber provisioning and NTFP provisioning. The 'niche complementarity' hypothesis after Tilman et al. (1997) predicts that plant communities with a higher biodiversity will have a higher variation in species traits, and will thus be able to better utilise limited available resources. This would result in increased productivity, which can in turn result in higher aboveground biomass (e.g. Cavanaugh et al., 2014; Finegan et al., 2015; Poorter et al., 2015; Shen et al., 2016; Sullivan et al., 2017; Van De Perre et al., 2018; van der Sande et al., 2017). The 'insurance' hypothesis after Yachi & Loreau (1999) predicts that biodiverse communities contain species that can complement each other in productivity, providing higher resilience against environmental fluctuations. This enables biodiverse communities to maintain a high productivity across time, and ultimately, a higher aboveground biomass (e.g. Poorter et al., 2015; van der Sande et al., 2017). Last, according to the 'selection effect' hypothesis after Tilman et al. (1997), biodiverse communities have a higher chance of including specific species or traits from the larger species pool that are highly productive, which can result in a higher aboveground biomass (e.g. Cavanaugh et al., 2014; Poorter et al., 2015; Shen et al., 2016; Sullivan et al., 2017; Van De Perre et al., 2018). Yet, our understanding of the relationships between plant diversity and these three ecosystem services in tropical forests is incomplete, which is partly due to the three general knowledge gaps mentioned above. Therefore, it remains unclear to what extent ecosystem service-based conservation measures can be expected to contribute to tropical forest conservation and to what extent additional conservation efforts will be needed.

First important contextual background information on ecosystem services and plant diversity is presented in sections 1.2 and 1.3. Subsequently, the three knowledge gaps mentioned above are further explored for tropical forest plant diversity-ecosystem service relationships in sections 1.4, 1.5 and 1.6. Last, section 1.7 presents the aim and research questions of this thesis, followed by a description of the adopted approach.

1.2 What constitutes ecosystem services

The concept of ecosystem services, the expression of benefits that are derived from ecosystems and their biodiversity, has become a highly influential concept in the science-policy discourse. Although the term 'ecosystem services' was introduced into the scientific literature in the 1990s by

Costanza et al. (1997) and Daily (1997), the concept has its roots in the economic and ecological literature since at least the 1970s (Braat & de Groot, 2012; Costanza et al., 2017). The Millennium Ecosystem Assessment (MEA) of 2005 used the concept to analyse and quantify the state of the world's ecosystems and their biodiversity, and this has become increasingly popularised in the policy area (Braat & de Groot, 2012; Ingram et al., 2012). The MEA broadly defined ecosystem services as 'all the indirect and direct benefits that ecosystems provide to human wellbeing' (MEA, 2005) and recognised the following four types: provisioning, regulating, cultural and supporting services. Provisioning services provide useful goods such as food, freshwater and genetic resources; regulating services are related to beneficial ecosystem processes, such as carbon storage, water regulation and pollination; cultural services are the non-material benefits people derive from ecosystems, such as recreation, inspiration and cultural heritage; and supporting services are ecosystem processes that indirectly provide benefits by supporting other ecosystem services, such as soil formation, nutrient cycling and primary production.

Currently, the classification of the MEA still lies at the heart of most of the science-policy interface initiatives that work with ecosystem services, such as the Economics of Ecosystems and Biodiversity (TEEB), the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), and the Natural Capital Project (Costanza et al., 2017). Recently, IPBES has advocated the use of the term 'nature's contribution to people' instead of 'ecosystem services', in order to be more inclusive to different social perceptions (Díaz et al., 2018). However, the use of this term has been criticised as having no added practical value while the term ecosystem services is widely used and recognised in the science-policy interface (e.g. see Braat, 2018, and Kenter, 2018). Therefore, this thesis will use the term 'ecosystem services', following the classification of the MEA.

Ecosystem services are delivered by a complex interplay of ecological and socio-economic factors, making their quantification and valuation challenging (Bennett et al., 2015; Costanza et al., 2017; Guerry et al., 2015; Potschin & Haines-Young, 2016; Reyers et al., 2013; Ricketts et al., 2016). To facilitate their quantification and valuation, multiple conceptual frameworks are in use. However, these frameworks differ in their focus and the terms that they use for different concepts (see for example Costanza et al., 2017; Guerry et al., 2015; Potschin & Haines-Young, 2016). In this thesis, the interpretation and terminology of Hein et al. (2016) and Costanza et al. (2017) are mainly used, and these are described below.

By their nature, ecosystem services are generated by functions and processes of ecosystems that ultimately deliver benefits to human wellbeing. However, it is important to make a distinction between ecosystem 'functions' and ecosystem 'services'. Ecosystem functions are the processes or functions that generate a potential for ecosystem services, while ecosystem services are the processes or functions that are actually enjoyed or used by a human beneficiary (Costanza et al., 2017). In the terminology of Hein et al. (2016), ecosystem functions generate a ‘potential supply’ of ecosystem services, which may or may not deliver benefits. Ecosystem services are also often interpreted in the terms of economic capital. Here, ecosystems represent ‘natural capital’, in which a ‘stock’ and ‘flow’ component can be recognised (Costanza et al., 2017). An ecosystem service stock is a state indicator of the potential of the ecosystem to provide a certain service (e.g. X timber species ha^{-1}) and the flow is the yield of that stock over time that delivers benefits (e.g. Y m^3 timber ha^{-1} yr^{-1}). In this sense, flow can be the amount of service extracted (e.g. with provisioning services) or received (e.g. with regulating services) by people (Hein et al., 2016).

By definition, ecosystem functions only deliver services when they benefit human wellbeing. Thus, ecosystem functions only deliver benefits after human interaction (Bennett et al., 2015; Costanza et al., 2017; Mace et al., 2012). The amount and kind of human interaction needed to deliver benefits differs between ecosystem services, but also between types of ecosystem services. For example, in regulating ecosystem services such as carbon storage, no human interaction is needed for the process of carbon storage to deliver benefits (except for their quantification and valuation). Yet, in provisioning ecosystem services such as NTFP provisioning, NTFPs first need to be harvested before they can ultimately lead to benefits. This requires labour, knowledge and potential tools. In addition, the potential benefits of harvesting need to outweigh the potential costs. In the terminology of economic capital, there can only be a flow of ecosystem service benefits from natural capital after interaction with other forms of capital, for example ‘human capital’, ‘built or manufactured capital’ and ‘social or cultural capital’ (Costanza et al., 2017). In this way, ecosystem services are delivered by means of an interaction between both ecological factors that determine ecosystem functions and socio-economic factors that determine the flow of benefits from these ecosystem functions.

Therefore, to quantify ecosystem services and determine their relationship to biodiversity, knowledge is needed about the ecological and socio-economic factors that determine its stock, its potential supply and/or its flow. For example, when quantifying the stock of plant-based NTFP provisioning, knowledge is needed on which plant species are used to harvest NTFP from, which is determined by their demand (a socio-economic factor), and the number of such species (an ecological factor).

In general, an ecosystem service stock is determined mainly by ecological factors, while ecosystem service flow is often strongly codetermined by socio-economic factors (Ricketts et al., 2016). Therefore, in theory, socio-economic factors could weaken, nullify or even change the direction of the ecologically-driven relationships between plant diversity and the stock component. For example, supposing that species-rich tropical forests contain a high number of timber tree individuals, then this will lead to a general positive relationship between species richness and timber stock. If such species-rich forests are located too far away for human interaction to make extraction profitable (a socio-economic circumstance), there may not be a positive relationship between species richness and timber provisioning. This nullifies the relationships between plant diversity and the stock component for the entire service of NTFP provisioning. In support of the potential nullification of relationships, Ricketts et al. (2016) carried out a meta-analysis of biodiversity-ecosystem services relationships and found that for some ecosystem services, significant relationships of biodiversity which were found for the stock component could not be found for the flow component.

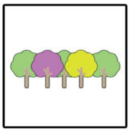
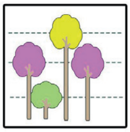
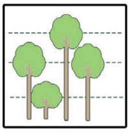
Last, ecosystem services, including their stock, potential supply and flow, are often valued in order to make benefits to specific users explicit, which can then be used to assess potential trade-offs between different uses and/or users of ecosystem services (Costanza et al., 2017). Here, a 'value' of an ecosystem service is a particular interpretation of its expected or realised benefit for a particular group of users (Costanza et al., 2017). According to Costanza et al. (2017), ecosystem services can be valued in multiple ways, expressing the benefits in for example monetary units, time units, labour units or relative terms based on various indicators. Nevertheless, in the literature of biodiversity-ecosystem service relationships, ecosystem services are often valued economically, in particular by using a monetary unit (e.g. Z USD ha^{-1} yr^{-1})(Braat & de Groot, 2012). Reasons for this include the fact that monetary values of ecosystem services are globally comparative and understandable (Laurila-Pant et al., 2015), and have proven to be highly influential to policy makers (e.g. Sheil & Wunder, 2002). Depending on the type of ecosystem services, different techniques for monetary valuation can have advantages. For ecosystem services coupled to markets, such as commercial timber and NTFPs provisioning, it is preferable to use direct market valuation techniques such as the market price (Laurila-Pant et al., 2015). For ecosystem services without markets, such as pollination, techniques such as revealed preference and stated preference can be used (Laurila-Pant et al., 2015).

1.3 What constitutes plant diversity

The MEA approached biodiversity after the definition given by the Convention of Biological Diversity (CBD), being "*the variability among living organisms from all sources including*, inter alia, terrestrial, marine and other aquatic *ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems*" (CBD, 1992). Under this interpretation, when analysing relationships between biodiversity and ecosystem services, biodiversity should be analysed according to its total variation within an ecosystem. However, in practice, biodiversity is often considered synonymous to taxonomic diversity, for example species richness, species diversity or the presence of iconic species (Isbell et al., 2017; Lyashevska & Farnsworth, 2012; Pascual et al., 2021). Such approaches ignore a large part of the variation included in biodiversity, potentially missing important relationships between biodiversity and ecosystem services. For example, Slik et al. (2013) found that the density of large trees in a community (trees with a diameter of 70 cm or more), which represents structural plant diversity, can be an important predictor of carbon stock in tropical forests. In addition, Fauset et al. (2015) found that the maximum diameter that specific tree species in tropical forests can attain, which is a representative of plant functional diversity, can also be an important predictor of carbon stock. Even though species richness can be used as a rough surrogate for diversity in general because species-rich communities are often also rich in functional traits and structural complexity (Tilman et al., 1997), it can only represent diversity to a limited extent (Isbell et al., 2017; Pascual et al., 2021). For instance, species richness does not incorporate species abundances (Isbell et al., 2017), and positive associations between species richness and functional diversity are not always found (Mayfield et al., 2010). Therefore, in this thesis, I include indicators that collectively represent multiple dimensions of plant diversity, including a taxonomic, functional and structural dimension.

It may appear that confusion is possible when recognising functional and structural indicators. After all, both indicators include measurements of structural properties of plants, including morphological, physiological and phenological properties. However, functional indicators are based on structural properties of specific taxa (e.g. species, genera, families) that are interpreted in light of an ecological or evolutionary strategy (i.e. 'traits') (Pérez-Harguindeguy et al., 2016), while structural indicators are based on the structural properties of the entire community, i.e. regardless of taxonomic identity. For example, the community-weighted mean (CWM) of wood density, which is a measure of the dominant value in wood density, is considered a functional diversity indicator (Duncan et al., 2015), while the number of stems or basal area is considered a structural indicator (van der Sande et al., 2017). To facilitate the recognition of the three plant diversity dimensions in this thesis, a simple framework was used. This framework assigns plant diversity indicators to one of the three plant diversity dimensions on the basis of the extent to which taxonomic identity and physical properties of the plant individual are included in the indicator (**Table 1-1**). According to the framework, taxonomic indicators are based on measurements of taxonomic identity, but not physical properties (except those needed for taxonomic identification). Functional indicators are based on both measurements of taxonomic identity and physical properties, as without either one, an ecological or evolutionary role cannot be assigned or interpreted. Last, structural indicators are based solely on physical properties, ignoring taxonomic identity. In this way, this framework identifies the number of different taxa as taxonomic diversity, the variation in wood density as functional diversity, and the average height of the community as structural diversity.

Table 1-1. Three dimensions of plant diversity included in this thesis (taxonomic, functional and structural), which can be recognised according to the importance of taxonomic identity and physical properties of the plant individual (+ = important, 0 = not important). The plant diversity dimensions are depicted by pictograms: taxonomic diversity with trees of different colours (i.e. different colours representing different taxa), functional diversity with trees of different colours and heights, structural diversity with trees of different heights.

	Biodiversity dimension		
	Taxonomic	**Functional**	**Structural**
			
Taxonomic identity	+	+	0
Physical properties	0	+	+
Examples of plant diversity indicators	Species richness Shannon diversity Camargo evenness	Average height of the dominant species Community-weighted mean wood density Functional dispersion of selected leaf area	Mean height Mean basal area Mean stem density Number of large trees (diameter > 70 cm)

1.4 Fragmented and incomplete evidence of specific plant diversity-ecosystem service relationships in tropical forests

As stated above (section 1.1), the empirical evidence in the literature for relationships between plant diversity and carbon storage, timber provisioning and NTFP provisioning in old-growth tropical forests appears fragmented and incomplete. On the basis of my assessment, three important aspects of fragmented and/or incomplete evidence can be identified, and these are addressed below.

First, most contemporary studies on the relationships between plant diversity and ecosystem services in old-growth tropical forests focus on ecosystem service stocks, while less attention is given to ecosystem service flows. For example, most of the recent studies that focus on the service of carbon storage only address relationships with carbon stock, whereas relationships with carbon flow (i.e. carbon sequestration) are hardly ever addressed (e.g. Shen et al., 2016; Sullivan et al., 2017; Van De Perre et al., 2018). This is not surprising, as carbon storage in tropical forests is usually quantified using plots (i.e. vegetation surveys of a certain area), and quantifying carbon stocks requires only one measurement whereas quantifying carbon flows requires repeated measurements. Nevertheless, relationships of plant diversity with stock and flow components of ecosystem services could differ as ecosystem service stocks lack a temporal dimension in contrast to flows, and flows can be strongly codetermined by socio-economic aspects (See section 1.2). According to Ricketts et al. (2016), any existing relationships between biodiversity and ecosystem service stock could become weakened or even nullified for the flow component because generally the flow component is more influenced by socio-economic circumstances (Section 1.2). This could lead to different relevant plant diversity for stock and flow components of ecosystem services. In support, Finegan et al. (2015) studied the relationships of several functional plant diversity indicators with both carbon stock and sequestration (i.e. carbon stock and flow) in tropical forests, and found that the CWM of maximum attainable height of the trees was most important for carbon stock, whereas the CWMs of several leaf traits were more important for carbon sequestration. This raises the question to what extent relationships of plant diversity with the three ecosystem services differ between the stock and flow components of the services.

Second, although there is scattered evidence that taxonomic, functional and structural plant diversity can show relationships to ecosystem services, the evidence has been incompletely assessed. There are only a few studies that address relationships of plant diversity with timber and NTFP provisioning (e.g. Baraloto et al., 2014), and studies of plant diversity-ecosystem service relationships often only assess the relationships of plant diversity according to one or two of the three plant diversity dimensions (e.g. Cavanaugh et al., 2014; Finegan et al., 2015; Poorter et al., 2015; Shen et al., 2016; Sullivan et al., 2017). Yet, contemporary evidence suggests that different plant diversity dimensions can show significant but distinct relationships with ecosystem services. Van der Sande et al. (2017) carried out a systematic review of reported relationships between plant diversity and carbon stock and flow across different kinds of tropical forests and plantations. Their review indicated that taxonomic indicators showed mainly positive relationships with carbon stock and flow, functional indicators showed a mix of positive, negative and non-significant relationships, and structural indicators showed mainly positive relationships. The review by van der Sande et al. (2017) illustrates how different dimensions of plant diversity can be related to carbon stock and flow in tropical vegetation; however, it cannot be concluded on the basis of this review how taxonomic, functional and structural plant diversity are related to carbon stock and flow in old-growth tropical forests. In their review, van der Sande et al. (2017) pooled relationships from old-growth tropical forests, secondary tropical forests and tropical plantations. As species composition and vegetation structure can be expected to differ between these three kinds of vegetation, the pooling of these vegetation types obscures potentially unique relationships for old-growth tropical forests. Therefore, the question remains how taxonomic, functional and structural plant diversity is related to carbon storage, timber provisioning and NTFP provisioning in old-growth tropical forests.

Third, most studies focus on the relationships between plant diversity and one particular ecosystem service, whereas relationships of plant diversity with multiple ecosystem services remain incompletely studied. If biodiversity underpins ecosystem services, then it could be expected that biodiversity could support multiple ecosystem services at the same time, potentially providing 'bundles' of ecosystem services (Bennett et al., 2015; Duncan et al., 2015; C. Raudsepp-Hearne et al., 2010). However, most contemporary studies of plant diversity-ecosystem services relationships in old-growth tropical forests focus on carbon storage only (e.g. Shen et al., 2016; Sullivan et al., 2017; Van De Perre et al., 2018; van der Sande et al., 2017), obscuring how plant diversity is related to multiple ecosystem services simultaneously. One rare study that assessed the relationships of plant diversity with multiple ecosystem services in tropical forests is that by Baraloto et al. (2014), who explored the relationships between tree genera and aboveground biomass, timber stock and the abundance of NTFP-producing plant species (NTFP abundance). The study found no evidence that particular plant diversity indicators showed similar or even dissimilar relationships to multiple ecosystem services, but focused on plant diversity on the genus level rather than the more detailed level of species. The study also concentrated on a limited set of plant diversity indicators, including only two indicators (a taxonomic and a functional diversity indicator), and was limited to a particular area of tropical forests (South-West Amazonia).

As long as the empirical evidence for relationships of taxonomic, functional and structural plant diversity with the selected ecosystem services remains fragmented and incomplete, our ability to generalise how plant diversity and ecosystem services are related is also limited (Duncan et al., 2015). In addition, it remains unclear to what extent ecosystem service bundles may be expected. The existence of ecosystem services bundles could greatly facilitate the development of conservation measures by representing an opportunity to safeguard multiple ecosystem services at the same time. By contrast, if relationships of biodiversity with multiple ecosystems services would differ in direction, for example including a positive relationship to one ecosystem service while including a negative relationship to another, then trade-offs could be expected in conservation goals, and additional conservation measures would be needed to conserve multiple ecosystem services.

1.5 Uncertainty about the effects of spatial scale aspects in plant diversity-ecosystem service relationships

Biodiversity and ecosystem services show spatial variation, and there has been increasing awareness that this variation can affect relationships between biodiversity and ecosystem services (Bennett et al., 2015; Cardinale et al., 2012). By incorporating an increasingly larger spatial scale, a larger part of the natural variation in biodiversity and ecosystem services will be captured, which in turn could lead to different relationships. In addition, the amount of environmental heterogeneity is expected to increase, which may also influence relationships. Across spatial scales, different mechanisms may drive variation in biodiversity and/or ecosystem services (McGill, 2010; Whittaker et al., 2001). At local scales (i.e. within one plot or study site), interspecies interactions such as competition and predation are thought to be relatively important, while environmental heterogeneity is expected to be relatively low. By contrast, at landscape to intercontinental scales, environmental heterogeneity such as in topography, disturbance, biogeographical isolation and evolutionary history is considered to be much higher, and thus it is expected to be more important (Scheiner et al., 2011; Whittaker et al., 2001). In this way, it may be expected that the relationships between biodiversity and ecosystem services are affected by the spatial scale aspects of plot size and geographical extent that are included in the analysis (Chisholm et al., 2013; Isbell et al., 2017; Mittelbach et al., 2001; Scheiner et al., 2011). Here, the plot size is the unit of sampling, and the geographical extent is the study area or the geographical area from which samples were taken and compared. Effects of plot size and geographical extent could explain why relationships between biodiversity and ecosystem services can differ between studies (Chisholm et al., 2013; Scheiner et al., 2011; Whittaker, 2010), for example when one study finds a significant positive relationship between a specific biodiversity indicator and ecosystem service while a different study finds this relationship to be non-significant.

However, my preliminary assessment of the literature on the relationships between plant diversity and carbon storage, timber provisioning and NTFP provisioning suggests that the effects of these spatial scale aspects has not yet been analysed thoroughly. The effects of plot size have been analysed only for carbon stock. For example, the relationship between plant species richness and tropical forest carbon stock was found to change from predominantly positive at plot sizes of ≤ 0.1 ha to non-significant at a plot size of 1 ha (Poorter et al., 2015; Sullivan et al., 2017), showing a moderating effect of plot size. However, despite increasing attention for matters of spatial scale, the potential effect of geographical extent has received much less attention. To my knowledge, there has been no statistical analysis of the effect of geographical extent on the relationships between plant diversity and ecosystem services in tropical forests.

As long as the effects of plot size and geographical extent on the relationships between plant diversity and the three ecosystem services in tropical forests remain incompletely studied, it cannot be assessed to what extent relationships are generally valid across tropical forests and spatial scales. Yet, insight into the direction and strength of biodiversity-ecosystem service relationships at specific spatial scales is key to managing ecosystem services, as management usually takes place in administrative units of a certain spatial scale, such as national parks, provinces or nations (Malinga et al., 2015; Ciara Raudsepp-Hearne & Peterson, 2016). For example, if tropical forests are managed on a regional spatial scale, then a potential relationship that can only be found at local spatial scales will be less relevant.

1.6 Incomplete understanding of how plant diversity is related to provisioning ecosystem services in different ecological and socio-economic circumstances

As stated above in section 1.2, ecosystem services delivery is determined by a complex interplay of ecological and socio-economic factors (Costanza et al., 2017; Mace et al., 2012; Renard et al., 2015). However, most studies of ecosystem services either focus on the ecological part of ecosystem services, for example how ecosystems and/or their biodiversity represent a stock or can generate a potential supply, or the socio-economic part, for example the magnitude of ecosystem service flow (Bennett et al., 2015). As a consequence, there is a general lack of knowledge of how stock, potential supply and flow of ecosystem services are linked. This limits the generalisation of relationships between biodiversity and ecosystem services across other areas, including ecosystem service stocks, uses and values. Moreover, without considering the flow of ecosystem services, it remains unclear as to what extent ecosystem services are or can be used sustainably (Bennett et al., 2015; Duncan et al., 2015; Hein et al., 2016). For instance, although a natural ecosystem and its biodiversity may produce a certain sustainable potential supply of ecosystem services, the actual use (flow) can be higher than the potential supply, leading to overexploitation. This can result in degradation or even permanent loss of the ecosystem service and its related biodiversity (Hein et al., 2016). Here, related biodiversity includes both the biodiversity that is helping to generate the ecosystem service, as well as the biodiversity that is co-dependent on it. For example, overexploitation of food NTFPs may also be detrimental to other organisms that feed on these NTFPs.

My preliminary assessment of the relationships between plant diversity and the three ecosystem services in old-growth tropical forests (section 1.4) found that most attention has been given to the relationships between plant diversity and carbon storage. As carbon storage is a regulating ecosystem service in which the actual use is equal to the potential supply (Hein et al., 2016), it can be expected that relationships between plant diversity and carbon sequestration can be generalised across other tropical forests without much attention for socio-economic circumstances (save those socio-economic factors that are important for monitoring and valuation). By contrast, the delivery of the provisioning services of timber and NTFPs are greatly influenced by socio-economic circumstances. However, the relationships of plant diversity with timber provisioning and NTFP provisioning have been incompletely studied. Most, if not all, studies of timber and NTFP provisioning in old-growth tropical forests have focused on either quantifying the potential supply or on quantifying actual use. For example, studies that focus on NTFP provisioning have either focused on quantifying NTFP stocks (e.g. Baraloto et al., 2014), potential NTFP supply (e.g. Jaramillo-Giraldo et al., 2017; Lopes et al., 2019; Peters et al., 1989; Strand et al., 2018) or NTFP use (i.e. flow; e.g. Gavin, 2004; Godoy et al., 2000; Gram, 2001; Gram et al., 2001; Padoch & de Jong, 1989; Schaafsma et al., 2014; Shanley et al., 2002; van Andel et al., 2007). Across these studies of NTFP provisioning, only NTFP stocks have been quantitatively related to plant diversity (e.g. Baraloto et al., 2014). This state of knowledge obscures how plant diversity is related to the ecosystem services of timber provisioning and NTFP provisioning, and to what extent they are used sustainably. Therefore, there is a need for studies that address how timber or NTFPs are delivered in relation to both ecological and socio-economic factors, relating plant diversity to stock, potential supply and flow of the service.

1.7 Seeing the forest through the trees: aim, research questions and approach

According to my preliminary assessment of the literature on relationships between plant diversity and ecosystem services in tropical forests, three major knowledge gaps were identified that hamper the assessment of plant diversity-ecosystem service relationships and their relevance for tropical forest conservation. In other words, there is a need to 'see the forest through the trees', in other words to discern overall patterns in plant diversity-ecosystem services relationships in tropical forests in the various details, in order to arrive at conclusions about their potential contribution to tropical forest conservation.

Consequently, this thesis aims to explore the relationships between plant diversity and the ecosystem services of carbon storage, timber provisioning and NTFP provisioning in old-growth tropical forests.

To facilitate this aim, the following four research questions related to the identified knowledge gaps, have been formulated:

RQ 1: *How are taxonomic, structural and functional plant diversity related to the stock and flow components of carbon storage, timber provisioning and NTFP provisioning in tropical forests?*

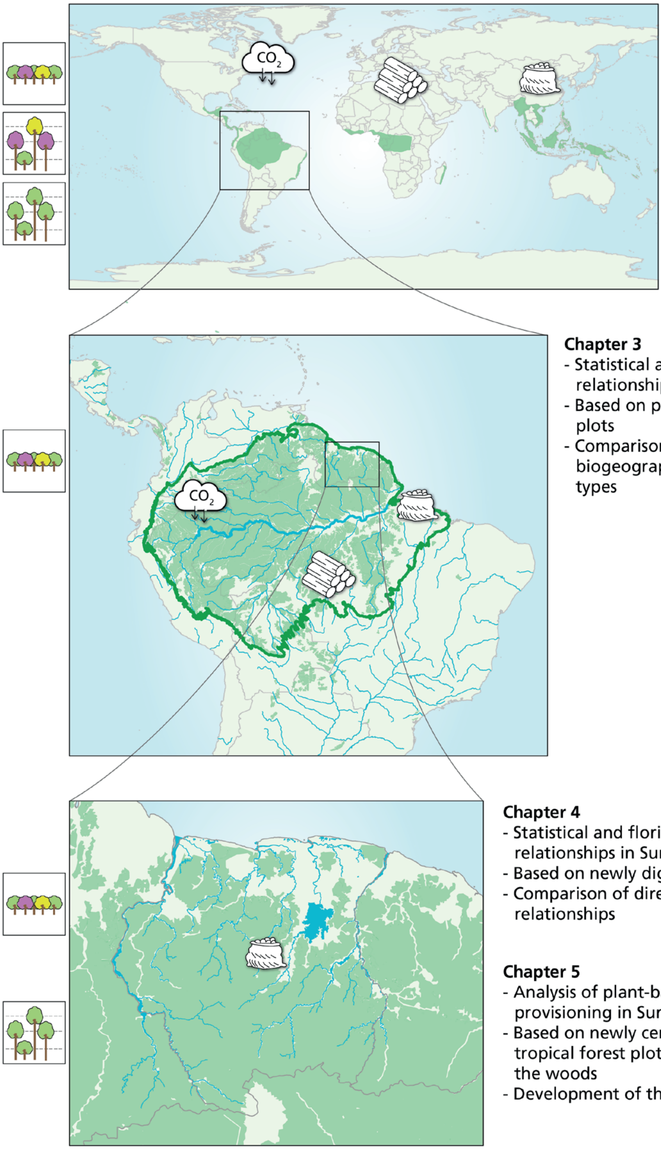
RQ 2: *How is plant diversity related to multiple ecosystem services in tropical forests, such as carbon storage, timber provisioning and NTFP provisioning?*

RQ 3: *What are the effects of the spatial scale aspects of plot size and geographical extent on the observed relationships between plant diversity and carbon storage, timber provisioning and NTFP provisioning in tropical forests?*

RQ 4: *What are the relationships between plant diversity and the stock, potential supply and use of tropical forest NTFPs?*

From the preliminary assessment carried out in this General Introduction (**Chapter 1**), it became clear that answering these questions requires the application of various methods and the inclusion of different spatial scales (**Figure 1-1**). First, to better identify the knowledge gaps, a systematic review was needed of the empirical evidence in the literature. Hence, a systematic review was conducted of empirical studies across the tropics, discerning specific plant diversity dimensions and ecosystem service components. On the basis of the studies found, a meta-analysis was performed to statistically assess the evidence, including the potential effects of plot size and geographical extent. Both the systematic review and the meta-analysis are presented in **Chapter 2**.

This paved the way for effectively analysing any remaining knowledge gaps using 'primary' plot data (as opposed to 'secondary' data taken from the literature). Here, **Chapter 3** delves more deeply into how the taxonomic plant diversity indicator of woody species richness, i.e. the richness of tree and arborescent palms, is related to tropical forest carbon stock, timber stock and NTFP abundance (a proxy for NTFP stock). In this chapter, particular attention is given to species-rich and carbon-rich tropical forests. This helps answer the question to what extent overlap in both types of forests can be expected and to what extent these forest types co-vary in timber stock and NTFP stock. In addition, **Chapter 3** analyses how differences in geographical extent can affect the relationships between woody species richness and the three ecosystem services. It studies the influence of environmental heterogeneity by discerning relationships across and within multiple forest types and geographical strata (regions and subregions) at two spatial scales in the Neotropics, including the regional scale of the Guiana Shield and the continental scale of Amazonia. To achieve these aims, Chapter 3 uses a dataset of 283 previously published tropical forest plots.



Chapter 2
- Systematic review and meta-analysis of pantropical relationships
- Based on the literature
- Comparison across and within plant diversity dimensions and ecosystem service components

Chapter 3
- Statistical analysis of Amazonian relationships
- Based on pre-existing tropical forest plots
- Comparison across and within biogeographical strata and forest types

Chapter 4
- Statistical and floristic analyses of relationships in Suriname
- Based on newly digitized tropical forest plots
- Comparison of direct and indirect relationships

Chapter 5
- Analysis of plant-based ecosystem service provisioning in Suriname
- Based on newly censused and pre-existing tropical forest plots, interviews & walks in the woods
- Development of theoretical framework

Figure 1-1. Graphical representation of the four chapters of this thesis. Showing the three focal scales (pantropical, Amazonia and Suriname) and providing the main methods used. The addressed plant diversity and ecosystem services per chapter are depicted by pictograms: taxonomic diversity with trees of different colours, functional diversity with trees of different colours and heights, structural diversity with trees of different heights, carbon storage with a CO_2 cloud, timber provisioning with a stack of timber boles, and non-timber forest product (NTFP) provisioning with a bag of fruits. Approximation of tropical forests extent shown in green, where for the pantropical scale the extent is shown after the historical tropical forest extent recognised by Corlett & Primack (2011) and for Amazonia and Suriname the after Global Forest Watch (2021).

Chapters 4 and 5 further address the knowledge gap of how plant diversity is related to provisioning ecosystem services as opposed to the regulating ecosystem service of carbon storage. Specifically, these chapters focus on the relationships between plant diversity and NTFP provisioning. NTFPs can constitute multiple kinds of benefits, including cultural and economic values, increasing their relevance to local stakeholders and thus to tropical forest conservation. First, in **Chapter 4**, a detailed analysis is performed of the direct and indirect relationships of taxonomic and structural woody plant diversity with NTFP abundance in Suriname tropical forests. However, the analysis of how plant diversity delivers NTFPs under the complex interaction of both ecological and socio-economic factors requires a theoretical framework that describes the flow of plant-based NTFPs from forest stock to final market. This framework is developed in **Chapter 5**, where it is applied to the case-study of plant-based NTFPs that are sourced from old-growth tropical forests and are traded at the market in Suriname. To achieve these aims, Chapters 4 and 5 use an as yet unpublished dataset of 287 tropical forest plots from the 1970s, which was newly digitised and updated during this research. Chapter 5 uses an additional 62 previously published tropical forests plots, as well as six plots that were newly censused during this research. In addition, for Chapter 5 a dataset of walks-in-the-woods with harvesters and interviews with harvesters and market vendors of NTFPs in Suriname was compiled during this research.

In this way, the four research questions of this thesis are addressed in multiple research chapters (**Table 1-2**). In **Chapter 6**, the main findings of these research chapters are synthesised and discussed in the light of the research questions and their relevance to tropical forest conservation, leading to recommendations for resource managers, scientists and policy makers. Last, the main findings and their implications are summarised for a broader audience, both in English and in Dutch.

Table 1-2. Overview of research questions and chapters in which these are addressed.

Chapter & Title		Research questions			
		RQ 1	RQ 2	RQ 3	RQ 4
2	*Shedding light on relationships between plant diversity and tropical forest ecosystem services across spatial scales and plot sizes*	●		●	
3	*Relationships between species richness and ecosystem services in Amazonian forests strongly influenced by environmental heterogeneity*		●	●	
4	*Exploring relationships between abundance of non-timber forest product species and tropical forest plant diversity*				●
5	*From forest stock to market: assessing the economic value of plant-based non-timber forest products and their conservation relevance in Suriname*				●

View across the tropical forests of the Guiana Shield from the Fredberg, Suriname, facing North-West. Photo by Evelien Bos.

2

Shedding light on relationships between plant diversity and tropical forest ecosystem services across spatial scales and plot sizes

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Abstract

This chapter sheds light on the state of our knowledge of relationships between plant diversity and tropical forests ecosystem services. We systematically reviewed the empirical evidence of relationships between three ecosystem services: carbon stock and sequestration, timber provisioning and non-timber forest product (NTFP) provisioning, and three dimensions of plant diversity: taxonomic, functional and structural. We carried out meta-analyses to assess their validity across spatial scales and plot sizes. We found that indicators of all three dimensions of plant diversity have reported relationships with at least two of the studied ecosystem services, but there has been limited and inconsistent use of plant diversity indicators and little attention for relationships with timber and NTFP services. Nevertheless, we found that tree species richness showed robust significant positive correlations with carbon stock across the tropics, and that the geographical extent of the study area had a significant negative effect on the strength of this relationship, where the strength of the relationship decreased with increasing geographical extent. This chapter reveals a knowledge gap for services other than carbon stock and shows that at local to regional spatial scales, synergies can be achieved between policies focused on biodiversity conservation and maintenance of carbon stocks.

2.1 Introduction

There is increasing concern that the biodiversity decline caused by the ongoing global degradation of ecosystems drives and accelerates the loss of ecosystem services, thereby threatening human wellbeing and worsening the conditions for life on Earth (Cardinale et al., 2012; MEA, 2005; Rockström et al., 2009). In response, ecosystem services are being put forward by policymakers, academia and non-governmental organizations as the focal point for conservation efforts (IPBES, 2019; MEA, 2005). Central to this idea are the presumed positive relationships between ecosystem services and biodiversity; biodiversity has been considered to be either the basis for ecosystem services provisioning or a service in itself, and may therefore show covariation with other ecosystem services (Díaz et al., 2005; Mace et al., 2012). As such, preservation of ecosystem services would not only help to safeguard human wellbeing and the conditions of life on earth, but also aid the conservation of biodiversity. In support, during the last few decades several reviews and meta-analyses have shown that there is indeed evidence of positive relationships between ecosystem services and biodiversity (Balvanera et al., 2006; Cardinale et al., 2012; Harrison et al., 2014; Quijas et al., 2010). However, questions remain as to the validity of these relationships for specific ecosystems, which is hampered by two important issues. First, current evidence is fragmented as most studies address limited parts of the wide spectrum of biodiversity-ecosystem service relationships (Balvanera et al., 2014; Bennett et al., 2015; Harrison et al., 2014; Ricketts et al., 2016), which obscures the full potential of the concept of ecosystem services to support conservation efforts. Second, there is insufficient knowledge on how spatial aspects, such as spatial scale and plot size affect the biodiversity-ecosystem service relationships (Bennett et al., 2015; Cardinale et al., 2012; Isbell et al., 2015; McGill, 2010; Scheiner et al., 2011).

These issues are especially relevant to conservation efforts focused on tropical forests, as these forests are among the most species-rich biomes on Earth (Myers et al., 2000), and provide globally important ecosystem services such as carbon stock and sequestration, timber and non-timber forest products (NTFPs) (Baraloto et al., 2014; Bonan, 2008; Brandon, 2014). Yet tropical forests are under increasing pressure of deforestation and degradation, which drives species extinction and conversion of ecosystems, thus affecting the provisioning of ecosystem services (Barlow et al., 2018; Corlett, 2016). Regarding plant diversity, tropical forests are specifically bountiful in species richness, functionality and structure (Corlett, 2016; Corlett & Primack, 2011; Myers et al., 2000). Thus, plant diversity is expected to show strong relationships with the provisioning of ecosystem services as it represents the primary producers and the building blocks of not only tropical forests but all terrestrial ecosystems. In support of this expectation, a meta-analysis across various ecosystems found positive relationships between pooled plant diversity indicators (i.e. combinations of similar variables) and the provisioning and regulating ecosystem services (Quijas et al., 2010).

However, knowledge on how plant diversity might be related to tropical forest ecosystem services relationships is fragmented in three important ways. First, most contemporary studies seem to focus exclusively on carbon stocks (e.g., Shen et al., 2016; Sullivan et al., 2017; Van De Perre et al., 2018; van der Sande et al., 2017), while there is evidence that different plant diversity indicators can show different relationships with different ecosystem services. For example, Baraloto et al. (2014) found that Simpson diversity of tree genera was negatively correlated with above-ground biomass of small stems, while it showed no significant correlation with the services of timber or NTFPs provisioning. Second, plant diversity consists of multiple dimensions of diversity, including a taxonomic (e.g., species richness), functional (e.g., diversity in wood density) and structural (e.g., average height of the community) dimension (Lyashevska & Farnsworth, 2012). However, most studies focus variously on one or two of these three common plant diversity dimensions (e.g., Poorter et al. 2015; Shen et al. 2016; Sullivan et al. 2017), while there is evidence that all three dimensions of plant diversity have significant, yet distinct, relationships with a variety of ecosystem services in tropical forests. For example, the review by van der Sande et al. (2017) on pan-tropical plant diversity relationships with carbon stock and carbon flow, showed that taxonomic, functional and structural plant diversity indicators can show different relationships per dimension, including positive, negative and non-significant relationships. The general pattern was that the taxonomic dimension showed mainly significant positive relationships, the functional dimension showed a mix of significantly positive, significantly negative and non-significant relationships, and the structural dimension showed mainly positive relationships with carbon stock and flow. Third and last, similar plant diversity aspects have been approximated with different indicators, which are not necessarily comparable. For example, taxonomic richness has been correlated to tropical forest tree carbon stock, but on the basis of different indicators, where the relationship was found to be positive when species richness or Margalef's richness index was used (Chaturvedi & Raghubanshi, 2015; Gillison et al., 2013) but negative when the rarefaction of species richness was used (Ruiz-Jaen & Potvin, 2011). In addition, a recent meta-analysis on the evidence of more general biodiversity-ecosystem services relationships found that pooling different indicators to investigate more general patterns can obscure important differentiating relationships (Ricketts et al., 2016). As there has not been a quantitative systematic analysis of how different dimensions and specific indicators of plant diversity are related to multiple ecosystem services in tropical forests, this fragmented state of knowledge may lead to suboptimal conservation measures. For example, this is the case when contrasting findings cannot be explained (e.g. Ricketts et al., 2016) or when potential trade-offs between specific plant diversity indicators and ecosystem services are not acknowledged (e.g. Howe et al., 2014).

In addition, there is increasing awareness that biodiversity-ecosystem service relationships can behave differently across variation in spatial aspects, specifically across plot sizes and geographical extents (Bennett et al., 2015; Cardinale et al., 2012; Chisholm et al., 2013; Isbell et al., 2015; Scheiner et al., 2011). Here, the plot size is the unit of sampling, and the geographical extent is the study area or the geographical area over which samples are compared. Different mechanisms may drive the changes in biodiversity-ecosystem service relationships across spatial scale (McGill, 2010; Whittaker et al., 2001). It has been proposed that at the local scale, interspecies interactions (such as competition and predation) are relatively important as environmental heterogeneity is expected to be low, while at larger, landscape to intercontinental scales, environmental heterogeneity (such as in topography, disturbance, biogeographical isolation, evolutionary history) is considered to be higher and thus has a larger influence on these relationships (Scheiner et al., 2011; Whittaker et al., 2001). Regardless of the underlying mechanisms, insight into the behaviour of biodiversity-ecosystem service relationships at specific spatial scales is key to managing ecosystem services, as management usually takes place in units with administrative at varying spatial scales, such as national parks, provinces and nations boundaries (Malinga et al., 2015; Ciara Raudsepp-Hearne & Peterson, 2016).

Yet, the influence of spatial aspects on biodiversity-ecosystem service relationships across tropical forests has not yet been analysed thoroughly. Only for carbon stock the effects of plot size have been analysed. Here, the relationship between plant species richness and tropical forest carbon stock was found to change from predominantly positive at plot sizes of ≤0.1 ha to non-significant at a plot size of 1 ha across the tropics (Poorter et al., 2015; Sullivan et al., 2017), showing a moderating effect of plot size. However, despite increasing attention for matters of spatial scale, the potential effect of the geographical extent of the study area has received much less attention. With increasing geographical extent an increasing part of the spectrum of variation in plant species diversity and ecosystem services within tropical forests will be captured, which could lead to different relationships. In addition, with increasing geographical extent, the amount of environmental heterogeneity is expected to increase as well, which may also influence relationships. Therefore, we expect that the geographical extent in which samples have been collected may partly determine the observed biodiversity-ecosystem service relationships. However, to the best of our knowledge, there has been no statistical analysis of the effects of geographical extent on the relationships between plant diversity and ecosystem services in tropical forests.

This chapter focuses on two questions: 1) to what extent is there empirical evidence for relationships between tropical forest ecosystem services and plant diversity and, 2) to what extent are these relationships robust across spatial scales and plot sizes. Knowledge on these matters will help to assess the potential of ecosystem services to function as a focal point for biodiversity conservation. To quantify and statistically compare the effects of different spatial aspects across the tropical biome, a meta-analysis of published relationships was needed. To this end, our chapter consists of two components. First, we performed a systematic review of the peer-reviewed literature to identify which relationships had been studied. We focused our review on the services of carbon stock and sequestration, timber provisioning and NTFP provisioning, as initial scoping showed that plant diversity relationships are relatively well-documented for these services and because they are all related to above ground biomass, which facilitates comparison. Moreover, these three services are considered to be important for communities living in or near tropical forests (Baraloto et al., 2014). We included the dimensions of taxonomic, functional and structural plant diversity in our analysis to allow for a broad assessment of evidence. Second, as we could find only sufficient evidence regarding the stock aspect of carbon stock, we used meta-analysis to quantify specific relationships between plant diversity indicators and carbon stock across the tropics. In addition, for those pan-tropical carbon stock relationships that had sufficiently large datasets we analysed the effects of both plot size and the geographical extent on the relationships between plant diversity and carbon stock.

2.2 Material and Methods

Our approach consisted of two components: 1) a systematic review of the literature to take stock of empirical relationships between plant diversity and ecosystem services in tropical forests and, 2) meta-analyses of several specific relationships. Both review and meta-analyses followed the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) (Moher et al., 2009) as much as possible; Figure 1-1 shows the flow of information; Figure S2.1.2 in Annex S2.1 shows an infographic of the methods used in the systematic review and meta-analyses; Annex S2.1.7 show the PRISMA checklist for this study.

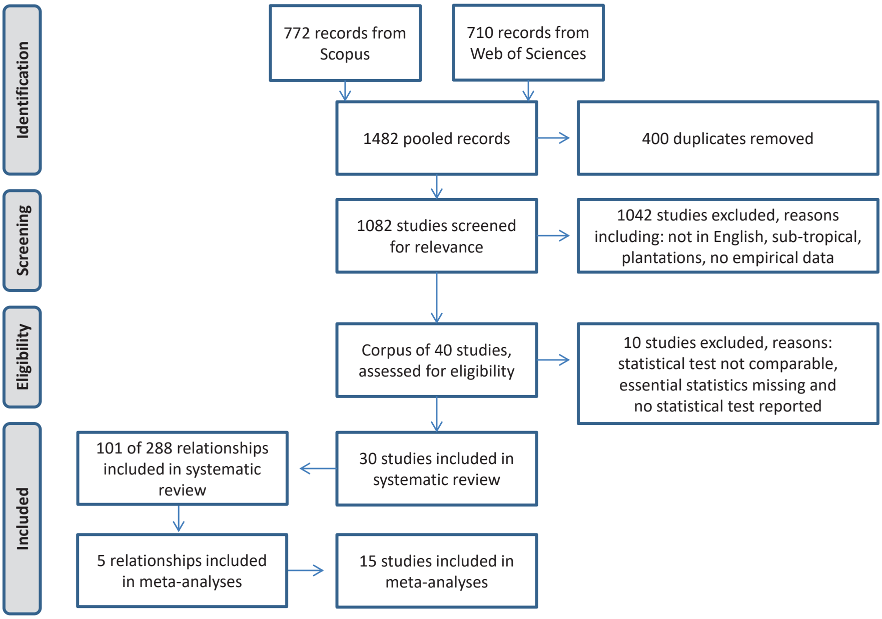


Figure 2-1. PRISMA information flow diagram of the systematic review and meta-analysis (after Moher et al., 2009).

Systematic review

To identify potentially relevant literature we used broad search strings, i.e. including overarching terms and synonyms, which we employed in both Scopus and Web of Sciences between June 2017 and May 2018 (search strings are provided in Figure S2.1.1). We managed and screened records in the programme R (R Core Team, 2018), with package 'stringr' (Hadley Wickham, 2019). We selected only peer-reviewed articles and excluded non-English records (27 of the 1082 records, i.e. 2.5%, were not written or not partly written in English), based on the meta-information provided by the search engines. To check the eligibility of the records, we downloaded the full texts with 'RCurl' (Temple Lang, 2018) and used the title, abstracts and table and figure headings to manually select the records that contained empirical data of relationships between tropical forest plant diversity and one of the three ecosystem services. As there is no common definition in the literature as to what a 'tropical forest' is, we filtered for records that contained data from forests that lie within countries that host parts of the estimated historical extent of evergreen tropical rain forests as identified in Corlett and Primack (2011) and excluded records that contained only plantation or non-forest tropical vegetation. To assess the scope of the corpus dataset, we noted: i.a. which continent was sampled, in which

Köppen climate class the forests were located, and the reported forest disturbance (i.e. primary and/or secondary). We interpreted primary forest as forests that are not under or to under little human impact (e.g., old-growth forest) and secondary forest as forests that have been selectively logged or harvested for other plant based products or forests that are regenerating after being clear cut. On the basis of the scope information we summarized that the forests ultimately compared in the systematic-review and meta-analyses included a wide spectrum of tropical forests, but were predominantly evergreen, terra-firme primary forests lying in the Köppen tropical climate zone ('A'). Some records also or only included secondary forests, which ranged from forests that where selectively logged (either presently by local communities or in the past 14 to 22 years ago)(most of the cases) to forests that have been regenerating after being clear-cut 10 to 120 years ago. More scoping information on the datasets that are used in the systematic review and meta-analyses is included in Annex S2.2.

This process resulted in a corpus of 40 relevant studies for which data was extracted and stored separately by two persons in order to avoid coding errors. We registered data for each reported relationship, including: (1) the type of ecosystem service and whether it concerned a stock (e.g., X Mg carbon ha^{-1}) or a flow (e.g., Y Mg carbon ha^{-1} yr^{-1}); (2) the plant diversity indicator and whether it represented taxonomic, functional or structural traits (according to the framework in Annex S2.1); (3) the type of statistical analysis and outcome; and (4) the spatial covariables, including the plot size (i.e. here the focal scale or the area size to which data are standardized prior to analysis, in ha) and the geographical extent (the area that encompasses the plots compared in a relationship, in km^2; after Whittaker, 2010 and Scheiner et al., 2011; see Figure S2.1.2 for a graphical representation of how plot size and geographical extent can vary per study). Here, 'plant diversity' included measures of diversity as well as richness and composition. As the geographical extent of the study area was not always reported, we calculated the minimum rectangle encompassing the compared plots using an online tool and applied a natural log ('ln') transformation to linearize the relationship between geographical extent and increasing study area (see Annex S2.1 for more information on data extraction, storage and pre-analysis). The corpus database is available as a separate Excel file in Annex S2.4.

We included only those relationships in the systematic review for which all necessary statistical information could be retrieved. This resulted in a dataset of 30 eligible studies that provided a total of 288 bivariate, multivariate, correlational and regression analyses of relationships between plant diversity dimensions and ecosystem services originating from the American, African, Asian and Australian tropical areas. Bivariate analyses formed the largest component of the corpus and were analysed in more detail. We pooled the plant diversity indicators of 247 bivariate analyses per taxonomic, functional and structural dimension, summing the number of significantly positive, significantly negative and non-significant relationships. To evaluate whether the significant outcomes consistently pointed towards a specific direction, we carried out a binomial t-test under the pragmatic assumption that outcomes were independent of each other. Specifically, we tested H_0: ratio (outcome 1 / (outcome 1 + outcome 2)) = 0.5, with a two-tailed t-test with 95% CI and an alpha = 0.05, where outcome 1 and 2 are either the number of significantly positive outcomes and number of significantly negative outcomes. As our data were nested, the outcome of the binomial t-test ran the risk of having inflated type I errors, i.e. rejecting H_0 while it is true. In this light, the binomial t-test outcomes can be interpreted as being conservative. In addition, we partitioned the 247 bivariate analyses into 101 subsets of specific relationships between plant diversity indicators and ecosystem services.

Meta-analyses of relationships across the tropics

We used multilevel random-effect models to establish overall relationships between carbon stocks and taxonomic (i.e. taxonomic richness, Shannon diversity, Simpson diversity) and structural (i.e. mean stand density, mean basal area) plant diversity indicators (see Annex S2.5). Pearson correlation coefficients (*r*) were used as input for the effect sizes as these provided the largest set of statistically comparable analyses. We retrieved *r* from the studies either directly or through conversion of other suitable bivariate statistical metrics, as described by Koricheva, Gurevitch and Mengersen (2013). We used Fisher's Z-transformation to transform *r* into effect sizes (henceforth '*Zr*') and used the sample size of *r* to calculate the asymptotic variance of *Zr*, which we used as weight of precision in our meta-analyses. For convenience of interpretation, reported *Zr* values were back-transformed to *r* values in graphical output, except for the analyses of spatial aspects for which back-transformation would reduce the readability of the graphs. Before meta-analyses, we scrutinized the data to avoid double counting within and between studies as much as possible, and we excluded any *r* that was based on a sample size too small to calculate the variance of *Zr* (i.e. number of samples ≤ 3).

We used restricted maximum likelihood estimation (REML) to calculate an overall effect size for each relationship subset that had five or more effect sizes ('*m*') originating from three or more studies ('*k*'; i.e. $m \geq 5$ and $k \geq 3$). Although an overall effect size can already be calculated with only two effect sizes (Koricheva et al., 2013), we took this conservative approach to reduce the potential for Type II errors (i.e. false positives). As some of the effect sizes originated from the same study (i.e. the data is nested), we used multilevel models to control for non-independence. Specifically, we used a three-level random effects model where variance in the data was contrasted in sampling variance between studies (level 1), variance between effect sizes within each study (level 2), and variance of effect sizes between studies (level 3) (after Assink and Wibbelink, 2016). We used forward model selection to find the optimal model for each relationship, by selecting the optimal random structure on the basis of a Likelihood Ratio Test (LRT) and comparison of the Akaike

Information Criterion (AIC), and by selecting the optimal variance structure by testing for significant variance at level 2 and level 3, using one-sided LRT tests. Significance of the calculated overall effect size was tested using t-distribution (after Knapp and Hartung, 2003). Tests for significant heterogeneity among overall effect sizes was assessed using the Q-statistic.

Effects of spatial scale and plot size

We ran separate multilevel mixed-effect REML models to investigate whether spatial covariables explained part of the heterogeneity among effect sizes. We did this for each dataset that had seven or more effect sizes originating from three or more studies (i.e. $m \geq 7$ and $k \geq 3$). As we could not know the minimum number of effect sizes required before knowing the strength of the expected relationship (see Field, Miles and Field, 2012), we chose this threshold as a compromise between the risk of having an excessively small dataset (potentially leading to Type II errors) and the opportunity of investigating the effects of spatial scale on plant diversity and tropical forest ecosystem services relationships. We included each spatial covariable separately as a fixed-effect and used an omnibus F-test to determine (after Knapp and Hartung, 2003) whether its coefficient was significant. We included one single spatial covariable at a time as our dataset sizes were too small (i.e. $7 \leq m \leq 13$) to statistically warrant the inclusion of interactions between the moderators. To avoid potential interdependence between the spatial covariables as much as possible, we tested for collinearity between the spatial covariables in each subset. Although we found that the focal scale and ln-transformed geographical extent were correlated ($r \approx 0.8$), we maintained both spatial covariables, as we wanted to specifically test the effects of both plot size and geographical extent.

Sensitivity analyses

For all meta-analyses models we analysed the sensitivity of the models by identifying potentially influential cases on the basis of their Cook's Distance (i.e. Distance > $4/m$) and subsequent case-wise deletion of influential cases to investigate the impact on the model outcome (after Viechtbauer and Cheung, 2010). For all meta-analysis models, we analysed the impact of potential publication bias by using a trim-and-fill method (after Duval and Tweedie, 2000) where possible, else by visual inspection of funnel plots, and we compared calculated fail safe numbers to the conservative benchmark of $5k+10$ (after Rosenberg, 2005).

All analyses were carried out using '**metafor**' in R (Viechtbauer, 2010). Additional visual output was created by using '**gmodels**', '**ggrepel**' and '**ggplot2**' (Slowikowski, 2019; Warnes et al., 2018; H. Wickham, 2016). More information on the meta-analyses and sensitivity analyses is included in Annex S2.1.

2.3 Results

General relationships between plant diversity indicators and tropical forest ecosystem services

Of the 30 studies included in the systematic review and covering the tropical forest ecosystem services of carbon stock and sequestration, timber provisioning and NTFP provisioning, 90% addressed carbon stocks (i.e. 27 addressed carbon stocks, 3 addressed carbon flow, 1 addressed both timber stock and flow, and 3 addressed both NTFP stock and flow; Table 2-1). Only 1 study covered all three ecosystem services. In these 30 studies, carbon stock was quantified as biomass per surface area (e.g. Mg ha^{-1}) and carbon flow was quantified as the increase in carbon derived from multiple measurements over a period of 2-7 years. Carbon stocks were derived from measurements of the above ground biomass in stems, using allometric equations and commonly multiplying this with a biomass-to-carbon factor of ~0.5. Although most studies included only trees, some also included shrubs and palms (i.e. 9 and 1 out of the 27 studies, respectively). Timber stock was quantified as the density of adult timber tree species (stems ha^{-1}), and timber flow was approximated as the density of sub-adult timber tree species (stems ha^{-1}) which were expected to grow into an adult population after a non-specified number of years. NTFP stock was quantified as the density of useful species per surface area (individuals ha^{-1}), and NTFP flow was estimated by the regeneration of NTFPs, which was approximated through either repeated measurements or the density of juvenile trees that were expected to grow into an adult NTFP population after a non-specified number of years.

A total of 288 analyses were reported in the 30 studies, which were either correlative or regressional (162 and 126, respectively), showing significant positive, significant negative and non-significant relationships. Most of these analyses concerned bivariate relationships as opposed to multivariate relationships (247 vs 41), and most analyses concerned linear rather than non-linear relationships (269 vs 19). When we pooled plant diversity indicators per plant diversity dimension, we found that relationships between plant diversity dimension and carbon stock and between plant diversity dimension and carbon flow showed positive, negative and non-significant relationships (Table 2-1). For most pooled relationships the number of outcomes was too low to test any emergent trends. However, for carbon stock conservative binomial t-tests indicated that the numbers of positive and negative outcomes for the pooled relationships were consistent, i.e. not likely found due to chance (highlighted in bold in Table 2-1; See Annex S2.5 Table S2.5.1), and the overall emergent pattern indicated mostly positive relationships, i.e. more significant positive outcomes than significant negative ones. For carbon flow, relationships were not consistent, but indicated a trend towards mostly positive relationships. For both NTFP stocks and flow, the majority of the relationships with the diversity dimensions were non-significant, although a pattern of consistently negative relationships for NTFP flow with the structural dimension was observed. The number of relationships reported for timber stock and flow was very low, and therefore no emergent trends could be observed.

Table 2-1. Reported relationships in tropical forests based on correlation and regression analyses, set out per ecosystem service aspect and plant diversity dimension (total number of analyses considered is 288, from 30 eligible studies). Reported types of relationship are: significant positive '+', significant negative '-' and non-significant 'ø', highlighted in green. Significantly consistent outcomes on the basis of a binomial t-test are highlighted in bold. For each plant diversity dimension and ecosystem service aspect, the total number of analyses and the percentage of significant relationships is highlighted in blue. Some papers contained information on multiple services and service dimensions.

		Ecosystem service and aspect											
		Carbon				**Timber**				**NTFPs**			
		Stock		Flow		Stock		Flow		Stock		Flow	
		27 source studies		3 source studies		1 source study		1 source study		3 source studies		3 source studies	
Plant diversity dimension	**Taxonomic indicators**												
	n analyses	59	+ **22**	5	+ 4	1	+ 0	1	+ 0	5	+ 1	5	+ 1
	% significant	44%	- **4**	80%	- 0	0%	- 0	0%	- 0	20%	- 0	20%	- 0
			ø 33		ø 1		ø 1		ø 1		ø 4		ø 4
	Functional indicators												
	n analyses	87	+ **37**	12	+ 2	1	+ 0	1	+ 0	4	+ 0	4	+ 0
	% significant	66%	- **20**	42%	- 3	100%	- 1	0%	- 0	0%	- 0	0%	- 0
			ø 30		ø 7		ø 0		ø 1		ø 4		ø 4
	Structural indicators												
	n analyses	49	+ **32**	7	+ 6	2	+ 1	3	+ 1	16	+ 0	26	+ **0**
	% significant	67%	- **1**	100%	- 1	50%	- 0	33%	- 0	25%	- 4	23%	- **6**
			ø 16		ø 0		ø 1		ø 2		ø 12		ø 20

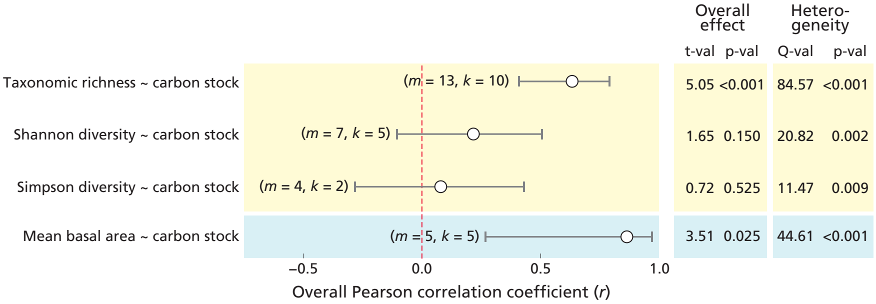
For the 247 bivariate analyses, we found that 70 unique plant diversity indicators were used, and only 33 of these were applied at least twice (Table S2.5.2). A relatively large number of functional indicators were used compared to the number of unique taxonomic and structural indicators (37 vs 13 and 16, respectively). Further analysis of the 247 bivariate analyses showed that most functional indicators were scarcely used (2.4 times on average, standard deviation ± 4.5) in comparison to the taxonomic and structural indicators (taxonomic 4.9 ± 6.4; structural 5.4 ± 8.8). When we partitioned the 70 indicators into 101 subsets of specific relationships between plant diversity indicators and ecosystem service aspects, we found that only 33 had been used at least twice, and only 5 indicators were studied for multiple ecosystem services: the Simpson taxonomic diversity, Rao's Q Functional diversity of leaf and wood functional traits, Mean stand density, Mean basal area and Mean biomass (Table S2.5.3). Although most relationships showed uniform directions, for most cases sample sets were too small to make generalizations (i.e. 14 relationships had two samples, 3 had three samples and 6 had four samples).

Specific relationships between plant diversity and ecosystem services across the tropics

On the basis of the number of analyses, five subsets of specific relationships were flagged as sufficiently large to perform a meta-analysis. Of these five, three relationships belong to the taxonomic dimension, i.e. taxonomic richness, Shannon diversity, Simpson diversity, and two belong to the structural dimension, i.e. mean basal area and mean stand density. All five considered the ecosystem service of carbon stock, and as a consequence, the follow-up meta-analysis of specific relationships was limited to this ecosystem service. After being checked for potential double-counting, the five subsets covered a total of 33 analyses (14.5% of 288) from 15 papers (50% of 30) and from at least two continents (See forest plots in Annex S2.6). From the meta-analysis it became clear that taxonomic richness, mean basal area and mean stand density showed overall significant positive correlations with carbon stock, whereas Shannon diversity and Simpson diversity showed a non-significant overall relationship (Figure 2-2). Sensitivity analysis showed that the relationships concerning taxonomic richness, Shannon diversity, Simpson diversity and mean basal area were robust and were not affected by a potential publication bias (analyses given in Annex S2.6). However, the relationship between mean stand density and carbon stock was found to be not robust, as Cook's Distances showed effect sizes that disproportionately affected the strength of the correlation. As the subsequent case-wise deletion of these effect sizes led to a non-significant correlation, we excluded this relationship from further analysis. In addition, the positive correlation between mean basal area and carbon stock is likely the result of the allometric equations that were used to calculate carbon stock of which basal area is a constituent, and we therefore also omitted this relationship from further analysis.

Regarding the statistically robust relationships, plant diversity included mostly trees, where for taxonomic richness 2 of the 13 effect sizes, for Shannon diversity 3 of the 7 effect sizes and for Simpson diversity all 4 effect sizes also included other plants (or 'stems') with a certain diameter at breast height (e.g. palms). Most plant diversity was represented at the species-level, where for taxonomic richness 1 of the 13 effect sizes, for Shannon diversity 3 of the 7 effect sizes and for Simson diversity 1 of the 4 effect sizes represented diversity at the genus-level. For the significant relationships between taxonomic richness and carbon stock, which was based on 13 effect sizes from 10 papers, we tested the effect of omitting the 1 effect size at the genus level, and found that this did not change the significance of the overall relationship (See Annex S2.6, S2.6.1.8).

In all three statistically robust relationships we detected significant heterogeneity (Figure 2-2), indicating significant unexplained variation among effect sizes. We visually checked whether different continents showed graphical patterns in effect sizes, as this may explain part of the observed heterogeneity. However, we observed no such patterns (See forest plots in Annex S2.6).



	Overall effect		Hetero-geneity	
	t-val	p-val	Q-val	p-val
Taxonomic richness ~ carbon stock	5.05	<0.001	84.57	<0.001
Shannon diversity ~ carbon stock	1.65	0.150	20.82	0.002
Simpson diversity ~ carbon stock	0.72	0.525	11.47	0.009
Mean basal area ~ carbon stock	3.51	0.025	44.61	<0.001

Figure 2-2. Overall effect sizes back-transformed to overall Pearson correlation coefficients (white circles) with their 95% confidence intervals (grey bars) for the five relationships in tropical forests for which a sufficient dataset was available. Shown in brackets are the number of effect sizes used, '*m*', and the total number of studies from which these originate, '*k*'. Also shown are the t-statistic for the overall effect size and its p-value, as well as the Q-statistic of the heterogeneity and its p-value (values rounded).

Effects of spatial scale and plot size

The datasets of the relationships between tree taxonomic richness and carbon stock and between tree Shannon diversity and carbon stock were large enough to analyse the potential effects of plot size and of geographical extent on these relationships. In these datasets the ranges in plot size and geographical extent represent different spatial aspects as they do not overlap in area, with plot size ranging from 0.06 to 1 ha and ln-transformed geographical extent ranging from 7 (corresponding to a non-transformed 702 km^2) to 18.5 (102.5x10^6 km^2).

We found that ln-transformed geographical extent had a significant linear negative effect on the overall correlation between tree taxonomic richness and carbon stock (Omnibus $F_{1,11}$ = 6.1924, p = 0.0301; see Figure 2-3a), which implies that the strength of the correlation decreases when a larger geographical area is covered by the study. These findings were found to be robust during the sensitivity analysis and for the impacts of potential publication bias (analyses given in Annex S2.6). The moderating effect of the geographical extent appears to be strongest in study area sizes up to approximately 1x10^6 km^2 (corresponding to a ca. 14 ln-transformed geographical extent, or a Euclidian distance between plots of 1000 km; see Figure S2.6.1.4 and Figure 2-3a). There was no significant effect of plot size on the correlation between tree taxonomic richness and carbon stock (Omnibus $F_{1,10}$ = 4.4650, p = 0.0607; see Figure 2-3b). Omitting the genus-richness effect size did not yield different results (ln-transformed geographical extent Omnibus $F_{1,10}$ = 5.1839, p = 0.0460; plot size Omnibus $F_{1,9}$ = 1.1649, p = 0.3085). The correlation between tree Shannon diversity and carbon stock was not significantly influenced by ln-transformed geographical extent or plot size (Omnibus $F_{1,5}$= 0.2302, p = 0.6517 and $F_{1,4}$= 1.0933, p = 0.3548, respectively; see Figure 2-3c and 2-3d).

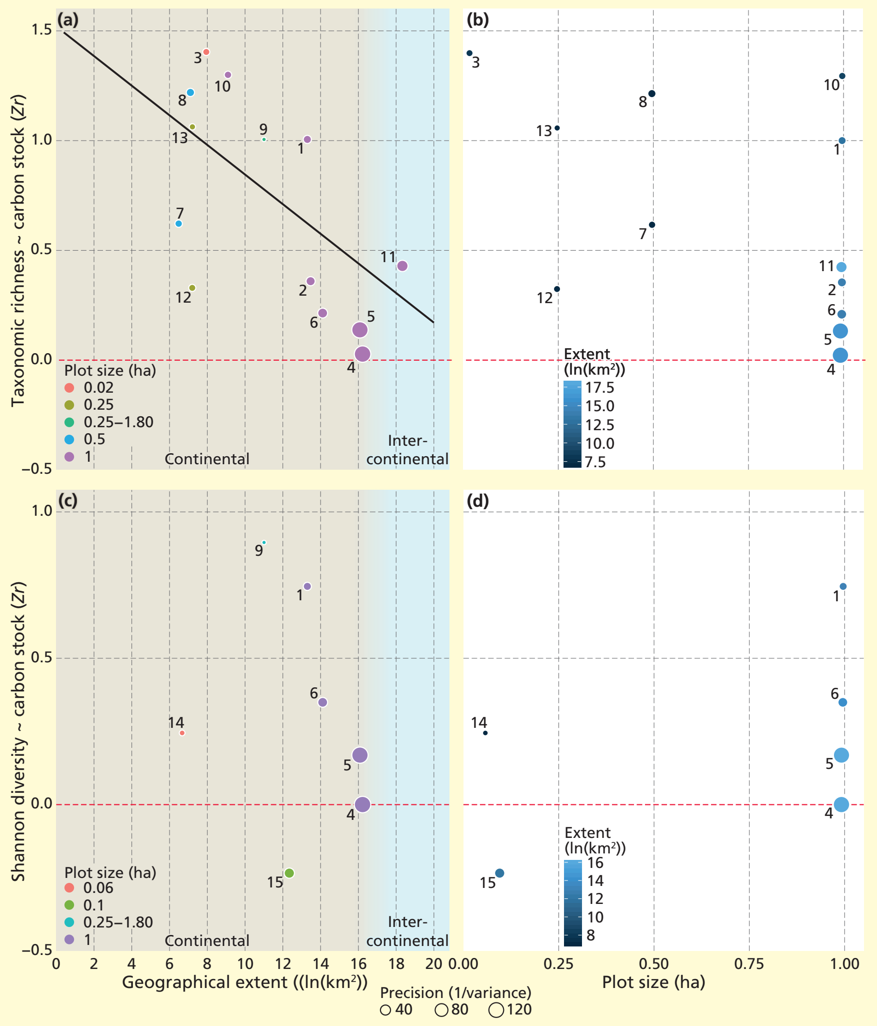


Figure 2-3. Effect sizes (Z-transformed Pearson correlation coefficients) of the relationships between tree taxonomic richness and carbon stock in tropical forests against ln-transformed geographical extent (in km^2; $m = 13$; panel a) and plot size (in ha; $m = 12$; panel b), and the relationships between tree Shannon diversity and carbon stock in tropical forests against ln-transformed geographical extent (in km^2; $m = 7$; panel c) and plot size (in ha; $m = 6$; panel d). Effect size cases are represented by a unique number and their size is drawn proportional to the inverse of the variance of the effect size (i.e. the larger the circle, the higher precision of the effect size). The plot size of effect size case 9 was aggregated from sizes between 0.25 to 1.80 ha and was therefore not used in the analyses, but it is shown in panels a and c for illustration purposes. In panels a and c the grey area in the graph represents study area sizes found at a continental scale; the light blue area in the graph represents study area sizes at an inter-continental scale. In panel a, the significant linear relationship between ln-transformed geographical extent and effect sizes is shown with a black line.

2.4 Discussion

Spatial scale matters in relationships between carbon stock and tree species diversity

The meta-analysis of 13 relationship outcomes reported in 10 studies yielded a robust positive correlation between carbon stock and tree taxonomic richness across the tropics. The strength of this relationship is linearly moderated by the ln-transformed geographical extent of the study area, where the correlation is strongest at extents corresponding to local to regional scales and approaches zero at extents corresponding to continental and intercontinental scales. Specifically, the relationship appears to be positively correlated for geographical extents up to around $1x10^6$ km^2 (i.e. regional scales), even though at these extents floristic composition and carbon stocks can show significant variation with abiotic variables (Guitet et al., 2015; Poorter et al., 2015; Slik et al., 2013). For example, it has been shown that at geographical extents of approximately $0.6x10^6$ km^2, edaphic and climatic variables such as soil fertility and rainfall can significantly influence carbon stocks (Slik et al., 2010), and that at extents of round $54x10^3$ km^2, topographic factors such as convexity and slope can significantly influence floristic composition (Guitet et al., 2015).

To our knowledge, this is the first study of tropical forests to statistically quantify the effect of geographical extent on the relationship between carbon stock and tree taxonomic richness and underlines that geographical extent can have a significant effect on relationships between plant diversity and ecosystem services. Previous studies suggested that geographical extent may have a significant effect on the relationship between carbon stock and tree species richness (Sullivan et al., 2017; van der Sande et al., 2017). When we reinterpret the results of the most comparable and elaborate of these studies (i.e. Sullivan et al., 2017), we find support for a moderating effect of geographical extent. In the study by Sullivan et al. (2017), the relationship between carbon stock and tree species richness was compared between plots in the American, African and Asian tropics, which correspond to geographical extents of $1.5x10^6$, $11.4x10^6$ and $13.1x10^6$ km^2 respectively, and between plots pan-tropically (i.e. across all three mentioned tropics). At these continental to pan-tropical scales, no significant relationships were found between carbon stock and tree species richness (Sullivan et al., 2017). In congruence, our results show that despite significant variation between effect sizes there is a significant positive correlation between carbon stock and tree species richness at relatively small geographical extents, starting at extents of about 700 km^2 (local scales). However, this positive correlation decreases with increasing ln-transformed geographical extent, which approaches zero at extents of about $1x10^6$ km^2 (regional scales) and above (continental to pan-tropical scales). A zero to weak positive correlation at a pan-tropical geographical extent is in contrast with an earlier finding in which a significant positive relationship was observed between tree genus richness and carbon stock at a pan-tropical extent (Cavanaugh et al. 2014). This contrasting finding may be explained by the fact that plant genus richness behaves differently across spatial scales than plant species richness (see for example Huang, Huang, Lu, & Ma, 2016; Mutke & Barthlott, 2005).

Although our meta-analysis has some data limitations, such as the restriction to only linear relationships and a lack of access to the primary data, it is possible to synthesize potential explanations for the observed pan-tropical relationship between tree species richness and carbon stock as well as the effect of geographical extent. First, several hypotheses have been put forward that could explain the positive correlation between tree species richness and carbon stock in tropical forests. These hypotheses include the niche complementarity hypothesis (i.e. forests with more tree species are more diverse in species traits, which allows higher primary productivity and thus higher carbon storage; Poorter et al., 2015; Shen et al., 2016; Sullivan et al., 2017; van der Sande et al., 2017), the selection effect hypothesis (i.e. tree species-rich communities are more likely to contain high-carbon storing species; Poorter et al., 2015; Shen et al., 2016; Sullivan et al., 2017), and the insurance hypothesis (i.e. species can complement each other in output across time, and thus species-rich communities ultimately have a greater output over time; Poorter et al., 2015; van der Sande et al., 2017). However, support for these hypotheses in our analyses remains inconclusive as these previous studies have incorporated different geographical extents and are therefore not directly comparable (Shen et al., 2016; Sullivan et al., 2017). Second, the relationship between tree species richness and carbon stock in tropical forests approaches zero at continental to intercontinental scales. We propose that this can be explained by the effect of the increasing amount of environmental heterogeneity that is captured. For example, it has been found that at the continental scale several environmental variables vary significantly with carbon stocks, although their relative importance differs across the continents. Sullivan et al. (2017) showed that at the continental geographical extents ($1.5x10^6$ to 13.1 $x10^6$ km^2) in the American and African tropics, carbon stocks are mainly influenced by cumulative water deficit, while in the Asian tropics it is mean annual precipitation, mean annual temperature and total exchangeable bases (a proxy for soil fertility) that mainly influence carbon stocks. We cannot rule out that variation in plant species richness and ecosystem service provisioning also partly explains the moderating effect observed, although it is expected that most interspecies interactions will have the strongest influence at landscape to regional geographical extents (Scheiner et al., 2011).

Previous studies that addressed the quantitative effect of plot size on plant diversity-carbon relationships found that with larger plot sizes relationships were more often non-significant (Poorter et al., 2015; Sullivan et al., 2017). In contrast, we found no effects of plot size on the correlation between tree taxonomic richness and carbon stock or between tree Shannon diversity and carbon stock. However, this is not surprising since most effect sizes in our analysis concerned plot sizes and sample sizes that are considered adequate to capture micro-scale level variation in carbon stocks in tropical forests (i.e. ≥ 0.5 ha, see Figure 2-3; sensu Chave et al., 2004; Clark & Clark, 2000; Grussu et al., 2016; Keller, Palace, & Hurtt, 2001). In support, omitting the cases with relatively small plot sizes (<0 .5 ha; i.e. cases 3, 12 and 13) did not yield significantly different results for the overall correlation between tree taxonomic richness and carbon stock (significant overall effect size 0.7006 *Zr* instead of 0.7553 *Zr*; Annex S6).

Although we found significant positive relationship between tree species richness and carbon stock across the tropics, no significant correlation between tree species diversity indicators (Shannon and Simpson) and carbon stock across the tropics were found. This is in line with previous analyses across the tropics (Poorter et al., 2015; Sullivan et al., 2017). The significant positive correlation between carbon stock and tree taxonomic richness on the one hand, and the non-significant correlation between carbon stock and both Shannon diversity and Simpson diversity together suggests that tree species abundance is less important than tree species richness for predicting carbon stocks across the tropics. However, it is possible that a yet unknown untested covariable moderates these relationships, as we detected significant unexplained variation in the relationships. Tree mean basal area showed a significant positive overall correlation with carbon stock despite significant variation among effect sizes. This finding can be explained by the fact that mean basal area is a constituent of the algorithms for biomass calculation (Poorter et al., 2015; Sullivan et al., 2017) and therefore, the outcome is not surprising.

The positive relationship between tree species richness and carbon stock in tropical forests has important implications for conservation policies. The possibility that high carbon and high biodiversity show spatial overlap has been a prospected win-win solution for policymakers under the UN REDD+ programme and has been put forward as having high potential for the conservation of tropical forests (Busch et al., 2011; Harvey et al., 2010; Scharlemann et al., 2010). However, up to now findings of such win-win situations have been limited because maps identifying the areas of spatial overlap at scales finer than the global scale are missing, and it is known that spatial overlap between high carbon and other biodiversity components (e.g. endemic or iconic species) does not always occur (Gardner et al., 2012; Harvey et al., 2010). In such cases where there is no spatial overlap, trade-offs between carbon and biodiversity conservation can be expected, limiting the effectiveness of conservation policies (Phelps et al., 2012). Here, we show empirical evidence of a spatial overlap between high tree species richness and high carbon stocks at the local to the regional scale, but not at the continental to global scales, which helps to funnel the search for win-win solutions. In addition, high tree species richness thus seems to facilitate high carbon, and therefore the loss of forests with high tree species richness can be expected to result in a strong decrease in carbon stock. This positive correlation indicates that forest with high tree species richness plays an important role in mitigating climate change by storing large amounts of carbon. This supports the argumentation that, in addition to reforestation of deforested or degenerated (secondary) forests (Bastin et al., 2019; Brancalion et al., 2019; Busch et al., 2019), conservation of remaining tree species rich forests is of high importance mitigating climate change.

Many indicators but limited consistency

Less than half of the seventy unique plant diversity indicators that were reported in the literature were used more than twice, and only five were used frequently to allow a meta-analysis (Table S2.5.2). In addition, only five indicators were used in bivariate analyses with multiple ecosystem services. Most relationships addressed the service of carbon stock, but less is known about the relationships between plant diversity indicators and carbon flow, timber provisioning and NTFP provisioning. This surprising finding shows that although there has been considerate attention for empirical relationships between plant diversity and tropical forest ecosystem services, the attention has been scattered over many different plant diversity indicators, which results in a lack of comparison. For instance, the functional dimension of plant diversity has been approximated by a myriad of scarcely used indicators (Annex S2.5). In addition, in some cases the difference between indicators was not directly apparent. For example, functional composition can be measured by the taking the Community Weighted Mean (CWM), but the CWM can use different weights (e.g. the number of individuals or the relative contribution to biomass) and the chosen weight was not always explicitly stated. Therefore, to facilitate meaningful comparisons in the future, a consensus should be established on the use of common functional indicators. Such common indicators could either be preferably used or, at the least, relationships including these indicators should be mentioned in the appendices of a paper. In addition, more published replicas of relationships are needed to substantiate the empirical evidence and to be able to investigate the potential heterogeneity between findings. A potential source of such additional information could be non-English papers, specifically Spanish papers. For example, a recent review of biodiversity-ecosystem service relationships reported for Latin-American dry tropical forests, found that 24% of all identified papers were published in Spanish (Quijas et al., 2019). Although the number of non-English papers retrieved by our English-based search strings was relatively low, i.e. 2.5%, including relevant non-English terms in search queries can be expected to increase this number, thereby increasing the chance to identify additional relevant information.

Despite the lack of consistent analyses of specific plant diversity-ecosystem service relationships, by pooling results by dimension and testing for consistency in significant outcomes, we found evidence that taxonomic, functional and structural indicators show distinct patterns in the direction of significant relationships with ecosystem services. Carbon stock showed consistent patterns of mainly positive relationships with the taxonomic, functional and structural dimensions, although for the functional dimension the pattern was less pronounced (i.e. a smaller difference in the number of positive and negative relationships) (Table 2-1). For carbon flow, relationships were not consistent, but indicated a trend towards mostly positive relationships. This is in line with previous findings in a review of pan-tropical relationships between plant diversity dimensions and carbon stock and flow (van der Sande et al., 2017). Our review added that NTFP stock and flow showed a general trend of non-significant relationships with the taxonomic, functional and structural plant diversity dimensions, although we found a pattern of negative relationships of the NTFP flow with the structural dimension. A post-hoc analysis of the pattern of negative relationships between the NTFP flow with the structural dimension showed that all negative relationships came from a single study, in which the regeneration of a single palm species was negatively correlated to stand density and basal area. In this situation a negative relationship may be expected on the basis of effects of competition for space, light and/or water. Nevertheless, we think that the evidence is too thin to substantiate such interpretations. Only when additional data would become available, these could be incorporated in a meta-analysis to verify to what extent such observed trends for NTFP can be statistically supported.

Concluding remarks

In our analysis, we set out to assess the evidence for (positive) relationships between plant diversity and multiple ecosystem services across variation in different spatial aspects. We found that the evidence gathered in contemporary literature is patchy, except for the service of carbon stock. Little evidence is available for carbon flow and timber and NTFP provisioning. The relationships that were found generally had few replications, were often inconclusive, or showed both positive and negative relationships. This limits the synthesis of relationships between plant diversity and ecosystem services. Yet, we found that plot-level tree species richness shows a strong positive correlation with carbon stock up to geographical extents corresponding to the regional scale. Tree species richness and carbon stock in tropical forests therefore represent opportunities for synergies between carbon and biodiversity conservation policies at the local to regional levels. This is relevant for protected areas designated at national level, such as national parks, forest reserves or other conservation units and for REDD+ projects. A better understanding of relationships between plant diversity and ecosystem services other than carbon is needed. The potential value of the ecosystem services concept as a focal point for biodiversity conservation can at present not be fully assessed and we may therefore risk missing important conservation trade-offs or synergies. As resources for research are limited, we stress the need to reach a consensus on common plant diversity indicators. We also plea for research into ecosystem services other than carbon stock, and we suggest to incorporate spatial aspect covariables, such as geographical extent, in future analyses of spatial variation of ecosystem services.

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SUPPLEMENTARY MATERIAL CHAPTER 2

Annex S2.1 Additional methods and methodology

Please note that Figure 2-1 in the main text shows the flow of information and Figure S2.1.2 shows an infographic of the methods used in the systematic review and meta-analyses.

S2.1.1 Search strings

Table S2.1.1 Search strings used in Scopus and Web of Science ('WoS'), including their and dates of submittal and the amount of returned hits.

Eco-system service	Search engine	Search string	Date final search string submitted and amount of records retrieved
Carbon	Scopus	TITLE-ABS-KEY("carbon storage" OR "carbon stock" OR "carbon store" OR "carbon sequestration" OR "carbon increase" OR "carbon increment" OR "carbon accumulation" OR "carbon accrual") AND TITLE-ABS-KEY("species richness" OR "species composition" OR "species diversity" OR "biodiversity" OR "species evenness" OR "species trait*" OR "species inventory" OR "functional richness" OR "functional composition" OR "functional diversity" OR "functional evenness" OR "functional trait*" OR "functional inventory" OR "vegetation structure") AND TITLE-ABS-KEY(forest) AND TITLE-ABS-KEY(tropic*)	6-6-2017; 477
	WoS	TS=("carbon storage" OR "carbon stock" OR "carbon store" OR "carbon sequestration" OR "carbon increase" OR "carbon increment" OR "carbon accumulation" OR "carbon accrual") AND TS=("species richness" OR "species composition" OR "species diversity" OR "biodiversity" OR "species evenness" OR "species trait*" OR "species inventory" OR "functional richness" OR "functional composition" OR "functional diversity" OR "functional evenness" OR "functional trait*" OR "functional inventory" OR "vegetation structure") AND TS=(forest) AND TS=(tropic*)	6-6-2017; 480
Timber	Scopus	TITLE-ABS-KEY("timber production" OR "timber volume*" OR "timber bole*" OR "timber trunk*"" OR "timber harvest*" OR "timber yield*" OR "wood production" OR "wood volume*" OR "wood bole*" OR "wood trunk*" OR "wood harvest*" OR "wood yield*") AND TITLE-ABS-KEY("species richness" OR "species composition" OR "species diversity" OR "biodiversity" OR "species evenness" OR "species trait*" OR "species inventory" OR "functional richness" OR "functional composition" OR "functional diversity" OR "functional evenness" OR "functional trait*" OR "functional inventory" OR "vegetation structure") AND TITLE-ABS-KEY(forest) AND TITLE-ABS-KEY(tropic*)	28-05-2018; 155

Eco-system service	Search engine	Search string	Date final search string submitted and amount of records retrieved
	WoS	TS=("timber production" OR "timber volume*" OR "timber bole*" OR "timber trunk*"' OR "timber harvest*" OR "timber yield*" OR "wood production" OR "wood volume*" OR "wood bole*" OR "wood trunk*" OR "wood harvest*" OR "wood yield*") AND TS=("species richness" OR "species composition" OR "species diversity" OR "biodiversity" OR "species evenness" OR "species trait*" OR "species inventory" OR "functional richness" OR "functional composition" OR "functional diversity" OR "functional evenness" OR "functional trait*" OR "functional inventory" OR "vegetation structure") AND TS=(forest) AND TS=(tropic*)	28-05-2018; 155
Non Timber Forest Products (NTFPs)	Scopus	TITLE-ABS-KEY("forest product" OR "NTFP*") AND TITLE-ABS-KEY("species richness" OR "species composition" OR "species diversity" OR "biodiversity" OR "species evenness" OR "species trait*" OR "species inventory" OR "functional richness" OR "functional composition" OR "functional diversity" OR "functional evenness" OR "functional trait*" OR "functional inventory" OR "vegetation structure") AND TITLE-ABS-KEY(forest) AND TITLE-ABS-KEY(tropic*)	11-7-2017; 140
	WoS	TS=("forest product" OR "NTFP*") AND TS=("species richness" OR "species composition" OR "species diversity" OR "biodiversity" OR "species evenness" OR "species trait*" OR "species inventory" OR "functional richness" OR "functional composition" OR "functional diversity" OR "functional evenness" OR "functional trait*" OR "functional inventory" OR "vegetation structure") AND TS=(forest) AND TS=(tropic*)	11-7-2017; 67

S2.1.2 Registering data for the corpus

For our corpus records we registered 4 types of data: the type of ecosystem service, the type of plant diversity indicator, the type of statistical analysis, and the type of spatial covariables. These data types included: the type of ecosystem service and whether it concerned stock (e.g. X Mg carbon ha^{-1}) or flow (e.g. Y Mg carbon ha^{-1} yr^{-1}); how the ecosystem service was approximated (e.g. for carbon: using a allometric model and biomass-to-carbon conversion factor, for Timber and Non-Timber Forest Products (NTFPs): which plant species or plant genus); which plant diversity indicator was used (e.g. species richness, leaf area index, basal area); which life forms of plant diversity indicator were considered (i.e. herbs, lianas, palms, trees); the reported minimum and maximum diameter of stems that were considered in the plant diversity indicator (in cm); the taxonomic precision of the plant diversity indicator (i.e. species, genus, family).

For the plant diversity indicators, we assigned them to a group specified by the plant diversity aspect that was measured (e.g. leaf-aspects, diameter aspects, taxonomic aspects), and we registered whether they represented traits from the taxonomic, functional or structural dimension. As the taxonomic, functional and structural plant diversity dimension where not always distinguished in the records, we classified the reported plant diversity indicators to one of these three dimension using a framework on the basis taxonomic identity and physical properties, which is visualized in Table S2.1.1. Here, the taxonomic and functional indicators are based on a taxonomic identity because without it, species cannot be quantified and physical attributes cannot be interpreted in the light of an ecological or evolutionary role. In contrast, the structural indicators can be measured regardless of taxonomic identity. Taxonomic indicators can be measured without measuring physical properties (except those needed for taxonomic identification) while for functional indicators and structural indicators physical properties always need to be quantified. Examples of how this framework classified different plant diversity indicators: the average height of a community was a structural indicator, the average height of a taxon (e.g. a species or genus) was a functional indicator and the number of different taxa was a taxonomic indicator (e.g. species richness or genus richness).

Table S2.1.2. Conceptual framework of to what extent taxonomic identity and physical properties are important in taxonomic, functional and structural indicators, where '++' stands for 'very important', '+'stands for 'important' and '0' stands for 'not important'.

Taxonomic identity		
++	+	0
Taxonomic indicators	**Functional indicators**	**Structural indicators**
0	+	++
		Physical properties

For the type of statistical analysis, we registered data on the amount of variables considered (i.e. univariate, bivariate, multiple variables); which relationship-test was used (e.g. correlation, regression, non-parametric); the type model used (e.g. Pearson correlation, Kendall's tau, OLS regression); if the relationship was reportedly significant; the linearity of the relationship (e.g., linear, exponential, logarithmic), the reported direction of the significant relationship (i.e. positive, negative); the trend of the relationship (ignoring statistical significance; i.e. positive, negative) taken as reported, or else from visual interpretation; the reported sample size used in the test (*'plot number'*); and any reported statistics of the test (e.g. correlation coefficient, p-value, t-value, F-value, Z-value, R^2, regressions coefficients, standard error).

For the spatial covariables, we registered data on the grain size (i.e. the area in which the data have been originally measured, or the *actual plot size*, in ha); the focal scale (the area size to which data are standardized prior to analysis, in ha; which we treat synonymous to 'plot size' in this chapter, see also under S2.1.5 Meta-regressions); and the geographical extent (the area that encompasses the *actual plots* compared in a relationship, in km^2; after Whittaker, 2010 and Scheiner et al., 2011). See Figure S1 for a graphical representation of how plot size, plot number and geographical extent can vary per study. As the geographical extent of the study area was not always reported, we calculated the minimum rectangle encompassing compared plots using the Daftlogic website-tool (Daftlogic, 2018; https://www.daftlogic.com/projects-google-maps-area-calculator-tool.htm, accessed 12-02-2017). As the geographical extent increases with a power function, we applied a natural log ('ln') transformation to linearize the relationship between geographical extent and study area.

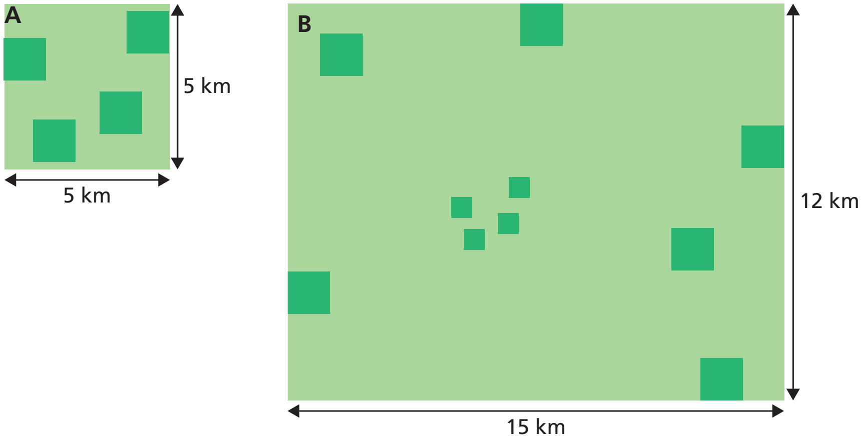

Figure S2.1.1. Graphical representation of how plot size, plot number and geographical extent can vary per study, showing two studies: A and B. In Study A, 4 plots (dark green squares) are compared, each are 1 ha, and the geographical extent (the smallest rectangle; light green rectangle) is 25 km^2 or 3.22 ln(km^2). In Study B, 10 plots are compared, where 6 plots are 1 ha and 4 plots are 0.25 ha, and the geographical extent is 180 km^2 or 5.19 ln(km^2).

Last, we included meta-information consisting of: a unique identifier per record (*i*); the title of the paper; a short citation reference to the paper and the year of publication; which tropical continent was sampled on the basis of the reported location (i.e. Australian tropics, Asian tropics, African tropics, American tropics or pan-tropical); and the reported forest disturbance (i.e. primary and/or secondary). We interpreted primary forest as forests that are under no to little human impact, e.g. 'old-growth forest', and secondary forest as forests that have been selectively logged or harvested for other plant based products or forests that are regenerating after being clear cut. The corpus database is provided in Annex S2.4.

S2.1.3 Systematic review

For inclusion in the systematic review, we first assessed the completeness of statistical information provided in the corpus. For a comparison to be included, it needed information the type of test used (e.g. a t-test), the test-value (e.g. the t-value) an exact significance value (i.e. the p-value, not 'ns' or '<0.05'). This resulted in a dataset of 40 relevant studies.

Second, as there is no common definition in the literature as to what a 'tropical forest' is, we filtered for studies that contained data from forests that lie within countries that host at least parts of the estimated historical extent of evergreen tropical rain forests as identified in Corlett and Primack (2011). Afterwards, we excluded records that contained only plantation or non-forest tropical vegetation. This resulted in a dataset of 30 eligible studies.

The scope of the final 30 studies that were used in the systematic review was assessed by first registering additional information on: the Köppen climate class, either reported or assigned on the basis of the location of the study; the reported local climate of the forest (i.e. Dry forest, Moist forest and Wet forest); the reported hydrology of the forest (i.e. terra firme or seasonally flooded); and second summarizing this and other relevant information already registered in the corpus, in Table S2.2. On the basis of Table S2.2, we can summarize that the forests ultimately compared in the systematic-analysis included a wide spectrum of forests, but are predominantly evergreen, terra-firme primary forests, from the Köppen tropical climate zone ('*A*'). Some studies also or only included secondary forests (i.e. 9 primary and secondary, 6 only secondary), which ranged from mostly forests that where selectively logged (either presently by local communities or in the past 14 to 22 years ago) to one forest that has been regenerating after being clear-cut 10 to 120 years ago.

We pooled the plant diversity indicators of 247 bivariate analyses per taxonomic, functional and structural dimension, summing the number of significantly positive, significantly negative and non-significant relationships. To see if the significant outcomes consistently pointed towards a specific direction, we carried out a binomial t-test under the pragmatic assumption that outcomes were independent of each other. Specifically, we tested H_0: ratio (outcome 1 / outcome 1 + outcome 2) = 0.5, with a two-tailed t-test with 95% CI and $\alpha = 0.05$, where outcome 1 and 2 are the number of significantly positive outcomes and number of significantly negative outcomes. As our data were nested, the outcome of the binomial t-test ran the risk of having inflated type I errors, i.e. rejecting H0, while it is true. In this light, the binomial t-test outcomes can be interpreted as running the risk of being over-conservative. In addition, we partitioned the 247 bivariate analyses into 101 subsets of specific relationships between plant diversity indicators and ecosystem services. Per subset we counted the total number of relationships reported, how many of these were statistically significant, and from how many studies the total number originated.

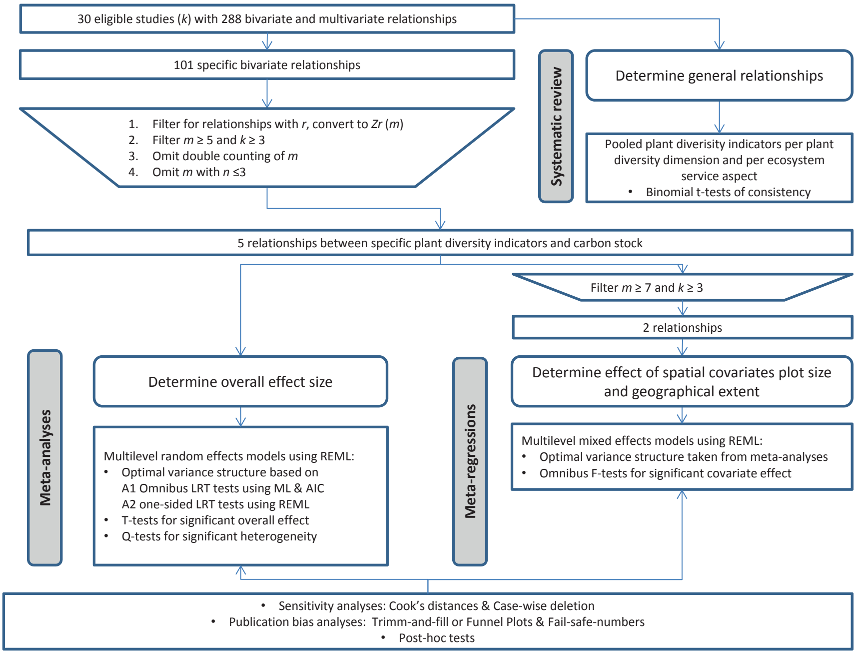

Figure S2.1.2. Infographic of the methods used in the systematic review and meta-analyses.

S2.1.4 Meta-analyses of relationships across the tropics

Pearson correlation coefficients (*r*) were used as input for the effect sizes of our meta-analysis, as these provided the largest set of statistically comparable analyses. We retrieved *r* from the studies either directly or derived or calculated it from other provided bivariate statistical metrics as described by Koricheva et al. (2013; see box 13.3). Since the Pearson correlation coefficient does not behave with desirable statistical properties (where if the coefficient approaches 1, its distribution becomes skewed), we transformed the Pearson correlation coefficients (*r*) using the Fisher's Z transformation (hereafter *Zr*). *Zr* is calculated by $Zr = 0.5 * \log[(1 + r) / (1 - r)]$, where *r* is the Pearson correlation coefficient and *Zr* can range between $-\infty$ and $+\infty$. The asymptotic variance of *Zr* (s^2_z) was calculated by $s^2_z = 1/(n - 3)$, where *n* is the amount of samples used. As the s^2_z of *Zr* has an inverse relationship of *n*, the s^2_z can be used as a weight of precision in comparing *Zr* (Castagneyrol & Jactel, 2012). If an *Zr* had a *n* of ≤3, we did not use it for analysis.

For our meta-analyses, we used multilevel random-effect models to establish overall relationships for specific plant diversity indicator-ecosystem service relationship. Here 'overall relationships' means the relationships across all effect sizes, in some cases meaning across the tropics. A random-effects model allows each sample in the model to behave independently, thereby enabling comparison of heterogeneous effect sizes. As some of the effect sizes originate from the same study (i.e. are nested) we used multilevel models (also called 'nested models' or 'hierarchical models') to control for non-independence. Specifically, we used a three-level random effects model where variance in the data was contrasted in: sampling variance between studies (level 1); variance between effect sizes within each study (level 2); and variance of effect sizes between studies (level 3) (after Assink & Wibbelink, 2016).

We used forward model-selection to find the optimal random structure for each relationship in two separate analyses. In one analysis (A1) we compared whether a multilevel model fitted the model better than a non-multilevel, 'unilevel' model and in the other analysis (A2) we tested if there was significant heterogeneity in effect sizes within each study an heterogeneity in effect sizes between studies (i.e. level 2 and level 3 variance).

For A1, we carried out an omnibus Likelihood Ratio Test (LRT) to see if a three-level random effects model (variance across all 3 levels) fitted the data differently than a fixed-effects model (no variance across any level), and if so, which model had the better fit. For the omnibus LRT, H_0 : fit multilevel model = fit unilevel model and H_1 : fit multilevel model ≠ fit unilevel model, at the significance level $\alpha = 0.05$; and fit is determined by the Deviance of the model: Deviance = -2 * log-likelihood, where likelihood was estimated by the Maximum Likelihood (ML) instead of Restricted Maximum Likelihood (REML) to allow comparison between the two types of models. When a significant difference was found in the omnibus LRT, we compared the Akaike Information Criterion (AIC) to see which model had the better fit, i.e. the lowest AIC. We used AIC instead of the more conservative Bayes Information Criterion (BIC) as our samples sizes were relatively small (i.e. $m < 14$) and in such cases little difference exists between AIC and BIC estimates. In addition, the AIC is more frequently used in the literature.

For A2, we carried out one-sided LRT tests to detect significant heterogeneity in effect sizes at level 2 and level 3. Here, we compared the heterogeneity (σ^2) of models that allowed variance to exist on specific levels (i.e. comparing a three-level random effects model with a random effects model without variance at level 2 and with a random effect model without variance at level 3) using one-sided LRTs. Here H_0: σ^2 alternative model = σ^2 baseline model and H_1 : σ^2 alternative model > σ^2 baseline model (as σ^2 cannot be negative), with $\alpha = 0.05$ at the boundary; and σ^2 is estimated using REML. The one-sided LRT p values were obtained by dividing the p-value of two-sided LRTs by 2 (after Zuur, Ieno, Walker, Saveliev, & Smith, 2009). We used a one-sided LRT test instead of a one-sided Cochran's Q-test because our datasets (number of effect sizes, *m*) are relatively small and in such cases both tests are conservative (i.e., when $m < 40$; Viechtbauer, 2007) and overall, to reduce the number of different tests used.

Although for the calculation of an overall effect size a minimum of 2 effect sizes is needed (Koricheva et al., 2013), a certain minimum is needed for a meta-analyses to have sufficient statistical power. If the statistical power is too low, there is a high chance for Type II errors, i.e. accepting H_0 while it is not true, thus being over-conservative. Because we cannot know the minimum a-priori and we wanted to calculate overall effect sizes spanning a wide geographical area, we used a guideline of at least 5 effect sizes (*m*) originating from at least three studies (*k*), i.e. $m \geq 5$ and $k \geq 3$. Significance of the calculated overall effect size was tested using an omnibus F-test, as after Knapp and Hartung (2003), the t-statistic was used. Here, H_0: $\mu = 0$ and H_1: $\mu \neq 0$, with $\alpha = 0.05$; and μ is estimated using REML.

For the overall effect size, the amount of heterogeneity was assessed using the Q-statistic. Here, we used a Chi-Squared test with $\alpha = 0.05$. Q values can be interpreted as the relative amount of heterogeneity under equal degrees of freedom. If the degrees of freedom increases, the Q value increases as well.

S2.1.5 Meta-regressions of spatial aspects

For our meta-regressions, we used multilevel mixed-effect models to investigate whether spatial scale covariables could explain part of the heterogeneity among effect sizes. To have sufficient statistical power to detect influence of a covariable, we only included relationships whose dataset had seven or more effect sizes originating from three or more studies (i.e. $m \geq 7$ and $k \geq 3$). As we could not know the minimum number of effect sizes required before knowing the strength of the expected relationship (cf. Field, Miles and Field, 2012), we chose this threshold as a compromise between the risks of having an excessively small dataset (potentially leading to Type II errors) and the opportunity of investigating effects of spatial scale on plant diversity and tropical forest ecosystem services relationships. All of our meta-regression models used REML.

Mixed-effect models contain a random-effects part and a fixed-effects part. In our models, the observed relationships in the dataset represent the random-effects part and the covariable(s) represent the fixed-effects part of the model. We included each spatial covariable as a fixed-effect separately and tested if its coefficient was significant using an omnibus F-test (as we used the t-statistic after Knapp and Hartung 2003). This kind of omnibus test takes two degrees of freedom into consideration: one based on the amount of moderators used (df1) and one based on the amount of effect sizes considered (df2). We included a single spatial covariable at a time as our dataset sizes were too small (i.e. $7 \leq m \leq 13$) to statistically warrant the inclusion of interactions between the moderators. To avoid potential interdependence between the spatial covariables as much as possible, we tested for correlations between the spatial covariables in each subset. We found that the grain size and focal scale were correlated ($r \geq 0.75$) and, as in most studies in our corpus the focal scale was most synonymous to the 'plot size', we omitted the grain size and treated the focal scale as the 'plot size' in this chapter. Although we found that the focal scale and ln-transformed geographical extent were correlated ($r \approx 0.8$), we maintained both spatial covariables, as we wanted to specifically test the effects of both plot size and geographical extent.

S2.1.6 Sensitivity and publication bias analyses

For all of our final models we analysed the sensitivity of the model and the effects of a potential publication bias. The sensitivity of the models was tested by comparing Cook's distances and case-wise deletion of any influential cases. Influential Cook's distances can be identified as distances larger than 1 or, more conservatively, larger than $4/m$. As we want to reduce the chance of interpreting non-robust outcomes, we used $4/m$ as the influential distance criterion. We considered a model to be robust when there were no influential cases or when after the removal of up to two influential cases the overall effect was still significant (after Viechtbauer & Cheung, 2010).

The effects of a potential publication bias were estimated by using a trim-and-fill method (Duval & Tweedie, 2000) where possible, else visual inspection of a funnel plot. We preferred to use the trim-and-fill method above the visual inspection of funnel plots as there are no statistical (objective) tests for funnel plots, funnel plots are hard to visually interpret, and funnel plots in ecological meta-analyses or meta-analyses with less than 30 studies tend to be asymmetrical anyway (Koricheva et al., 2013). In our analyses, due to at the time of writing the R package metafor did not support a trim-and-fill function for multivariate models, this meant that for our multivariate models (i.e. when effect sizes showed significant variance within studies) we used funnel plots, but in all other cases we used a trim-and-fill method. For our trim-and-fill method we used the R_0 estimator as we estimate that the amount of theoretical missing studies is less than 25% of those observed (Duval and Tweedie, 2000). For the funnel plot method, we made a visually interpretation. In addition to the quantitative trim-and-fill method, and specifically for the cases were we could only use the qualitative funnel plot method, Fail Safe Numbers were calculated to investigate a potential publication bias. With Fail Safe Numbers the number of studies with a significant effect needed to reach target $\alpha = 0.05$ is calculated and compared to a reference number, in our case the relatively conservative $5k+10$ number (after Rosenberg, 2005). Although Fail Safe Numbers were not originally developed for multivariate models and currently have not been specifically tested for such use, we decided to still use them in the absence of a better second quantitative method.

S2.7 PRISMA Checklist

The PRISMA checklist has been omitted to save paper. It can be accessed at the published version of this chapter (see the beginning of this chapter for a DOI and QR code).

Annex S2.2 Scoping table dataset used in systematic review and meta-analyses

Table S2.2 Scoping table of the 30 studies ultimately used for the systematic review and meta-analyses. NTFPs stands for Non-Timber Forest Products. Abbreviations hydrology: Terra Firme (TF) and Seasonally Flooded (SF). Bibliography of references given in Annex S3.

Reference	Ecosystem service	ES dimension included	Included in systematic review	Included in meta-analyses	Plant trait indicators included	Hydrology (reported or assigned)	Forest type (reported or assigned)	Forest disturbance	Matched Köppen climate classification	Continent sampled	No. of replicas	Grain size (ha)	Focal scale (ha)	Calculated geographical extent (km²)
Alamgir et al., 2016	Carbon	Stock	Y	N	structural	TF	Dry (sclerophyll), Wet forests	Primary, Secondary (selectively logged and regenerating, age not reported)	Aw	Australian	42	0.05	0.05	20,000
Aldana et al., 2017	Carbon	Stock	N	N	taxonomic, functional, structural	TF, SF	Wet forests	Primary	Af, Am	American	25	1	1	774,949
Álvarez-Yépiz et Dovciak, 2015	Carbon	Stock	Y	N	functional	TF	Dry forest	Primary	Bsh	American	27	0.04	0.04	930
Arul Pragasan, 2015	Carbon	Stock	Y	Y	taxonomic, structural	TF	Dry to Wet forests	Secondary (selectively logged)	Aw	Asian	24	0.5	0.5	1,318
Arul Pragasan, 2016	Carbon	Stock	Y	Y	taxonomic, structural	TF	Dry (Monsoon) forests	Primary	Aw	Asian	18	0.5	0.5	702
Asase et al., 2012	Carbon	Stock	Y	Y	taxonomic, structural	TF	Moist Forest	Primary, Secondary (commercially selectively logged 14 years ago)	Am/Aw	African	10	0.0025, 0.06	0.0025, 0.06	828
Baker et al., 2009	Carbon	Stock	Y	Y	functional, structural	TF, SF	Dry to Moist to Wet forests	Primary	Af, Am, Aw	American	60	1	1	5,760,000

Reference	Ecosystem service	ES dimension included	Included in systematic review	Included in meta-analyses	Plant trait indicators included	Hydrology (reported or assigned)	Forest type (reported or assigned)	Forest disturbance	Matched Köppen climate classification	Continent sampled	No. of replicas	Grain size (ha)	Focal scale (ha)	Calculated geographical extent (km²)
Baraloto et al., 2014	Carbon, NTFPs, Timber	Stock, Flow	Y	Y	taxonomic, functional	TF, SF	Humid forest	Secondary (selectively logged up to present)	Am, Aw	American	69	0.5	0.5	143,745
Behera et al., 2017	Carbon	Stock	Y	Y	taxonomic, structural	TF	Dry (Monsoon) forests	Primary	Cwa	Asian	3	1	1	355
Cavanaugh et al., 2014	Carbon	Stock	Y	Y	taxonomic, functional	TF	Dry to Moist to Wet Forests	Primary	Af, Am, Aw	Pantropical	59	1	1	102,500,000
Chaturvedi et Raghubanshi, 2015	Carbon	Stock, Flow	Y	Y	taxonomic, structural	TF	Dry (Monsoon), moist, Wet Forests	Primary	Cwa	Asian	45	0.1	0.1	253,693
Day et al., 2014	Carbon	Stock	N	N	taxonomic, structural	TF	Moist forests	Primary, Secondary (selectively logged 'in the past')	Af, Am, Aw	African	33	1	1	578,403
de Lima et al., 2013	Carbon	Stock	Y	Y	taxonomic	TF	Moist tot Wet forests	Primary, Secondary (regenerating, age not reported)	Am, Aw	African	Primary: 12; Secondary: 16	0.05	0.25	1,435
Fantini et Guries, 2007	NTFP	Stock, Flow	Y	N	structural	TF	Moist forest	Secondary (selectively logged 24-28 years ago)	Cfa	American	15, 12	0.16	0.16	NA
Fauset et al., 2015	Carbon	Stock	Y	Y	functional	TF	Moist forest	Primary	Af, Am, Aw	American	530	25 to 0.04; mean 0.69	25 to 0.04; mean 0.69	9,000,000
Finegan et al., 2015	Carbon	Stock, Flow	Y	Y	structural, functional	TF	Moist, Wet forests	Primary	Af, Am, Aw	American	Stock: 62; Flow: 21	Bolivia plots: 27; remainder: 1	1	7,578,911

Reference	Ecosystem service	ES dimension included	Included in systematic review	Included in meta-analyses	Plant trait indicators included	Hydrology (reported or assigned)	Forest type (reported or assigned)	Forest disturbance	Matched Köppen climate classification	Continent sampled	No. of replicas	Grain size (ha)	Focal scale (ha)	Calculated geographical extent (km²)
Gillison et al., 2013	Carbon	Stock	Y	Y	taxonomic, functional, structural	TF	Moist Forest	Primary, Secondary (selectively logged), Anthropogenic (plantations, grasslands, food gardens)	Af	Asian	16	0.02	0.02	3,018
Gonzalez et al., 2014	Carbon	Stock	Y	Y	taxonomic	TF	Moist forest	Primary, Secondary (regenerating, aged 10 to 42 yrs)	Aw	American	18	0.32; 0.36; 0.64; 0.9; 1; 1.08; 2; most 1	1	9,546
Jucker et al., 2016	Carbon	Flow	Y	N	taxonomic, structural	TF	Wet forests	Primary, Secondary (selectively logged 22 years ago)	Am	African	142	0.125	0.125	5,348
Kirby et Potvin, 2007	Carbon	Stock	N	N	taxonomic	TF	Moist Forest	Secondary (selectively logged)	Am	American	32	0.07	0.07	31.45
Martinez-Sanchez et al., 2015	Carbon	Stock	Y	Y	taxonomic, functional, structural	TF	Moist Forest	Primary, Secondary (regenerating, aged 20 to 120 yrs)	Af, Am	American	aggregated per site: 8	aggregated, minimum 0.25	aggregated, varying from 0.25 to 1.8 ha	6,2341
Peña et Duque, 2013	Carbon	Stock	Y	N	structural	TF	Moist to Wet forest	Secondary (regenerating from clear-cut 15 or 28 year)	Af	American	10	1	1	3,309
Poorter et al., 2015	Carbon	Stock	Y	N	taxonomic, structural	TF	Dry, Moist, Wet Forests	Primary	Af, Am, Aw	American	294, 1975	50 to 0.01; most 1	1, 0.1	23,253,032
Ruiz-Jaen et Potvin, 2010	Carbon	Stock	Y	Y	structural	TF	Wet forests	Primary	Af	American	117	0.04	4.95	0.06

Reference	Ecosystem service	ES dimension included	Included in systematic review	Included in meta-analyses	Plant trait indicators included	Hydrology (reported or assigned)	Forest type (reported or assigned)	Forest disturbance	Matched Köppen climate classification	Continent sampled	No. of replicas	Grain size (ha)	Focal scale (ha)	Calculated geographical extent (km²)
Ruiz-Jaen et Potvin, 2011	Carbon	Stock	Y	Y	taxonomic, functional	TF	Moist Forest	Primary	Af	American	815	50	0.04	0.5
Shen et al., 2016	Carbon	Stock	Y	Y	functional	TF	Moist Forest	Primary	Cwa	Asian	500	20	0.04	0.2
Stegen et al., 2009	Carbon	Stock	Y	Y	functional	TF	Dry, Moist, Wet Forests	Primary (predominantly; one site was frequently disturbed by hurricanes)	Af, Am, Aw	American	var 4 to 40; var 25 to 1000; var 5 to 115; var 25 to 500; var 15 to 320; var 12 to 250	4; 50; 5.95; 25; 16; 12	0.05; 2; 0.1; 0.1; 1; 0.5	0.04, 0.5, 0.059; 0.25; 0.16; 0.12
Sullivan et al., 2017	Carbon	Stock	Y	N	taxonomic, functional, structural	TF	Moist tot Wet forests	Primary	Af, Am, Aw	Asian, African, American	Asian: 40; African: 162; American: 158	1	1	Asian: 1,477,756; African: 13,135,977; American: 11,421,678
Toledo-Aceves et al., 2014	NTFP	Stock, Flow	Y	N	taxonomic	TF	Moist forest	Secondary (selectively logged, regenerating, ages not reported	Aw	American	64, 10	0.0004, 0.01	0.0004, 0.01	NA
van Con et al., 2013	Carbon	Stock	Y	Y	taxonomic, functional	TF	Dry to Moist to Wet Forests	Primary	Aw, Cwa	Asian	23	1	1	643,875

Annex S2.3 Studies used in systematic review and meta-analyses

See References at the end of this thesis.

Annex S2.4 Corpus database

Annex S2.4 has been omitted to save paper. It can be accessed at the published version of this chapter (see the beginning of this chapter for a DOI and QR code).

Annex S2.5 Reported number of analysis of plant diversity indicators across plant diversity dimensions

Table S2.5.1 Binomial t-test for the reported bivariate and multivariate relationships in tropical forests based on correlation and regression analyses, set out per ecosystem service aspect and plant diversity dimension. Here outcome 1 and 2 is either the number of significant positive relationships or number of significant negative relationships. Significant p-values are given in bold. NTFPs stands for Non-Timber Forest Products.

Table S2.5.1 has been omitted to save paper. It can be accessed at the published version of this chapter (see the beginning of this chapter for a DOI and QR code).

Table S2.5.2 Reported 70 plant diversity indicators used in 247 bivariate relationships between plant diversity indicators and ecosystem service aspects in tropical forests, showing the total number of use per plant diversity dimension. CWM stands for Community Weighted Mean.

	Number of analyses			
Plant diversity indicator group and indicators	**Taxonomic**	**Functional**	**Structural**	**Totals**
Taxonomic richness indicators group				**22**
Taxonomic richness (S)	17	0	0	17
Margalef's taxonomic richness (SR)	2	0	0	2
Mean percentage of individuals present in the canopy (% of pot spp)	1	0	0	1
Taxonomic richness rarefaction	1	0	0	1
Total number of individuals per canopy (spp)	1	0	0	1
Taxonomic diversity indicators group (rich*abun)				**39**
Simpson taxonomic diversity (D')	16	0	0	16
Shannon taxonomic diversity (H')	15	0	0	15
Shannon effective taxonomic diversity (exp(H'))	3	0	0	3
Whittaker's taxonomic evenness (Ew)	2	0	0	2
Shannon taxonomic equitability (Eh)	1	0	0	1
Simpson taxonomic dominance	1	0	0	1
Unknown taxonomic similarity index	1	0	0	1
Rarity dominance and endemism indicators group				**2**
Endemic taxonomic richness (spp/ha)	2	0	0	2
Functional richness indicators group				**1**
Unique PFT diversity (PFT are structural aspects attributed to species)	0	1	0	1
Functional diversity indicators group (rich* abun)				**22**
Rao's Q Functional diversity of leaf and wood functional traits	0	12	0	12
Functional dispersion of unknown indicators	0	2	0	2
Functional diversity related to taxonomic abundance	0	2	0	2
Functional evenness related to taxonomic abundance	0	2	0	2
Functional dispersion multivariate functional diversity (??)	0	1	0	1
Functional richness	0	1	0	1
Functional richness related to taxonomic abundance	0	1	0	1
Relative contribution of species to total number of stems (log)	0	1	0	1
Leaf indicators group				**29**
Functional dispersion Leaf dry mass per unit leaf fresh mass	0	3	0	3
CWM leaf area by individuals	0	2	0	2
CWM leaf dry mass per unit leaf fresh mass by biomass	0	2	0	2
CWM leaf dry mass per unit leaf fresh mass by individuals	0	2	0	2
CWM leaf force to tear by biomass	0	2	0	2
CWM leaf nitrogen concentration by biomass	0	2	0	2
CWM leaf nitrogen to phosphorous concentration ratio by biomass	0	2	0	2
CWM leaf phosphorous concentration by biomass	0	2	0	2
CWM selected leaf area per unit leaf mass by biomass	0	2	0	2
CWM selected leaf area per unit leaf mass by individuals	0	2	0	2
Functional dispersion Leaf area	0	2	0	2
Functional dispersion Selected leaf area per unit leaf mass	0	2	0	2
CWM leaf mass per area by basal area	0	1	0	1
Mean Leaf area	0	0	1	1
Mean litter fall	0	0	1	1
Mean Plant litter depth	0	0	1	1
Wood density indicators group				**33**
CWM wood density by biomass	0	28	0	28
CWM wood specific gravity by biomass	0	2	0	2
CWM wood density by individuals	0	1	0	1
Functional dispersion Wood density	0	1	0	1
Mean wood density	0	0	1	1
Height indicators group				**8**
CWM plant maximum height by biomass	0	2	0	2
CWM plant maximum height by basal area	0	1	0	1
Functional dispersion for plant maximum height	0	1	0	1
Mean plant maximum height	0	1	0	1
Mean Canopy height	0	0	1	1
Mean Plant height (m)	0	0	2	2
Biomass indicators group				**26**
Abundance-biomass-species diversity index (ABS)	0	1	0	1
Abundance-biomass-species index	0	1	0	1
Biomass-species diversity index (BS)	0	1	0	1
Biomass-species index	0	1	0	1
Initial AGB	0	0	1	1
Mean biomass (Mg/ha)	0	0	20	20
Mean volume (m3/ha)	0	0	1	1

	Number of analyses			
Plant diversity indicator group and indicators	**Taxonomic**	**Functional**	**Structural**	**Totals**
Diameter indicators group				**7**
CWM maximum diameter by individuals	0	2	0	2
Functional dispersion plant maximum diameter	0	1	0	1
Mean Plant diameter	0	0	2	2
Mean stand density of diameter > 70 cm (#/ha)	0	0	1	1
Mean stem diameter, quadratic (cm)	0	0	1	1
Complex indicators group				**3**
Functional divergence (FDiv=FDis) Plant height + Leaf nitrogen content (%N) + Carbon stable isotope ratio (?13C)	0	1	0	1
Plant Functional Complexity (PFC) index (based on PFT, PFT are structural aspects attributed to species)	0	1	0	1
Taxonomic diversity-plant functional traits index	0	1	0	1
Guild indicator group				**2**
CWM potential for nitrogen fixers by basal area	0	1	0	1
Functional dispersion potential for nitrogen fixers	0	1	0	1
Stand density indicators group				**24**
Mean stand density (#/ha)	0	0	24	24
Basal area indicators group				**25**
Mean basal area (m2/ha)	0	0	25	25
Canopy cover indicators group				**3**
Crown cover part of vegetation (%)	0	0	3	3
Misc indicators group				**1**
Bryophyte abundance	0	0	1	1
Analyses totals per plant diversity dimension	**63**	**98**	**86**	**247**
Total number of indicators used per plant diversity dimension	**13**	**41**	**16**	

Table S2.5.3 Reported bivariate relationships between plant diversity indicators and ecosystem service aspects in tropical forests, showing the total number positive outcomes ('+'), the number of non-significant outcomes ('Ø'), the number of negative outcomes ('-'), the total number of outcomes ('#'), and the total number of studies from which the relationships originate ('*k*'). Only those plant diversity indicators that were used at least twice in the 247 bivariate analyses are included (33 of the total 70 plant diversity indicators). Indicators are ranked by total number of bivariate relationships for each plant diversity dimension. Cells are flagged in light green if # ≥ 1 and *k* ≥ 1; cells are flagged in dark green if # ≥ 5 and *k* ≥ 3. CWM stands for Community Weighted Mean.

		Ecosystem service and aspect																													
		Carbon										**Timber**										**Non-Timber Forest Products**									
		Stock					Flow					Stock					Flow					Stock					Flow				
	Plant diversity indicator	**+**	**Ø**	**-**	**#**	***k***	**+**	**Ø**	**-**	**#**	***k***	**+**	**Ø**	**-**	**#**	***k***	**+**	**Ø**	**-**	**#**	***k***	**+**	**Ø**	**-**	**#**	***k***	**+**	**Ø**	**-**	**#**	***k***
Taxonomic	Taxonomic richness (S)	8	9	0	17	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Simpson taxonomic diversity (D')	2	3	1	6	3	0	0	0	0	0	0	1	0	1	1	0	1	0	1	1	0	4	0	4	1	0	4	0	4	1
	Shannon taxonomic diversity (H')	5	8	1	14	8	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Shannon effective taxonomic diversity (exp(H'))	1	0	0	1	2	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Endemic taxonomic richness	1	1	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Margalef's taxonomic richness (SR)	1	0	0	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Whittaker's taxonomic evenness (Ew)	1	0	0	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Functional	CWM wood density by biomass	14	9	5	28	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	CWM wood specific gravity by biomass	0	1	0	1	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Rao's Q Functional diversity of leaf and wood functional traits	0	1	1	2	1	0	0	0	0	0	0	0	1	1	1	0	1	0	1	1	0	4	0	4	1	0	4	0	4	1
	Functional dispersion Leaf dry mass per unit leaf fresh mass	1	2	0	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	CWM leaf area by individuals	0	1	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	CWM leaf dry mass per unit leaf fresh mass by biomass	0	1	0	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	CWM leaf dry mass per unit leaf fresh mass by individuals	2	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	CWM leaf force to tear by biomass	0	0	1	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	CWM leaf nitrogen concentration by biomass	0	0	1	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	CWM leaf nitrogen to phosphorous concentration ratio by biomass	0	1	0	1	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	CWM leaf phosphorous concentration by biomass	0	1	0	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	CWM maximum diameter by individuals	2	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	CWM plant maximum height by biomass	1	0	0	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	CWM selected leaf area per unit leaf mass by biomass	0	0	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	CWM selected leaf area per unit leaf mass by individuals	0	0	2	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Functional dispersion Leaf area	0	1	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Functional dispersion of unknown indicators	0	1	0	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Functional dispersion Selected leaf area per unit leaf mass	0	1	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Functional diversity related to taxonomic abundance	0	1	0	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Functional evenness related to taxonomic abundance	0	1	0	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Structural	Mean basal area (m2/ha)	8	2	0	10	7	3	0	0	3	2	0	0	0	0	0	0	0	0	0	0	0	2	2	4	1	0	4	4	8	1
	Mean stand density (#/ha)	2	6	0	8	6	2	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	2	2	4	1	0	8	2	10	1
	Mean biomass (Mg/ha)	0	0	0	0	0	0	0	0	0	0	1	1	0	2	1	1	1	0	2	1	0	8	0	8	1	0	8	0	8	1
	Crown cover part of vegetation (%)	3	0	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Mean Plant diameter	0	2	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Mean Plant height (m)	2	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Annex S2.6 Extended analyses per dataset

Please note that in contrast to the numbering of the cases from the references used in the main text, the numbering used in the extended analyses corresponds to the particular extended analysis. For example, case 5 in S1.6.1 refers to Sullivan et al. (2017), while in S1.6.2. it refers to van Asase et al. (2012).

S2.6.1 Taxonomic richness ~ Carbon Stock

S2.6.1.1 Assessing potential double-counting

After analysis of potential double-counting of data within source papers, we removed one of two effect sizes from Gillison et al. (2013), choosing to retain the *Zr* that was measured by taking all tree species versus taking all vascular plants, as this was the most comparable to the measurements of the other *Zr*. After analysis of potential double-counting of data between papers, we found that the plot locations used in Day et al. (2014) were also used by Sullivan et al. (2017). As the datasets of Sullivan et al. cover more plots and plot locations, we choose to retain the datasets of Sullivan et al. versus that from Day et al. In addition, we found partial double-counting of data between the datasets in Cavanaugh et al. (2014) and those in Sullivan et al. (2017). However, as this concerned only 16 of the 59 1-ha plots in the dataset of Cavanaugh et al., we choose to retain both datasets, but apply a post-hoc test to see if the omission would have made a difference in finding a substantial different overall effect size, which it did not (results not shown). Total omission of effect sizes: 2.

S2.6.1.2 Assessing the need for a multilevel model using ML

Comparing the fit of a fixed-effects model ('Reduced') vs a mixed-effects (multilevel) model ('Full')

	df	AIC	BIC	AICc	logLik	LRT	pval	QE
Full	3	18.2427	19.9375	20.9093	-6.1213			84.5734
Reduced	1	68.9570	69.5219	69.3206	-33.4785	54.7143	<.0001	84.5734

The multilevel model has lower AIC, BIC and Likelihood and is significantly different in likelihood ($p < 0.0001$) on the basis of a LRT. So we will use a multilevel model.

S2.6.1.3 Finding most optimal model using REML

One-tailed LRT comparison between the 'full' multilevel model and a 'reduced' model with fixed level 2 (differences within studies), to assess the influence of level 2 variance:

	df	AIC	BIC	AICc	logLik	LRT	adj.pval
Full	3	17.6911	19.1458	20.6911	-5.8455		
Reduced	2	15.6912	16.6610	17.0245	-5.8456	0.0001	0.4961

One-tailed LRT comparison between the 'full' multilevel model and a 'reduced' model with fixed level 3 (differences between studies), to assess the influence of level 3 variance:

	df	AIC	BIC	AICc	logLik	LRT	adj.pval
Full	3	17.6911	19.1458	20.6911	-5.8455		
Reduced	2	20.9919	21.9618	22.3253	-8.4960	5.3009	0.0107

Fixing level 3 significantly decreases the fit of the model (adjusted $p = 0.0107$, BIC 21.9618 vs 19.1458) while fixing level 2 does not (adjusted $p = 0.4961$), therefore, the most optimal model is one which allows variance at level 3.

S2.6.1.4 Estimating the overall effect size using REML

```
Test for Heterogeneity:
Q(df = 12) = 84.5734, p-val < .0001

Model Results:
estimate se        tval      pval      ci.lb     ci.ub
 0.7553   0.1494   5.0543    0.0003    0.4297    1.0809    ***

Back-transform Zr to r:
pred      ci.lb     ci.ub
0.6383    0.4051    0.7935
```

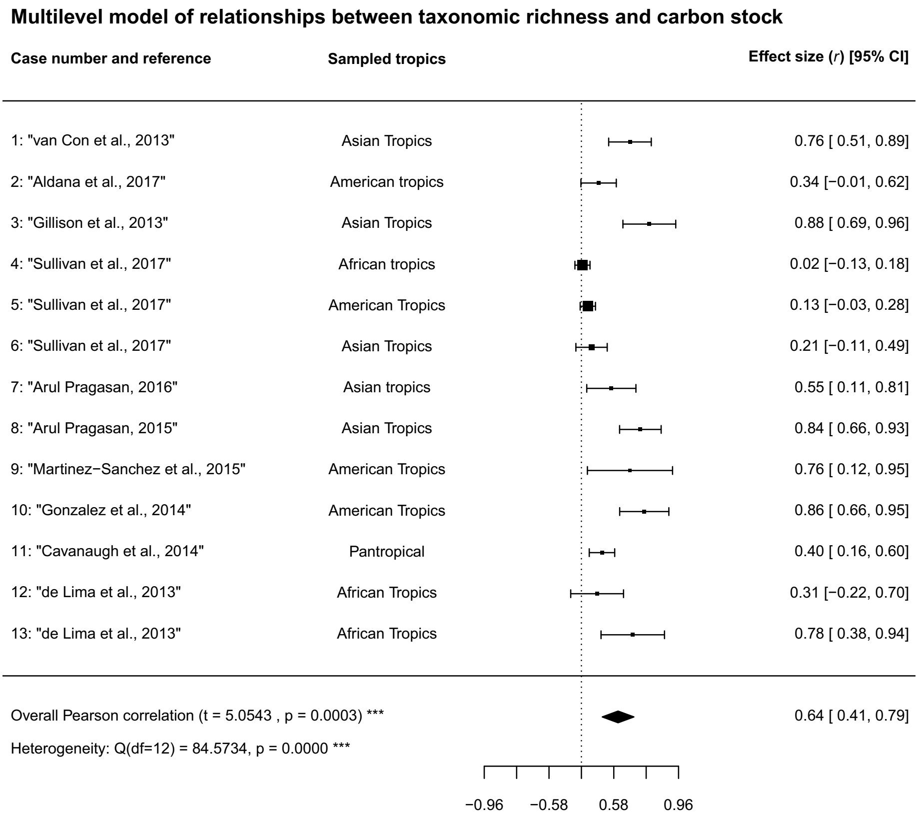

Figure S2.6.1.1. Forest plot of the overall effect size of the relationship between taxonomic richness and carbon stock. All Zr effect sizes and their 95% confidence intervals have been back-transformed to r values. Overall effect size calculated using multilevel model.

S2.6.1.5 Sensitivity and publication bias analysis overall model

As the trim-and-fill method is currently not available for multi-level models in metafor, we carried out a visual inspection of the funnel plot of the standard errors (See Figure S2.6.1.2 LEFT). The funnel plot shows that several cases lie outside the 95% pseudo-confidence interval (the white triangle), visualizing the heterogeneity present in the dataset. Analogous to the trim-and-fill method, if we wanted to make the observed funnel plot of the model more symmetric, we would add additional cases both left and right of the overall effect size, and as a result we do not expect that the overall effect size would significantly change. Thus, the visual inspection of the funnel plot does not give rise to doubt the robustness of the model and its overall effect size.

Rosenberg's weighted fail-safe number: 181
Conservative (5k+10) Rosenthal number: 75

The Rosenthal's fail-safe number is a factor 2.5 larger than the conservative number, indicating that when several of theoretical missing papers lying in a file drawer somewhere ("the file drawer problem") would be added to the model, it is unlikely that the overall effect size would become zero. Thus the fail-safe number indicates that the model is robust against the file drawer problem.

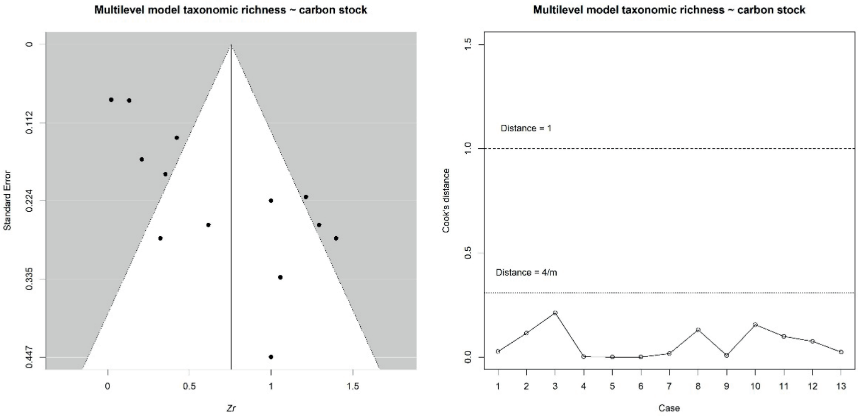

Figure S2.6.1.2. LEFT: Funnel plot of effect sizes used for the overall effect size of the relationship between taxonomic richness and carbon stock, using a multilevel model. The white area within the triangle represents the 95% pseudo-confidence interval of the calculated overall effect size. RIGHT: Plot of Cook's Distances of the final, multilevel model, comparing two thresholds for influential cases.

The plot of the Cook's distances (See Figure S2.6.1.2 RIGHT) show that all distances are below the threshold of 4/m (where *m* is the total amount of cases or effect sizes considered) and also the less conservative 1. Therefore we conclude that there are no influential cases in this model and that this model is robust.

S2.6.1.6 Meta-regression

Table S2.6.1.1. Collinearity check of moderators.

Pearson r	Grain size	Focal scale	Geographical extent
Grain size	1		
Focal scale	0.9880	1	
Geographical extent	0.5257	0.4685	1
ln Geographical extent	0.8685	0.8068	NA

On the basis of the collinearity check (table S2.6.1.1) we decided to exclude the grain size. Although ln geographical extent and the focal scale are collinear, we want to take the opportunity to investigate their effects in moderator analysis, although we cannot now be certain that effects are fully separate. Effect of Focal scale

```
Test for Residual Heterogeneity:
QE(df = 10) = 50.9731, p-val < .0001

Test of Moderators (coefficient(s) 2):
F(df1 = 1, df2 = 10) = 1.8699, p-val = 0.2014

Model Results:
                    estimate  se        tval      pval      ci.lb     ci.ub
intrcpt     1.1469  0.3349    3.4246    0.0065    0.4007    1.8931 **
Focal.scale.ha      -0.5693   0.4163    -1.3674   0.2014    -1.4970   0.3584
```

Back-transform *Zr* to *r*:

```
pred      ci.lb     ci.ub
-0.5149   -0.9046   0.3437
```

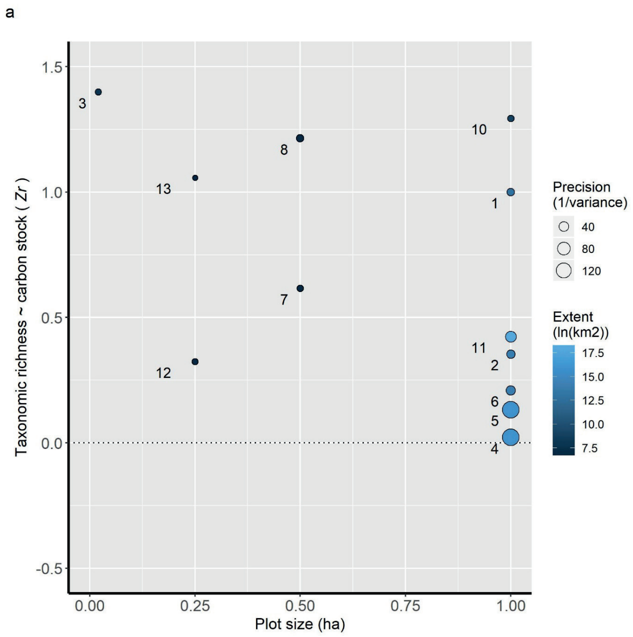

Figure S2.6.1.3. Plot of the focal scale against the Zr of 13 analyses of the relationship between taxonomic richness and carbon stock, using a multilevel model. Each analysis has a number corresponding to that used in the overall effect size model. Circles are drawn proportional to the inverse of the sampling variance, i.e. the Precision. Case 9 is omitted because the plot sizes were aggregated.

Effect of continuous Geographical extent:

```
Test for Residual Heterogeneity:
QE(df = 11) = 84.2514, p-val < .0001

Test of Moderators (coefficient(s) 2):
F(df1 = 1, df2 = 11) = 1.5569, p-val = 0.2380
```

```
Model Results:
                                estimate se          tval        pval        ci.lb       ci.ub
intrcpt                         0.8312      0.1620      5.1316      0.0003      0.4747      1.1877 ***
Geographic.area.extent.km2      -0.0000     0.0000      -1.2478     0.2380      -0.0000     0.0000
```

Back-transform *Zr* to *r*:

```
pred        ci.lb       ci.ub
-0.0000     -0.0000     0.0000
```

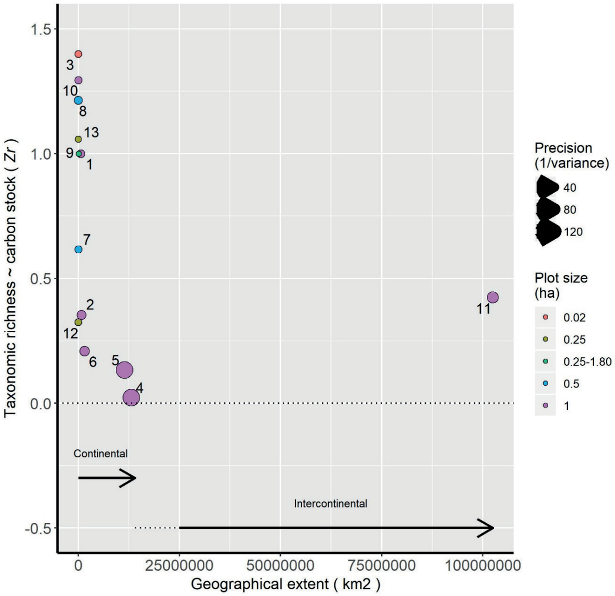

Figure S2.6.1.4. Plot of the continuous geographical extent against the Zr of 13 analyses of the relationship between taxonomic richness and carbon stock, using a multilevel model. Each analysis has a number corresponding to that used in the overall effect size model. Circles are drawn proportional to the inverse of the sampling variance, i.e. the Precision. The black arrows in the plot of geographical extent represent the approximated area of a continental and an intercontinental extent.

Effect of natural ln geographical extent:

```
Test for Residual Heterogeneity:
QE(df = 11) = 38.4497, p-val < .0001

Test of Moderators (coefficient(s) 2):
F(df1 = 1, df2 = 11) = 6.1924, p-val = 0.0301

Model Results:
                                estimate se          tval        pval        ci.lb       ci.ub
intrcpt         1.5147          0.3378      4.4847      0.0009      0.7713      2.2581 ***
log(Geographic.area.extent.km2) -0.0675     0.0271      -2.4884     0.0301      -0.1271     -0.0078  *
```

Back-transform *Zr* to *r*:

```
pred        ci.lb       ci.ub
-0.0674     -0.1264,    -0.0078
```

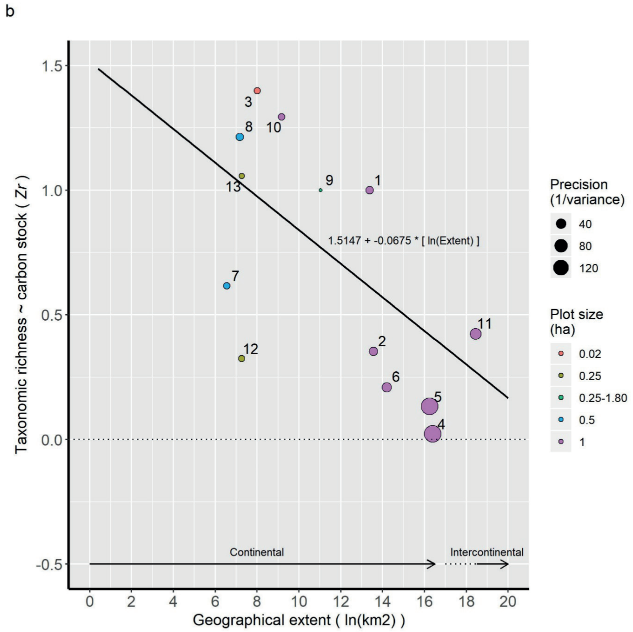

Figure S2.6.1.5. Plot of the natural log of the geographical extent against the Zr of 13 analyses of the relationship between taxonomic richness and carbon stock, using a multilevel model. Each analysis has a number corresponding to that used in the overall effect size model. Circles are drawn proportional to the inverse of the sampling variance, i.e. the Precision. The black arrows in the plot of geographical extent represent the approximated area of a continental and an intercontinental extent.

S2.6.1.7 Sensitivity and publication bias analysis meta-regression

We carried out a robustness analysis of the multilevel model of the effect of the natural ln geographical extent on the effect size of taxonomic richness ~ carbon stock as this effect was significant. Investigation of the Cook's distances identified three (weak) influential cases (i.e. showing distances below 1 but above 4/*m*): Case 7, 11 and 12. Therefore, we carried out a case-wise deletion of the most influential case which showed a significant effect of the natural log of geographical extent over the first four iterations (table S2.6.1.2). We therefore conclude that the outcome of the moderation analysis is relatively robust.

Table S2.6.1.2. Overview of case-wise deletion of the most influential case study, its effect on the outcome of the moderation analysis, and the number of influential studies remaining.

Iteration	Removal of case(s)	Omnibus test statistic	no. influential cases left
1	11	$F_{(1,10)} = 5.1839$, $p = 0.0460$	3
2	11, 12	$F_{(1,9)} = 23.4767$, $p = 0.0009$	3
3	11, 12, 7	$F_{(1,8)} = 72.9468$, $p < 0.0001$	2
4	11, 12, 7, 4	$F_{(1,7)} = 55.3688$, $p = 0.0001$	2

S2.6.1.8 Post-hoc tests

Effects of leaving dataset of Case 11 (Cavanaugh et al., 2014) out:
No difference in significance of overall effect size: estimate 0.8024 *Zr*, t = 4.8971, p = 0.0005.
No difference in moderation effect of focal size: Omnibus test $F_{(1,9)} = 1.1649$, p = 0.3085.
No difference in moderation effect of ln geographical extent: Omnibus test $F_{(1,10)} = 5.1839$, p = 0.0460.
No large difference in strength moderation effect of ln geographical extent: here -0.0787 instead of -0.0675

Effects of leaving out cases with relative small plot size (i.e. < 0.50 ha; case 3, 12, 13) after Whittaker 2010:
No difference in significance of overall effect size: estimate 0.7006 *Zr*, t = 4.1977, p = 0.0023.
No difference in moderation effect of ln geographical extent: Omnibus test $F_{(1,8)} = 5.7415$, p = 0.0434.
No large difference in strength moderation effect of ln geographical extent: here -0.0711 instead of -0.0675

S2.6.2 Shannon diversity ~ Carbon Stock

S2.6.2.1 Assessing potential double-counting and suitability of effect sizes

After analysis of potential double-counting of data within source papers, we removed three of four effect sizes from Asase et al. (2012), choosing to retain the *Zr* that was measured by taking all tree individual with DBH ≥ 10 cm versus taking a selection individuals with 5 ≤ DBH ≤ 10, and that that used the above ground biomass instead of the total biomass (including a compensation of belowground biomass), as this was the most comparable to the measurements of the other *Zr*. After analysis of potential double-counting of data between papers, we found that the plot locations used in Day et al. (2014) were also used by Sullivan et al. (2017). As the datasets of Sullivan et al. cover more plots and plot locations, we choose to retain the datasets of Sullivan et al. versus that from Day *et al*. Finally, we also omitted the case of Behera et al. (2017) as the used sample size (*n* = 3) is too small to calculate the variance of the *Zr*. Total omission of effect sizes: 3.

S2.6.2.2 Assessing the need for a multilevel model using ML

Comparing the fit of a fixed-effects model ('Reduced') vs a mixed-effects (multilevel) model ('Full')

```
         df     AIC      BIC      AICc     logLik   LRT     pval     QE
Full     3      10.8454  10.6831  18.8454  -2.4227                   20.8153
Reduced  1      11.6684  11.6143  12.4684  -4.8342  4.8231  0.0897   20.8153
```

The multilevel model has slightly lower AIC, BIC and Likelihood but is not significantly different in likelihood (p = 0.0897) on the basis of a LRT. So we will use a unilevel model.

S2.6.2.3 Estimating the overall effect size using REML

```
Test for Heterogeneity:
Q(df = 6) = 20.8153, p-val = 0.0020

Model Results:
estimate  se      tval    pval    ci.lb    ci.ub
0.2263    0.1371  1.6504  0.1499  -0.1092  0.5618
```

Back-transform *Zr* to *r*:

```
pred     ci.lb    ci.ub    cr.lb    cr.ub
0.2225   -0.1088  0.5093   -0.5057  0.7656
```

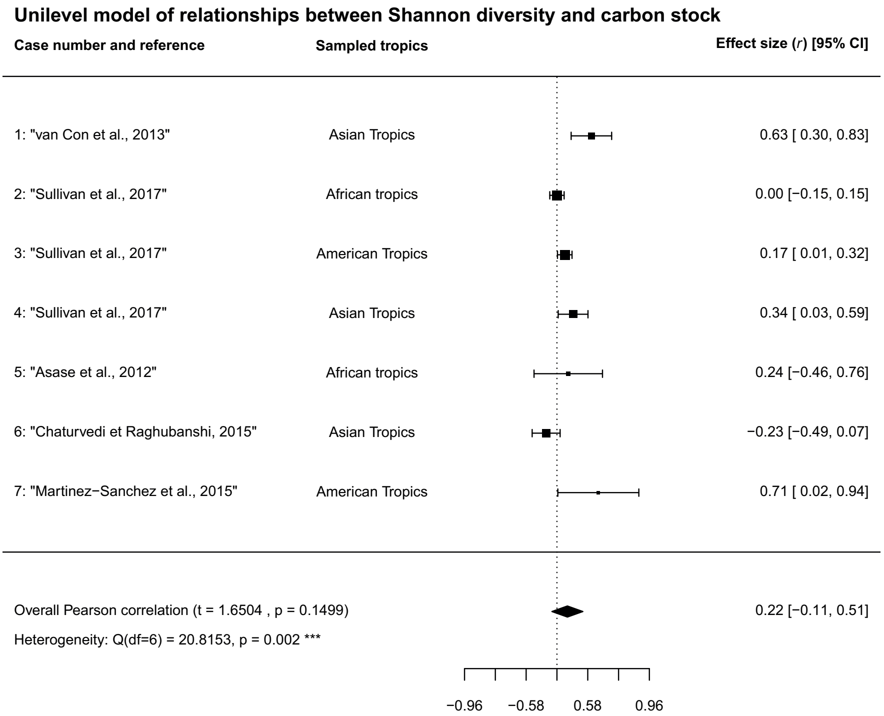

Figure S2.6.2.1. Forest plot of the overall effect size of the relationship between Shannon diversity (H') and carbon stock. All effect sizes and their 95% confidence intervals have been back-transformed to r values. Overall effect size calculated using an unilevel model.

S2.6.2.5 Sensitivity and publication bias analysis overall model

The trim-and-fill method predicts the additional cases to make the funnel plot symmetric. The trim-and-fill added a single case (See Figure S2.6.2.2 LEFT) and predicted an overall effect which did not greatly differed from the actual overall effect size (an back-transformed non-significant overall Pearson correlation of 0.1797 (95%CI [-0.0763, - 0.4240]; t = 1.3798, p = 0.1676). The funnel plot shows that two cases lie just outside the 95% pseudo-confidence interval (the white triangle), visualizing the relatively small amount of heterogeneity present in the dataset. Thus, the trim-and-fill test indicates that the model is not sensitive to the effects of the theoretical missing publications.

As the overall effect size was already non-significant we did not calculate a fail-safe number.

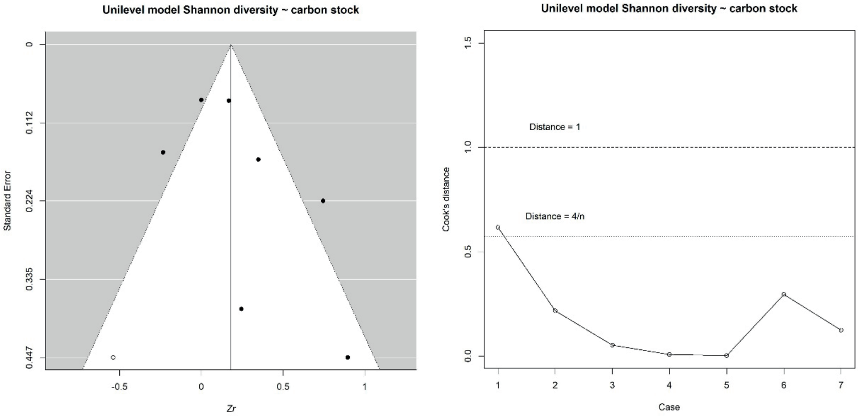

Figure S2.6.2.2. LEFT: Funnel plot of effect sizes used for the overall effect size of the relationship between Shannon diversity (H') and carbon stock, using a unilevel trim-and-fill model. The white area within the triangle represents the 95% pseudo-confidence interval of the calculated overall effect size. Black circles represent the effect sizes (cases) used in the model, open circles are simulated 'missing' cases added by the trim-and-fill method to correct the asymmetry of the funnel. RIGHT: Plot of the Cook's distances of the final, unilevel model, comparing two thresholds for influential cases.

The plot of the Cook's distances (See Figure S2.6.2.2 RIGHT) show that one case shows a distances that is above the threshold of 4/m (where *m* is the total amount of cases or effect sizes considered): case 4. All cases are less than the less conservative threshold of 1. We therefore carried out a sequential case-wise-deletion analysis where we omitted this case,

Investigation of the Cook's distances identified one (weak) influential cases (i.e. showing a distance below 1 but above 4/*m*): Case 1. Therefore, we carried out a case-wise deletion of the most influential cases which showed that after one iteration no more influential cases could be identified on the basis of Cook's distances and removal of this Case did not resulted in a significant different overall effect size (and back-transformed non-significant overall Pearson correlation of 0.1181 (95%CI [-0.1738, -0.3910]; t = 1.0367, p = 0.3474; table B3i). Therefore we conclude that that this model is robust.

Table S2.6.2.1. Overview of case-wise deletion of the most influential case study, its effect on the outcome of the moderation analysis, and the number of influential studies remaining.

Iteration	Removal of case(s)	t-test statistic	no. influential cases left
1	1	t-val = 1.0367, p = 0.3474	0

S2.6.2.6 Meta-regression

Table S2.6.2.2. Collinearity check of moderators

Pearson r	Grain size	Focal scale	Geographical extent
Grain size	1		
Focal scale	1	1	
Geographical extent	0.6734	0.6734	1
ln Geographical extent	0.8002	0.8002	NA

On the basis of the collinearity check (table S2.6.1.1) we decided to exclude the grain size. Although ln geographical extent and the focal scale are collinear we want to take the opportunity to investigate their effects in moderator analysis, although we cannot now be certain that effects are fully separate.

Effect of Focal scale

```
Test for Residual Heterogeneity:
QE(df = 4) = 13.6441, p-val = 0.0085

Test of Moderators (coefficient(s) 2):
F(df1 = 1, df2 = 4) = 1.0933, p-val = 0.3548

Model Results:
              estimate   se       tval      pval      ci.lb      ci.ub
intrcpt       -0.0980    0.3413   -0.2872   0.7883    -1.0455    0.8495
Focal.scale.ha 0.4739 0.4532      1.0456    0.3548    -0.7845    1.7323
```

Back-transform *Zr* to *r*:

```
pred      ci.lb      ci.ub
0.4413    -0.6552    0.9393
```

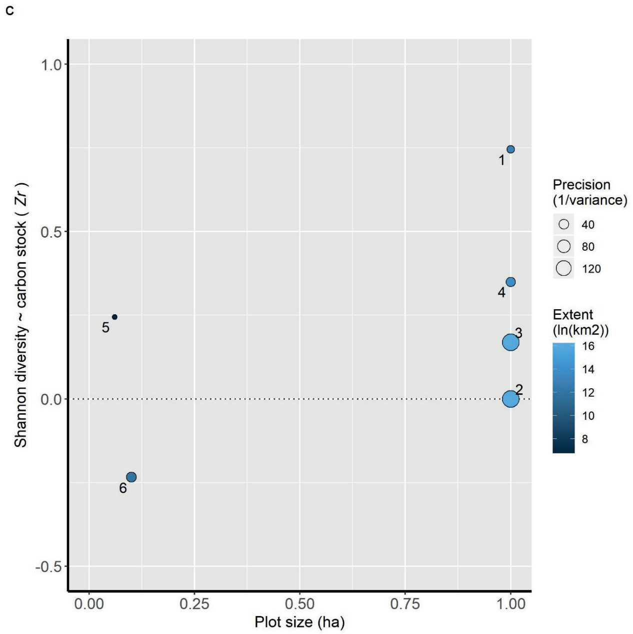

Figure S2.6.2.3. Plot of the focal scale against the Zr of 6 analyses of the relationship between taxonomic richness and carbon stock, using a multilevel model. Each analysis has a number corresponding to that used in the overall effect size model. Circles are drawn proportional to the inverse of the sampling variance, i.e. the Precision. In some of the moderator analyses single cases may be missing due to non-suitable data (e.g. moderator information was aggregated).

Effect of continuous Geographical extent:

```
Test for Residual Heterogeneity:
QE(df = 5) = 19.0466, p-val = 0.0019
```

```
Test of Moderators (coefficient(s) 2):
F(df1 = 1, df2 = 5) = 0.6918, p-val = 0.4435

Model Results:
                          estimate se        tval      pval      ci.lb     ci.ub
intrcpt                    0.3395   0.1906   1.7813    0.1350    -0.1504   0.8294
Geographic.area.extent.km2         -0.0000   0.0000    -0.8317   0.4435    -0.0000   0.0000
```

Back-transform *Zr* to *r*:

```
pred      ci.lb     ci.ub
-0.0000   -0.0000   0.0000
```

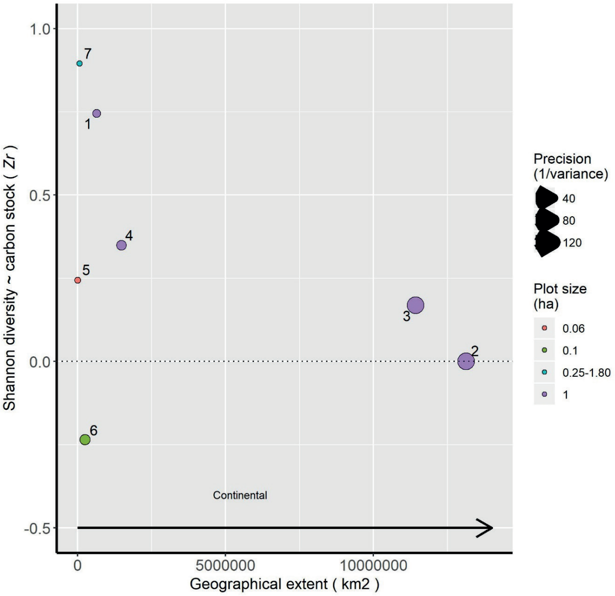

Figure S2.6.2.4. Plot of the continuous geographical extent against the Zr of 13 analyses of the relationship between taxonomic richness and carbon stock, using a multilevel model. Each analysis has a number corresponding to that used in the overall effect size model. Circles are drawn proportional to the inverse of the sampling variance, i.e. the Precision. The black arrows in the plot of geographical extent represent the approximated area of a continental and an intercontinental extent. In Case 7 plot sizes were aggregated and the Case was therefore not used in the final model, but is shown here for informational purposes.

Effect of natural ln geographical extent:

```
Test for Residual Heterogeneity:
QE(df = 5) = 20.2347, p-val = 0.0011

Test of Moderators (coefficient(s) 2):
F(df1 = 1, df2 = 5) = 0.2302, p-val = 0.6517
```

```
Model Results:
                     estimate se          tval        pval        ci.lb       ci.ub
intrcpt      0.5907     0.7583     0.7789     0.4713      -1.3587     2.5400
log(Geographic.area.extent.km2)  -0.0259   0.0540      -0.4797     0.6517      -0.1648     0.1130
```

Back-transform *Zr* to *r*:

```
pred       ci.lb      ci.ub
-0.0259    -0.1633    0.1125
```

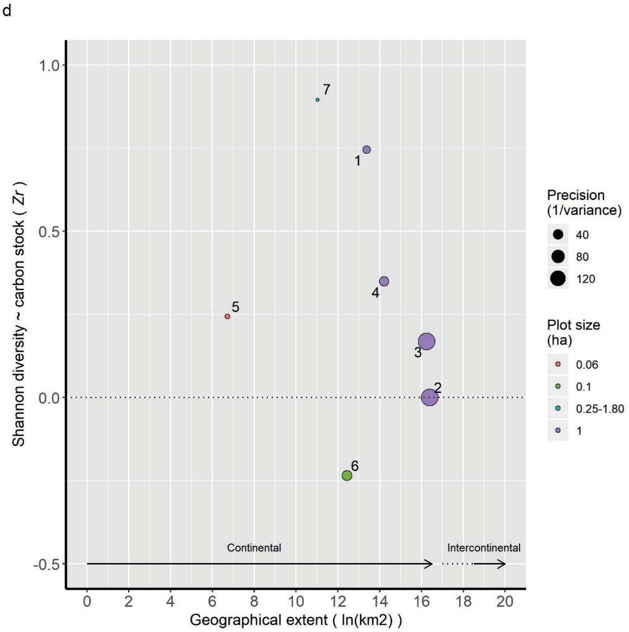

Figure S2.6.2.5. Plot of the natural log of the geographical extent against the Zr of 13 analyses of the relationship between taxonomic richness and carbon stock, using a multilevel model. Each analysis has a number corresponding to that used in the overall effect size model. Circles are drawn proportional to the inverse of the sampling variance, i.e. the Precision. The black arrows in the plot of geographical extent represent the approximated area of a continental and an intercontinental extent. In Case 7 plot sizes were aggregated and the Case was therefore not used in the final model, but is shown here for informational purposes.

S2.6.2.7 Sensitivity and publication bias analysis meta-regression

We did not investigate the robustness of the models as we found non-significant moderation effects.

S2.6.3 Simpson diversity ~ Carbon Stock

S2.6.3.1 Assessing potential double-counting

After analysis of potential double-counting of data within source papers, we removed one effect size from Baraloto et al. (2014), choosing to retain the Zr that was measured by taking all tree individual with DBH ≥ 10 cm versus taking a selection individuals with 2.5 ≤ DBH ≤ 10, as this was the most comparable to the measurements of the other Zr. Total omission of effect sizes: 1.

S2.6.3.2 Assessing the need for a multilevel model using ML

Comparing the fit of a fixed-effects model ('Reduced') vs a mixed-effects (multilevel) model ('Full')

	df	AIC	BIC	AICc	logLik	LRT	pval	QE
Full	3	4.6053	2.7642	28.6053	0.6974			11.4699
Reduced	1	2.9085	2.2948	4.9085	-0.4543	2.3033	0.3161	11.4699

The multilevel model has slightly lower AIC, BIC and Likelihood but is not significantly different in likelihood (p = 2.3033) on the basis of a LRT. So we will use a unilevel model.

S2.6.3.4 Estimating the overall effect size using REML

Test for Heterogeneity:
Q(df = 3) = 11.4699, p-val = 0.0094

Model Results:

estimate	se	tval	pval	ci.lb	ci.ub
0.0851	0.1187	0.7172	0.5250	-0.2926	0.4629

Back-transform *Zr* to *r*:

pred	ci.lb	ci.ub	cr.lb	cr.ub
0.0849	-0.2846	0.4325	-0.5676	0.6720

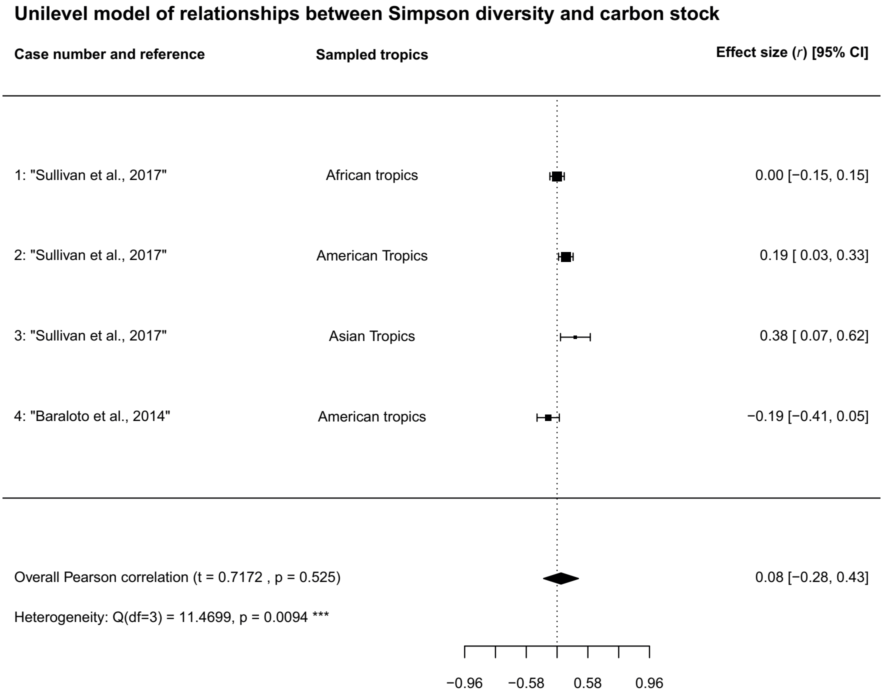

Figure S2.6.3.1. Forest plot of the overall effect size of the relationship between Simpson diversity (D') and carbon stock. All effect sizes and their 95% confidence intervals have been back-transformed to r values. Overall effect size calculated using an unilevel model.

S2.6.3.5 Sensitivity and publication bias analysis overall model

The trim-and-fill method added no cases (See Figure S2.6.3.2 LEFT). The funnel plot shows that one cases lies just outside the 95% pseudo-confidence interval (the white triangle), visualizing the relatively small amount of heterogeneity present in the dataset. Thus, the trim-and-fill test indicates that the model is not sensitive to the effects of the theoretical missing publications.

As the overall effect size was already non-significant we did not calculate a fail-safe number.

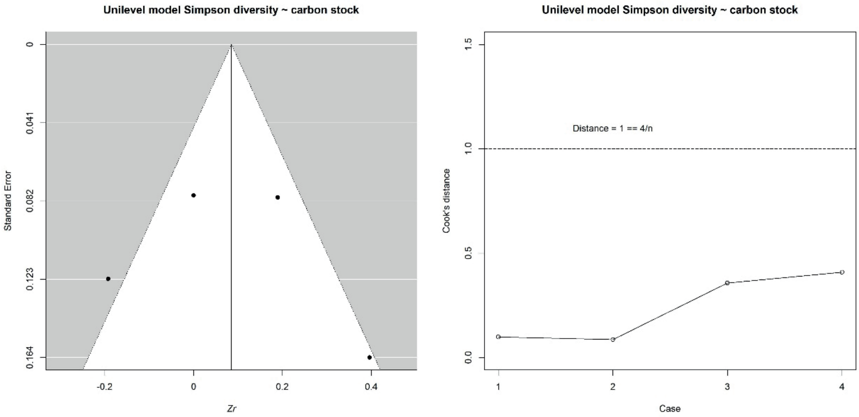

Figure S2.6.3.2. LEFT: Funnel plot of effect sizes used for the overall effect size of the relationship between Shannon diversity (H') and carbon stock, using a unilevel trim-and-fill model. The white area within the triangle represents the 95% pseudo-confidence interval of the calculated overall effect size. Black circles represent the cases used in the model, open circles are simulated 'missing' cases added by the trim-and-fill method to correct the asymmetry of the funnel. RIGHT: Plot of the Cook's distances of the final, unilevel model, comparing two thresholds for influential cases.

The plot of the Cook's distances (See Figure S2.6.3.2 RIGHT) show that all distances are below the threshold of 4/m (where *m* is the total amount of cases or effect sizes considered) and also the less conservative 1. Therefore we conclude that there are no influential cases in this model and that this model is robust.

S2.6.4 Mean stand density (#/ha) ~ Carbon Stock

S2.6.4.1 Assessing potential double-counting

After analysis of potential double-counting of data within and between source papers, we did not find any double-counting. We omitted the case of Behera et al. (2017) as the used sample size ($n = 3$) is too small to calculate the variance of the *Zr*. Total omission of effect sizes: 1.

S2.6.4.2 Assessing the need for a multilevel model using ML

The remaining effect sizes are not nested so we used a unilevel model.

S2.6.4.4 Estimating the overall effect size using REML

Test for Heterogeneity:
Q(df = 3) = 21.2300, p-val < .0001

```
Model Results:
estimate   se        tval      pval      ci.lb     ci.ub
0.5867     0.1758    3.3373    0.0445    0.0272    1.1462 *
```

Back-transform *Zr* to *r*:

```
pred       ci.lb     ci.ub     cr.lb     cr.ub
0.5275     0.0272    0.8165    -0.5390   0.9443
```

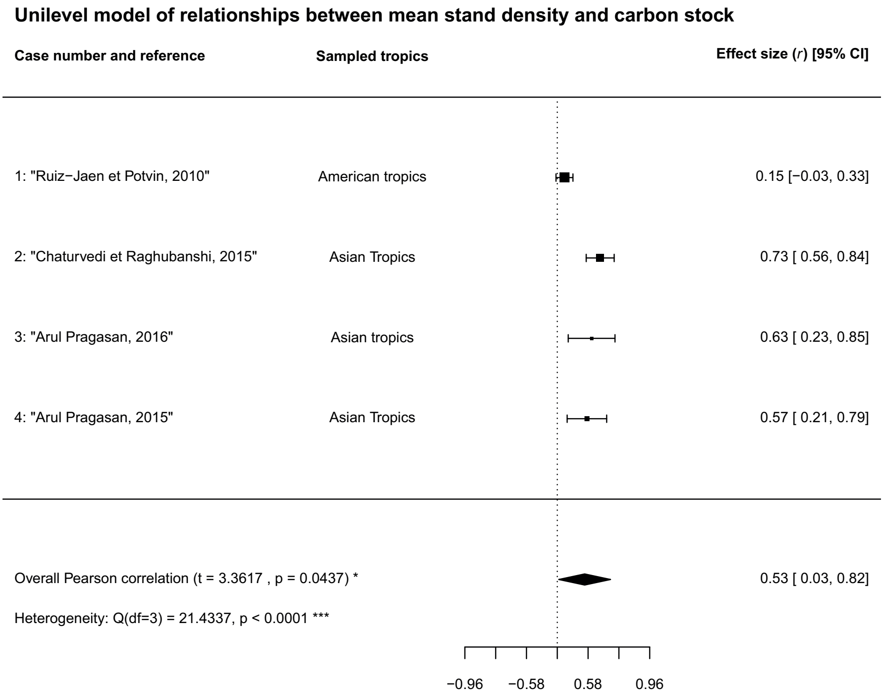

Figure S2.6.4.1. Forest plot of the overall effect size of the relationship between mean stand density and carbon stock. All Zr effect sizes and their 95% confidence intervals have been back-transformed to r values. Overall effect size calculated using a multilevel model.

S2.6.4.5 Sensitivity and publication bias analysis overall model

The trim-and-fill method predicts the additional cases to make the funnel plot symmetric. The trim-and-fill added no case to the funnel plot (See Figure S2.6.4.2 LEFT). The funnel plot shows that two cases lie just outside the 95% pseudo-confidence interval (the white triangle), visualizing the relatively small amount of heterogeneity present in the dataset. Thus, the trim-and-fill test indicates that the model is not sensitive to the effects of the theoretical missing publications.

Rosenberg's weighted fail-safe number: 32
Conservative (5k+10) Rosenthal number: 30

The Rosenthal's fail-safe number is close to the conservative number, indicating that when several of theoretical missing papers lying in a file drawer somewhere ("the file drawer problem") would be added to the model, it is likely that the overall effect size would become zero. Thus the fail-safe number indicates that the model is not robust against the file drawer problem.

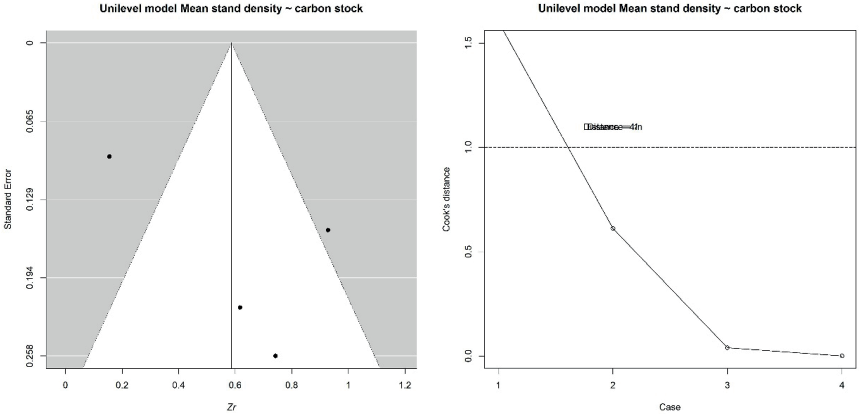

Figure S2.6.4.2. LEFT: Funnel plot of effect sizes used for the overall effect size of the relationship between mean stand density and carbon stock, using a unilevel trim-and-fill model. The white area within the triangle represents the 95% pseudo-confidence interval of the calculated overall effect size. Black circles represent the cases used in the model, open circles are simulated 'missing' cases added by the trim-and-fill method to correct the asymmetry of the funnel. RIGHT: Plot of the Cook's distances of the final, unilevel model, comparing two thresholds for influential cases.

The plot of the Cook's distances (See Figure S2.6.4.2 RIGHT) show that one case shows a distances that is above the threshold of 4/m (where *m* is the total amount of cases or effect sizes considered): case 4. All cases are less than the less conservative threshold of 1. We therefore carried out a sequential case-wise-deletion analysis where we omitted this case,

Investigation of the Cook's distances identified one influential case: Case 1. Therefore, we carried out a case-wise deletion of the most influential cases which showed that after two iterations the effect was no longer significant. Therefore we conclude that that this model is not robust.

Table S2.6.4.1. Overview of case-wise deletion of the most influential case study, its effect on the outcome of the moderation analysis, and the number of influential studies remaining.

Iteration	Removal of case(s)	t-test statistic	no. influential cases left
1	1	t-val = 8.4349, p = 0.0138	1
2	1	t-val = 10.8583, p = 0.0585	1

S2.6.5 Mean basal area (m2/ha)~ Carbon Stock

S2.6.5.1 Assessing potential double-counting

After analysis of potential double-counting of data within source papers, we removed one of two effect sizes from Asase et al. (2012), choosing to retain the Zr that was measured by taking all tree individual with DBH ≥ 10 cm versus taking a selection individuals with 5 ≤ DBH ≤ 10, as this was the most comparable to the measurements of the other Zr. We did not find any double-counting between source papers. We omitted the case of Behera et al. (2017) as the used sample size (n = 3) is too small to calculate the variance of the Zr. Total omission of effect sizes:2.

S2.6.5.2 Assessing the need for a multilevel model using ML

The remaining effect sizes are not nested so we used a unilevel model.

S2.6.5.4 Estimating the overall effect size using REML

```
Test for Heterogeneity:
Q(df = 4) = 44.6117, p-val < .0001

Model Results:
estimate   se       tval     pval     ci.lb    ci.ub
1.3593     0.3868   3.5140   0.0246   0.2853   2.4334 *
```

Back-transform *Zr* to *r*:

```
pred     ci.lb    ci.ub    cr.lb     cr.ub
0.8762   0.2778   0.9847   -0.8166   0.9991
```

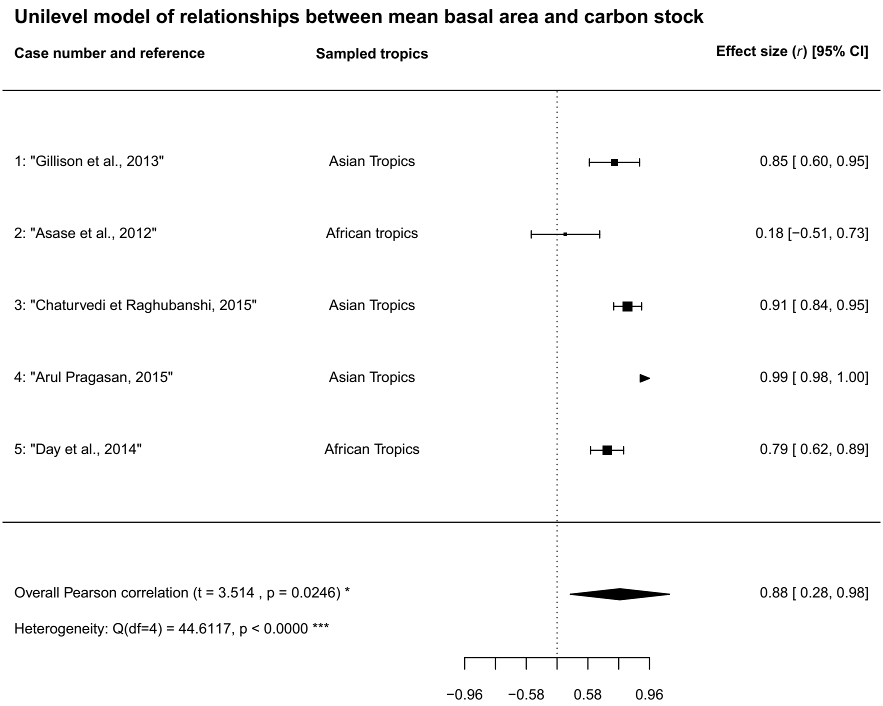

Figure S2.6.5.1. Forest plot of the overall effect size of the relationship between mean basal area and carbon stock. All Zr effect sizes and their 95% confidence intervals have been back-transformed to r values. Overall effect size calculated using a multilevel model.

S2.6.5.5 Sensitivity and publication bias analysis overall model

The trim-and-fill method predicts the additional cases to make the funnel plot symmetric. The trim-and-fill added no cases to the funnel plot (See Figure S2.6.5.2 LEFT). The funnel plot shows that two cases lie just outside the 95% pseudo-confidence interval (the white triangle), visualizing the relatively small amount of heterogeneity present in the dataset. Thus, the trim-and-fill test indicates that the model is not sensitive to the effects of the theoretical missing publications.

Rosenberg's weighted fail-safe number: 325
Conservative (5k+10) Rosenthal number: 35

The Rosenthal's fail-safe number is a factor 9 larger than the conservative number, indicating that when several of theoretical missing papers lying in a file drawer somewhere ("the file drawer problem") would be added to the model, it is unlikely that the overall effect size would become zero. Thus, the fail-safe number indicates that the model is robust against the file drawer problem.

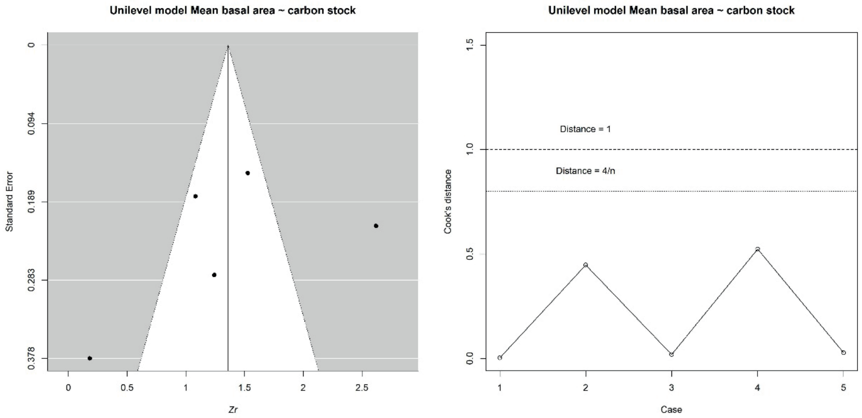

Figure S2.6.5.2. LEFT: Funnel plot of effect sizes used for the overall effect size of the relationship between mean basal area and carbon stock, using a unilevel trim-and-fill model. The white area within the triangle represents the 95% pseudo-confidence interval of the calculated overall effect size. Black circles represent the cases used in the model, open circles are simulated 'missing' cases added by the trim-and-fill method to correct the asymmetry of the funnel. RIGHT: Plot of Cook's distances of the final, unilevel model, comparing two thresholds for influential cases.

The plot of the Cook's distances (See Figure S2.6.5.2 RIGHT) show that all distances are below the threshold of 4/*m* (where *m* is the total amount of cases or effect sizes considered) and also the less conservative threshold of 1. Therefore, we conclude that there are no influential cases in this model and that this model is robust.

View across the Brokopondo lake from Brownsberg, Suriname. Photo by Lieke Guinée.

3

Relationships between species richness and ecosystem services in Amazonian forests strongly influenced by biogeographical strata and forest types

This chapter has been published open access in adapted form in the journal Scientific Reports as:
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Abstract

Despite increasing attention for relationships between species richness and ecosystem services, for tropical forests such relationships are still under discussion. Contradicting relationships have been reported concerning carbon stock, while little is known about relationships concerning timber stock and the abundance of non-timber forest product producing plant species (NTFP abundance). Using 151 1-ha plots, we related tree and arborescent palm species richness to carbon stock, timber stock and NTFP abundance across the Guiana Shield, and using 283 1-ha plots, to carbon stock across all of Amazonia. We analysed how environmental heterogeneity influenced these relationships, assessing differences across and within multiple forest types, biogeographic regions and subregions. Species richness showed significant relationships with all three ecosystem services, but relationships differed between forest types and among biogeographical strata. We found that species richness was positively associated to carbon stock in all biogeographical strata. This association became obscured by variation across biogeographical regions at the scale of Amazonia, resembling a Simpson's paradox. By contrast, species richness was weakly or not significantly related to timber stock and NTFP abundance, suggesting that species richness is not a good predictor for these ecosystem services. Our findings illustrate the importance of environmental stratification in analysing biodiversity-ecosystem services relationships.

3.1 Introduction

Despite considerable scientific attention for the relationships between biodiversity and ecosystem services, the extent to which such relationships exist in tropical forests remains unclear. Tropical forests are one of the most species-rich ecosystems on Earth (Myers et al., 2000), store an estimated 54% of the global aboveground carbon stock (Liu et al., 2015) and provide valuable timber (Putz et al., 2012) and non-timber forest products (Ros-Tonen & Wiersum, 2005), such as food, medicines and cultural ornaments. However, tropical forests are increasingly being degraded or lost (Mitchard, 2018), threatening their biodiversity and their goods and services that benefit human wellbeing. Under the expectation that ecosystem services are generally positively linked to biodiversity, there is increasing attention for ecosystem services as a rationale to help conserve tropical forest biodiversity (Barlow et al., 2018; Quijas et al., 2019; Steur et al., 2020). For example, contemporary conservation approaches, such as UN REDD+, focus on tropical forests with high carbon stocks, assuming that such forests will be biodiverse as well (Phelps et al., 2012). However, it is uncertain to what extent the number of tree and arborescent palm species, hereafter referred to as 'woody species richness', is related to carbon storage, timber provisioning and non-timber forest product (NTFP) provisioning in tropical forests, obscuring the extent to which conservation of ecosystem services can help protect tropical forest biodiversity.

In tropical forests, woody species are the main components of the aboveground plant biomass, and can therefore, be expected to be related to biomass-based ecosystem services, such as carbon storage, timber provisioning, and the supply of non-timber forest products ('NTFPs'). Several hypotheses have been proposed to explain how plant diversity can enhance biomass and therefore the relationship between woody species richness and aboveground biomass in tropical forests would be expected to be positive. According to the 'niche complementary' hypothesis (Tilman et al., 1997), species-rich communities have a higher variation in species traits, and thus, could better utilise limited available resources. This would result in increased productivity, which can in turn, result in higher aboveground biomass (Poorter et al., 2015; Shen et al., 2016; Sullivan et al., 2017; van der Sande et al., 2017). In addition, according to the 'insurance' hypothesis (Yachi and Loreau 1999), a higher variation in species traits allows a community to be more resilient against environmental fluctuations, maintain a high productivity across time and thus, enable a higher aboveground biomass (Poorter et al., 2015; van der Sande et al., 2017). Last, according to the 'selection effect' hypothesis (Tilman et al., 1997), species-rich communities have a higher chance of including species with higher biomass, resulting in higher sampled average aboveground biomass (Poorter et al., 2015; Shen et al., 2016; Sullivan et al., 2017).

However, although there has been considerable support for positive species-biomass relationships in grasslands and non-tropical forests and plantations (Bravo-Oviedo et al., 2021; Cardinale et al., 2012; Chisholm et al., 2013; Gamfeldt et al., 2013; Isbell et al., 2011), the empirical evidence for relationships between woody species richness and carbon storage, timber provisioning, and NTFP provisioning in tropical forests remains inconclusive. The review and meta-analysis of such relationships across tropical forests by Steur et al. (2020) identified contrasting results and knowledge gaps across Amazonia, the tropical forest area comprising of the Amazon River basin and the Guiana Shield. Most studies have focused on the aboveground carbon stock, hereafter referred to as 'carbon stock'. In recent studies, both positive and non-significant relationships have been reported for woody species richness and carbon stock (Aldana et al., 2017; Gonzalez et al., 2014; Poorter et al., 2015; Ruiz-Jaen & Potvin, 2011; Sullivan et al., 2017). By contrast, little to no attention has been given to the relationship of woody species richness with commercially relevant timber stock, hereafter referred to as 'timber stock', or its relationship with the abundance of tree and arborescent palms that produce commercially relevant NTFPs, hereafter referred to as 'NTFP abundance' (Steur et al., 2020). As for timber and NTFP provisioning, only a subset of the available plant species will be relevant, while no a-priori prediction can be made for the relationships with species richness. Although a more recent study by Steur et al. (2021) reported a negative relationship between woody species richness and NTFP abundance in Suriname lowland tropical forests, the extent of this relationship across other tropical forests and different spatial scales remains unclear.

To date, the contrasting results for the relationship between woody species richness and carbon stock across Amazonia have remained unexplained. Although previous studies found that plot size can moderate the 'species-carbon relationship' (e.g. Chisholm et al., 2013; Poorter et al., 2015; Sullivan et al., 2017), contrasting results have been found for studies that use the same plot size (Steur et al., 2020). For example, in studies using 1-ha plots, Aldana et al. (2017) found a positive relationship across Colombian tropical lowland forests, while Poorter et al. (2015) and Sullivan et al. (2017) did not find a significant bivariate relationship across a wide range of Neotropical forests. Although Poorter et al. (2015) ultimately found a positive relationship when variation in rainfall, stem density and stem diameter was accounted for, Sullivan et al. (2017) did not find any such positive relationship, even when variation in multiple climatic and edaphic variables were accounted for. As a possible explanation, the meta-analysis by Steur et al. (2020) suggested that contrasting results on the species-carbon relationship may be due to differences in geographical extent covered by the study area. The meta-analysis showed a positive species-carbon relationship across the tropics, but the strength of this relationship decreased with increasing amount of geographical extent covered. Such a pattern can also be observed in the aforementioned studies: Aldana et al. (2017) found a significant positive relationship at the geographical extent of Colombia, while Poorter et al. (2015) and Sullivan et al. (2017) found no significant bivariate relationship at larger extents ranging the Neotropics.

Steur et al. (2020) postulated that, with increasing geographical extent, an increasing amount of environmental heterogeneity is sampled, which ultimately moderates the relationship between woody species richness and carbon stock. In Amazonia, woody species diversity and aboveground biomass vary across environmental gradients likely to be increasingly sampled when the geographical extent of the study increases. For example, significant differences in woody species fisher's alpha and aboveground biomass have been observed across soil and forest types (Hawes et al., 2012; Quesada et al., 2012; Stropp et al., 2009) and across biogeographical regions and subregions of Amazonia (Mitchard et al., 2014; Stropp, 2011; Stropp et al., 2009; ter Steege et al., 2006). Specifically for forest types, Aldana et al. (2017) found a positive species-carbon relationship for Colombian terra firme forests, but no such relationship when terra firme forests were aggregated with flooded forests. However, a systematic analysis of the influence of soil type, forest type and biogeographical strata on relationships between woody species richness and ecosystem services for Amazonian tropical forests has not been conducted.

This study aims to provide insights into the relationships between species richness and multiple ecosystem services while accounting for the influence of environmental stratification at different spatial scales with respect to the tropical forests of Amazonia. For our analyses, we use two datasets of collectively 283 1-ha Amazonian lowland tropical forest plots: one spanning the Guiana Shield region composed of primary plot data and the other spanning all of Amazonia that was created by combining the Guiana Shield data with secondary published plot data. With the primary data from the Guiana Shield, we calculated woody species richness, carbon stock, timber stock and NTFP abundance, and tested their relationships across and within two main forest types and four biogeographical subregions. In addition, with the secondary data, we also tested the species-carbon relationship across and within six biogeographical regions of Amazonia. Unfortunately, local commercial demand for timber stock and NTFP abundance could only be adequately determined for the Guiana Shield region and was not available for the scale of Amazonia.

3.2 Method

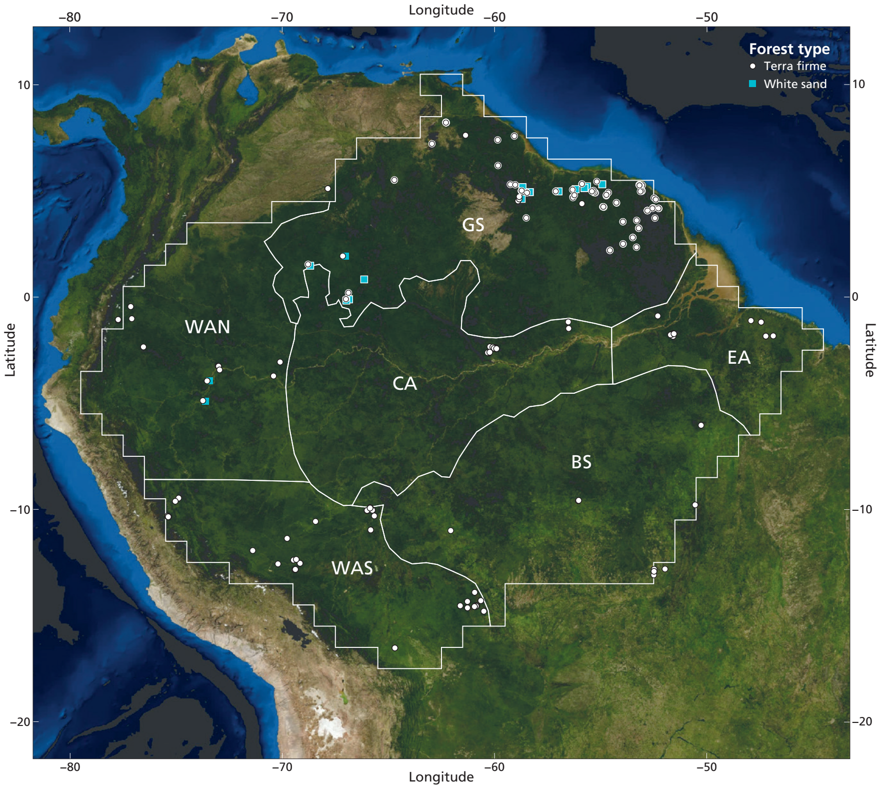

Figure 3-1. Map of the 283 1-ha old-growth lowland tropical forest plots across Amazonia. The plots of the Guiana Shield dataset are marked with an additional white contour (See Supporting Information Annex S1, Figure S1.1 for the Guiana Shield dataset plots only). For each plot, the forest type is indicated by symbols, where white circle = terra firme forest, and blue square = white sand forest. Approximate borders of the six biogeographical regions of Amazonia, reproduced from (ter Steege et al., 2019a), are indicated with white lines. Abbreviations for the regions are GS = Guiana Shield, BS = Brazilian Shield, WAN = north-western Amazonia, WAS = south-western Amazonia, CA = central Amazonia, and EA = eastern Amazonia. Figure created in R (R Core Team, 2020), background satellite imagery of South America by NASA (Stöckli et al., 2005).

Guiana Shield dataset

We compiled a dataset of 151 1-ha lowland tropical forest plots spanning the Guiana Shield biogeographical region in Amazonia, most from the Amazon Tree Diversity Network (ATDN) (Figure 3-1; Table 3-1; references provided in Table S3.1.3). These plots represent old-growth tropical forest vegetation on terra firme soils with limited signs of anthropogenic disturbance. In each plot, all trees and arborescent palms, hereafter referred to as 'woody species', with a diameter at breast height ('DBH'; 1.3 m) of ≥ 10 cm, were measured and identified to at least a unique morphospecies. In line with previous large-scale assessments of relationships between plant diversity and ecosystem services (Poorter et al., 2015; Sullivan et al., 2017), at least 60% of the stems had been identified up to the species level, at least 80% up to the genus level and 100% up to the family level. Taxonomy followed the 'Dynamic Amazon Tree Checklist' (ter Steege et al. 2019b; updated version 20200422).

Table 3-1. Overview of the two datasets used in this study, showing sample size, geographical extent and the number of biogeographical strata and forest types included. Biogeographical strata and forest types were recognized after Stropp (2011), ter Steege et al. (2013; 2019a), ter Steege & Zondervan (2000). In addition, for each of the three ecosystem service stock components and woody species richness showing their mean value and standard deviation (mean ± SD). See Table S3.1.3 for a summary of the plot data, including references. NTFP abundance = abundance of species that produce non-timber forest products.

	Guiana Shield dataset	**Amazonia dataset**
Number of 1-ha plots	151	283
Rectangular geographical extent	1.7 x 10^6 km^2	9.4 x 10^6 km^2
Number of biogeographical strata	4 subregions	6 regions
Number of forest types	2	2
	Mean ± SD	**Mean ± SD**
Aboveground carbon stock (Mg ha^{-1})	212.2 ± 49.48	175.34 ± 59.13
Timber stock (m^3 ha^{-1})	119.8 ± 67.82	NA
NTFP abundance (stems ha^{-1})	102.71 ± 57.94	NA
Woody species richness (species ha^{-1})	123.93 ± 50.37	141.60 ± 62.96

For these plots, we calculated woody species richness (species ha^{-1}), and the stock component of the ecosystem services carbon storage, timber provisioning, and non-timber forest product ('NTFP') provisioning. Aboveground carbon stock per plot (Mg ha^{-1}), hereafter referred to as 'carbon stock', was calculated following Sullivan et al. (2017): aboveground biomass was estimated from stem diameter, height, and wood density using the pantropical allometric equation of Chave et al. (2014). For this, stem height was estimated from stem diameter using biogeographical region-specific 'Weibull' equations developed by Feldpausch et al. (2012), and carbon stock was estimated by multiplying the biomass with a factor of 0.471. Wood density was retrieved from an appended version of the global wood density database by Chave et al. (2009) (ter Steege et al. in prep.; version 20200401). Applying a different allometric equation calibrated for the neotropics that did not require separate height estimation did not result in significantly different estimates (Supporting Information Annex S3.1).

Timber stock per plot (m^3 ha^{-1}), hereafter referred to as 'timber stock', was estimated by calculating the volume of tree species that had been recently commercially traded. Following Piponiot et al. (2019), we identified commercially relevant timber species as all timber tree species that have been reportedly commercially traded over the last 25 years (1995-2020) in at least one of the geographical areas included (See Table S1.1 for the references), and we considered trees with DBH ≥ 50 cm eligible for harvest under local forestry laws. This identified 727 commercially relevant timber tree species in our plots (9.4% of all morphospecies). Tree volume was estimated from tree diameter using the moist-forest allometric equation of Chave et al. (2005). Following Steur et al. (2021), the number of tree and arborescent palm individuals that produce commercially relevant NTFPs, hereafter referred to as 'NTFP abundance', was counted per plot (stems ha^{-1}) as a proxy for NTFP stock. For this, we counted the tree and palm individuals of species that are known to produce NTFPs, hereafter referred to as 'NTFP species', that have been commercially traded over the last 25 years (1995-2020) in at least one of the geographical areas included. This identified 295 commercially relevant NTFP species present in our plots (3.8% of all morphospecies), which were mainly used as food, crafts, medicines and for cultural services (e.g. for rituals)(See Table S3.1.2, including references).

Amazonia dataset

We combined the Guiana Shield data with data from 132 1-ha tropical forest plots published by Sullivan et al. (2017) to create a dataset of 283 plot measurements of woody species richness and carbon stock across Amazonia (Figure 3-1; Table 3-1; references provided in Table S3.1.3). This also added 14 additional plots for the Guiana Shield region. Taxonomic precision and the minimum DBH used by Sullivan et al. (2017) were comparable to the Guiana Shield dataset, see Annex S3.1 for more information.

Environmental covariables

To investigate how relationships with woody species richness changed according to environmental heterogeneity, we used forest type and biogeographical strata as categorical environmental covariables.

After ter Steege et al. (2013, 2019a), we classified all plots into two main forest types on well-drained soils (Figure 3-1): forests on brown soils, hereafter referred to as 'terra firme forests' (TF; n = 130 for Guiana Shield dataset, n = 257 for Amazonia dataset) and forests on white sands, hereafter referred to as 'white sand forests' (PZ; n = 21 for Guiana Shield dataset, n = 26 for Amazonia dataset). These forest types differ mainly in physiognomy, species composition, and substrate origin, and their sample sizes reflect the geographical coverage of these forest types, where terra firme forests cover more than 50% of Amazonia and white sand forests just under 5% (ter Steege et al., 2019a). In addition, we classified all plots into six biogeographical regions (Figure 3-1), and the plots from the Guiana Shield database into four biogeographical subregions (Figure S3.1.1). After ter Steege et al. (2013, 2019a) we recognised the following Amazonian biogeographical regions: the Guiana Shield (GS; n = 165), the Brazilian Shield (BS; n = 9), north-western Amazonia (WAN; n =

21), south-western Amazonia (WAS; n = 51), central Amazonia (CA; n = 22) and eastern Amazonia (EA; n = 15). Based on the Guiana Shield 'forest regions' identified by ter Steege & Zondervan (2000) and revised after floristic analyses carried out by Stropp (2011), we recognized the following forest subregions: forests of the northern Pleistocene sands (NPS, n = 56), south-western Pleistocene sands in the upper Rio Negro region (SWPS, n = 11), southern Guiana Shield (SGS, n = 63) and north-western Guiana Shield (NWGS, n = 21). These biogeographical strata have been identified according to differences in substrate history, geological age and floristic composition. More information on forest types and biogeographical strata is provided in Annex S3.1.

Although soil type information was also available for the Guiana Shield dataset, we found high collinearity of soil class with both biogeographical subregions and forest types. Therefore, we excluded it from further analyses. For reference, information on soil type is included in Annex S3.1.

Statistical analyses

We used standard linear models to analyse relationships between species richness and ecosystem service stock components and to explore how biogeographical strata and forest types influenced these relationships. To analyse how species richness was related to the different ecosystem services while accounting for potential confounding variables, we used multiple linear regression models that were optimised using a backward model selection procedure proposed by Crawley (2015). All dependent variables followed an approximate normal distribution, independent variables were checked for multicollinearity, and each model showed approximately homogenous variances. We used the relative contribution to the total amount of variation explained as a measure of the relative importance of the variables. The relative contribution was calculated according to the amount of explained variation added when a variable is included, taking the average of this amount across all possible variable orders in the model. In this way, the relative contribution of the variable to R^2 is compensated for the amount of variation already explained by other variables in the model (Lindeman et al., 1980).

We tested for significant variation in ecosystem service components and woody species richness across biogeographical strata and forest types by using analysis of variance F-tests and applied post-hoc Tukey tests to assess any differences among the groups. The Tukey post-hoc test adjusts the p-value for multiple testing, controlling for the increased chance of obtaining a false positive when multiple tests are conducted in sequence (Type I error). We checked for spatial autocorrelation in the model residuals by plotting them in a map and by performing Moran's I tests. Although we found significant spatial autocorrelation for the three models based on the Guiana Shield data and the model based on the Amazonia data (all four $p < 0.0200$), sensitivity analyses by leaving one biogeographical stratum out at a time did not result in significant differences. The spatial autocorrelation is believed to be inherent to our data, because some of the plots have the same longitude and latitude due to GPS limitations at the time of their census (e.g. the plots ALP-01 and ALP-30 from Sullivan et al. (2017).

All statistical analyses were conducted using R (R Core Team, 2020). Additional details on the statistical analyses and software used are included in Annex S3.1. Supplementary Results are provided in Annex S3.2.

3.3 Results

Relationships across the Guiana Shield

For the Guiana Shield, species richness showed a positive relationship with carbon stock and timber stock across all biogeographical subregions and forest types (explaining 15.8 and 18.2% of variation, respectively; both coefficients $p \leq 0.0003$; Table S2.1), but relationships differed for the two forest types and four biogeographical subregions (Figure 3-2). Species richness was positively related to carbon stock in three of the four subregions (all three coefficients $p \leq 0.0186$), whereas it was positively related to timber stock only in one subregion (coefficient $p < 0.0001$). In addition, it was positively related to carbon stock and timber stock in terra firme forests, but not significantly related in white sand forests. By contrast, species richness was not significantly related to NTFP abundance across the biogeographical subregions and forest types (coefficient $p = 0.8570$; Table S2.1), only showing a significant but negative relationship with NTFP abundance in white sand forests (coefficient $p = 0.0351$).

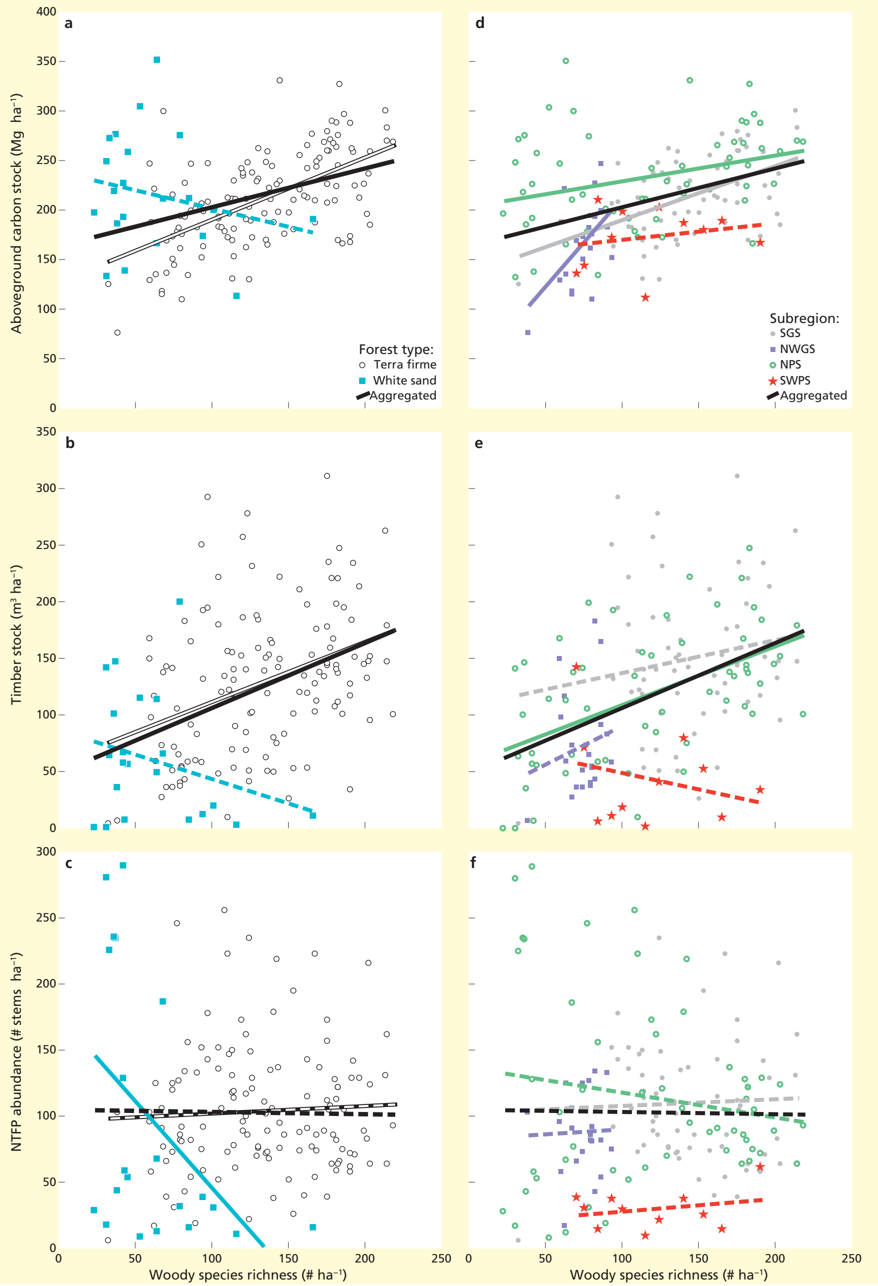
a
b
c
d
e
f
Aboveground carbon stock (Mg ha⁻¹)
Timber stock (m³ ha⁻¹)
NTFP abundance (# stems ha⁻¹)
400
350
300
250
200
150
100
50
0
350
300
250
200
150
100
50
0
300
250
200
150
100
50
0
0
50
100
150
200
250
Woody species richness (# ha⁻¹)
Forest type:
Terra firme
White sand
Aggregated
Subregion:
SGS
NWGS
NPS
SWPS
Aggregated

Figure 3-2. Previous page: Visualisation of linear bivariate relationships between species richness and carbon stock, timber stock, and non-timber forest products ('NTFP') abundance, across and within two forest types and four biogeographical subregions of the Guiana Shield. Showing relationships between species richness and carbon stock (panels a and d), between species richness and timber stock (panels b and e), and between species richness and NTFP abundance (panels c and f). Relationships across all forest types and subregions indicated by black lines (n = 151), within terra firme forests by white lines (n = 130), within white sand forests by blue lines (n = 21), within the Southern Guiana Shield by gray lines (n = 63; SGS), within the north-western Guiana Shield by purple lines (n = 21; NWGS), within the northern Pleistocene sands by green lines (n = 56; NPS), and within the south-western Pleistocene sands in the upper Rio Negro region by red lines (n = 11; SWPS). Solid lines indicate significant relationships ($p < 0.05$) and dashed lines non-significant relationships ($p \geq 0.05$). Forest plots are coloured according to forest type or subregion. Model details are included in Table S3.2.4 and S3.2.7.

Results showed that variation in carbon stock and timber stock was explained by a combination of species richness, biogeographical subregion and forest type, while variation in NTFP abundance was explained by biogeographical subregions only (Table 3-2). However, accounting for variation in biogeographical subregions and forest types did not result in significantly different relationships between species richness, carbon stock, timber stock and NTFP abundance across the Guiana Shield (Table 3-2 vs. Table S3.2.1). In all three relationships, biogeographical subregions explained a substantial part of the total variation (ranging between 14.7 and 19.3%). For carbon stock, species richness explained a similar amount of variation as when variation in forest type and biogeographical subregion was not accounted for (15.1 vs. 15.8%; Table 3-2 vs. Table S3.2.1). For timber stock, the contribution of species richness was considerably less (9.3 vs. 18.2%; Table 3-2 vs. Table S3.2.1). Last, forest type explained a small amount of variation in carbon stock and timber stock (2.4 and 6.5%, respectively; Table 3-2).

Table 3-2. Summary of optimized multiple linear models of carbon stock, timber stock and NTFP abundance predicted by species richness and environmental covariables across the Guiana Shield dataset (n = 151 1-ha plots). Originally included predictors were species richness, forest type, and subregion. For each retained predictor, a summary of the relationship and the relative contribution to total model R2 (%) is given. NTFP abundance = abundance of species that produce non-timber forest products. Model details are included in Table S3.2.2.

	Relationship summary	Rel. contr. R^2 (%)	Total R^2 (%)
Carbon stock			
Subregions	Significant variable	19.3	
Species richness	Significant positive	15.1	
Forest type	Significant variable	2.4	
			36.8
Timber stock			
Subregions	Significant variable	18.1	
Species richness	Significant positive	9.3	
Forest type	Significant variable	6.5	
			33.9
NTFP abundance			
Subregions	Significant variable	14.7	
			14.7

Relationships across Amazonia

In contrast to the positive relationship between species richness and carbon stock observed across the Guiana Shield (Table 3-2), across Amazonia species richness showed no significant relationship with carbon stock (slope -0.007, p = 0.8950; Table S3.2.10). However, the relationship differed for single biogeographical regions, where the relationship was either positive, or non-significant but weakly positive (all slopes > 0.013; Table S3.2.13; Figure 3-3). When variation in carbon stock across biogeographical regions was accounted for, a positive relationship between species richness and carbon stock was found across Amazonia (slope 0.289, p < 0.0001; Table S3.2.12). By contrast, the relationship between species richness and carbon stock did not differ between forest types (Figure S3.2.5), and accounting for variation in carbon stock between forest types did not lead to a significant relationship (Table S3.2.12).

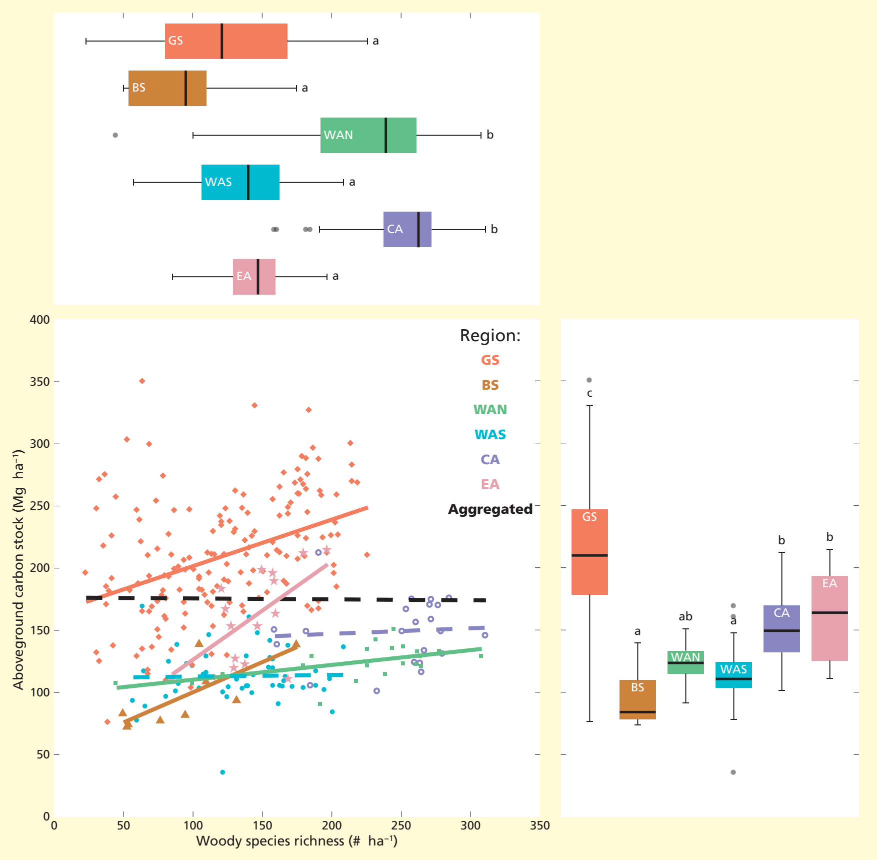

Figure 3-3. Visualisation of linear bivariate relationships between carbon stock and species richness for different biogeographical regions in the Amazonia dataset. Relationships across all biogeographical regions (Agg., n = 283): black line; for Guiana Shield (GS, n = 165): red line, Brazilian Shield (BS, n = 9): dark yellow line, north-western Amazonia (WAN, n = 21): green line, south-western Amazonia (WAS, n = 51): light blue line, central Amazonia (CA, n = 22): purple line, and eastern Amazonia (EA, n = 15): pink line. Showing boxplots for carbon stock (bottom left) and species richness (upper panel) across the regions with differences according to Tukey post-hoc tests indicated by different letters. Model details are included in Tables S3.2.13-S3.2.15.

Results showed that 60.0% of variation in carbon stock was explained by species richness, biogeographical regions and forest types (Table 3-3). Here, variation in carbon stock was for a large part explained by variation across biogeographical regions (54.9%), while species richness and forest type had small contributions (3.4 and 1.7%, respectively).

Table 3-3. Summary of the optimized multiple linear model of carbon stock predicted by species richness and environmental covariables across the Amazonia dataset (n = 283 1-ha plots). Originally included predictors were species richness, forest type and biogeographical region. For each predictor, a summary of the relationship and the relative contribution to total model R^2 (%) is given. Model details included in Table S3.2.11.

	Relationship summary	Rel. contr. R^2 (%)	Total R^2 (%)
Carbon stock			
Biogeographical region	Significant variable	54.9	
Species richness	Significant positive	3.4	
Forest type	Significant variable	1.7	
			60.0

3.4 Discussion

In this study we analysed how tree and arborescent palm species richness was related to aboveground carbon stock, commercially relevant timber stock, and commercially relevant NTFP abundance in tropical forests, and how these relationships were influenced by environmental stratification at different spatial scales. We found that species richness showed significant relationships with all three ecosystem services stock components, but its relationships were strongly influenced by variation across forest types and biogeographical strata. This is further explained below.

Across the Guiana Shield, species richness showed a positive relationship with carbon stock and timber, but not with NTFP abundance. Although relationships only differed in significance among the biogeographical subregions, they differed in direction between terra firme forests and white sand forests. Species richness was positively related to carbon stock and timber stock in terra firme forests, whereas it was negatively related to NTFP abundance in white sand forests. The positive species-carbon relationship across forests of the Guiana Shield is in line with the effects described by hypotheses such as the 'niche complementarity' and 'selection effect' (Tilman et al., 1997) and is in line with previous findings at regional spatial scales (Aldana et al., 2017; Steur et al., 2020). To our knowledge, the relationship between species richness and timber stock has not been previously analysed for tropical forests. Interestingly, the observed positive species-timber relationship in terra firme forests of the Guiana Shield contrasts with the negative species-timber relationship found for subtropical forests in both the U.S.A. and Spain (Bravo-Oviedo et al., 2021), although this may be explained by the difference in ecosystems. The non-significant species-NTFP abundance relationship across the Guiana Shield and the negative relationship within white sand forests seems to contradict previous findings. Steur et al. (2021) found a negative species-NTFP abundance relationship for tropical forests in Suriname. However, this negative relationship was found across multiple forest types, including flooded forests that had low species richness and high NTFP abundance. These flooded forests most likely influenced the species-NTFP abundance relationship across all forest types.

In contrast to the relationship between species richness and carbon stock, no mechanism has been proposed for how species richness would influence commercial timber stock and NTFP abundance. Although our results suggest that species richness had a positive relationship with timber, the relationship was not found within multiple biogeographical subregions. For NTFP abundance, species richness did not contribute to explaining variation when variation across biogeographical subregions was accounted for (i.e. was included as an explanatory variable). We here tentatively propose that both commercial relevant timber stock and NTFP abundance are driven by variation in species floristic composition, rather than by species richness. For services such as commercial timber and NTFP provisioning, only a subset of all species is relevant (in this study, 9.4% of all morphospecies for timber and 3.8% for NTFPs), and such subsets are likely not random selections. For example, for Suriname, it was found that variation in commercially relevant NTFP abundance was driven by a particularly small selection of NTFP producing species with high abundances (referred to as 'NTFP oligarchs'; Steur et al., 2021), and for commercial relevant timber stock, it is commonly known that selections tend to include more abundant than rare species. Additionally, as the relative abundance of species tends to vary across floristic regions in Amazonia, where, for example, certain species are dominant in particular forest types and biogeographical regions (ter Steege et al., 2013, 2019a), it can be expected that commercial timber stock and NTFP abundance are determined by floristic composition. In support, for NTFP abundance in Suriname tropical forests, Steur et al. (2021) found that floristic composition was a stronger predictor of NTFP abundance than species richness.

Across all of Amazonia, species richness had a positive relationship with carbon stock, but only when variation among biogeographical regions was accounted for. The positive species-carbon relationship across Amazonia partly contrasts with previous findings at continental spatial scales (Poorter et al., 2015; Sullivan et al., 2017). When variation across climatic and/or edaphic variables was accounted for, Sullivan et al. (2017) found no significant species-carbon relationship across South-America, while Poorter et al. (2015) did find a positive relationship across Meso- and South-America. Here, we propose that accounting for differences among biogeographical regions can explain the previously found contrasts at continental spatial scales. In our dataset, for individual regions, we found either a positive relationship or a non-significant, but weakly positive, relationship between carbon stock and species richness (Figure 3-3). However, when the data were aggregated across all regions, this resulted in a non-significant, and weakly negative, relationship. This reflects a known statistical phenomenon referred to as a 'Simpson's paradox' (Simpson, 1951), in which a relationship appears in multiple distinct groups but disappears or reverses when the groups are combined. Additional post-hoc tests of leaving one region out at a time showed that this pattern was not dependent of any particular biogeographical region. This is the first time that an analysis based on empirical data provides evidence for a Simpson's paradox in species-ecosystem service relationships.

It is likely that the observed differences in carbon stock across the biogeographical regions of Amazonia are influenced by multiple factors. For example, the biogeographical regions used in our analyses were recognised according to differences in substrate history, geological age and floristic composition, which could all contribute to variation in carbon stock. The substrate history and geological age of the biogeographical regions have been related to differences in soil fertility (Quesada et al., 2011), while multiple spatial gradients in floristic composition identified across the Amazon coincide with a spatial gradient in wood density (ter Steege et al., 2006). However, further analysis is needed to obtain better insight into the relative contributions of these and other variables to explain the observed variation in carbon stock across the biogeographical regions. This requires data on multiple environmental variables, including floristic composition, climatic variables such as the length of the dry period, soil conditions, and intensity of disturbance.

In our analyses, terra firme forests determined the relationship of species richness with the carbon stock, timber stock, and NTFP abundance across the datasets. Although this is most likely the effect of unequal sample sizes, with terra firme forests being the dominant forest type in terms of sample size (n = 130 vs. n = 21 for the Guiana Shield dataset; n = 257 vs. n = 26 for the Amazonia dataset), we expect that the observed relationships reflect the general pattern. Terra firme forests are the most dominant forest type in terms of geographical area (ter Steege et al., 2019a) and were representatively sampled. Regardless, the analyses per forest type had added value. The significant relationship between species richness and NTFP abundance in white sand forests across the Guiana Shield would otherwise have been overlooked.

Due to the known scarcity of reliable and adequate information on which timber and NTFP species are being commercially traded (Piponiot et al., 2019; Selaya et al., 2017; Strand et al., 2018; van Andel et al., 2003), we used a fixed set of timber and NTFP species to apply across the Guiana Shield plots. However, in reality, timber and NTFP species can be expected to vary according to socio-economic factors, such as culture, access, and harvest costs, which may change over space and time. Therefore, estimates of timber stock and NTFP abundance can be expected to differ across spatial gradients, and thus, their possible relationships with species richness cannot be easily generalised. To circumvent this, timber stock and NTFP abundance would have to be estimated on the basis of 'flexible' species selections that can change according to local socio-economic contexts. To this end, detailed information on both commercially relevant timber and NTFP species is urgently needed. Yet, for our study area, we did not observe major differences in selected species, and we included broad selections of species, which should make timber stock and NTFP abundance robust against small deviations in species selection. It must be noted that our approach of quantifying commercial relevant timber stock and NTFP abundance does not consider the value of timber and NTFPs for subsistence use. In addition, NTFPs can also be derived from other growth forms, such as lianas, shrubs and herbs. Last, because NTFP production data was not available we used NTFP abundance as a proxy for NTFP stock, following similar assessments of NTFP stock (Baraloto et al., 2014; Steur et al., 2021). A limitation of this approach is that each NTFP species individual has an equal contribution to NTFP stock, whereas it can be expected that large individuals may have a larger contribution than smaller individuals and that production volumes can differ for different types of NTFPs, for example barks vs. seeds.

Our findings illustrate the importance of considering environmental stratification and spatial scale when analysing relationships between biodiversity and ecosystem services. First, environmental stratification can help detect relationships that are otherwise obscured by environmental heterogeneity. For example, although the association between species richness and carbon stock across Amazonia was relatively weak (explaining ~3% of total variation vs. ~15% in the Guiana Shield) and was obscured by variation in carbon stock across biogeographical strata, by using environmental stratification the positive relationship remained detectable. Second, environmental heterogeneity tends to vary with spatial scale; therefore, its importance needs to be checked according to spatial scale. For example, at the regional scale of the Guiana Shield, biogeographical subregions explained a moderate amount of variation in carbon stock (~20%), while at the spatial scale of Amazonia, biogeographical regions explained more than half of total variation in carbon stock (~55%). Such an increase and ultimate importance of variation across biogeographical strata might also explain the absence of a significant relationship between species richness and carbon stock across African and/or Asian tropical forests as reported by Sullivan et al. (2017).

In our analyses, we found evidence of a positive relationship between species richness and carbon stock across and within Amazonia. This supports the notion that win-win scenarios are possible in conservation approaches, where, for example, REDD+ can be expected to help conserve tropical forests that contain large amounts of carbon stock and high concentrations of species (Phelps et al., 2012). However, we conclude that species richness is not always a strong predictor of biomass-based ecosystem services. In our analyses, NTFP abundance was not driven by species richness, and we ultimately expect the same for timber stock. We expect that differences in floristic composition, linked to differences across forest types and biogeographical strata, will be more relevant than species richness in explaining variation in timber stock and NTFP abundance. This would mean that conserving timber and NTFP related ecosystem services requires the development of additional region-specific strategies that account for differences in floristic composition. For example, areas with high concentrations of timber or NTFPs could be considered in the designation of multiple use protected areas (Oldekop et al., 2016), such as the extractive reserves in Brazil, or be included as 'high conservation value areas' (HCVAs) in sustainable forest management certification (Areendran et al., 2020).

Acknowledgements

This chapter is the result of the work of many different scientists and research institutions in the Amazon over the past 40 years. Without their hard work this analysis would have been impossible. D.S. & J-F.M. benefited from an "Investissement d'Avenir" grant managed by the Agence Nationale de la Recherche (CEBA: ANR-10-LABX-25-01).

SUPPLEMENTARY MATERIAL CHAPTER 3

Annex S3.1: Methodology and Material

Guiana Shield dataset

We compiled a dataset of 151 1-ha lowland tropical forest plots spanning the Guiana Shield region in Amazonia (Figure S3.1.1). These plots had been previously recorded by various authors, and most are included in the Amazon Tree Diversity Network (ATDN) (Table S3.1.3). Of the 151 plots, two were 0.98 ha in size but were treated as 1 ha plots. All of the plots represented old-growth tropical forest vegetation on terra firme soils, where all but two had shown visual signs of limited anthropogenic disturbance. In each plot, all trees and arborescent palms with a minimum diameter at breast height of 10 cm ('DBH', 1.3 m), hereafter referred to as 'woody species', had been measured and identified. In line with previous plant diversity and ecosystem services assessments at relatively large geographical extents (Poorter et al., 2015; Sullivan et al., 2017) at least 60% of the stems had been identified up to the species level, at least 80% up to the genus level and 100% up to the family level. Taxonomy of the woody species was updated following the 'Dynamic Amazon Tree Checklist' (ter Steege et al., 2019b; updated version 20200422).

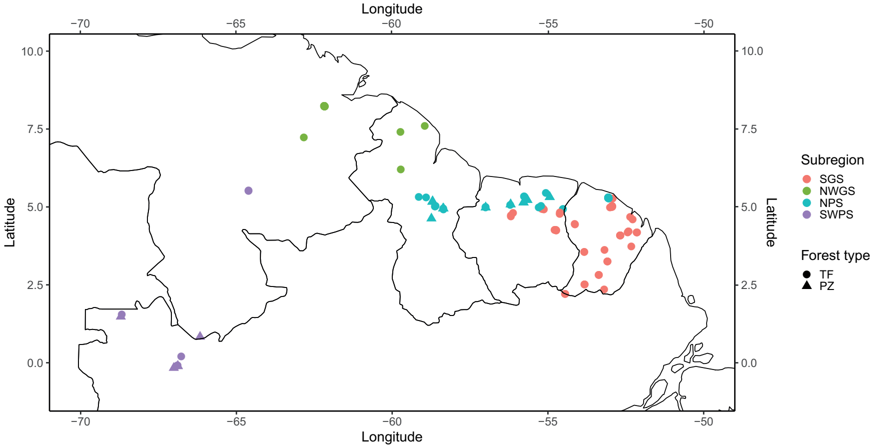

Figure S3.1.1. Map of the 151 1-ha Guiana Shield dataset plots. For each plot, the forest type is indicated by symbols, where circle = terra firme forest (TF, n = 130), and triangle = white sand forest (PZ, n = 21), and subregion is indicated by colour, where red = forests of the southern Guiana Shield (SGS, n = 63), green = forests of the north-western Guiana Shield (NWGS, n = 21), turquoise = forests of the northern Pleistocene sands (NPS, n = 56), and purple = forests of the south-western Pleistocene sands (SWPS, n = 11). Country borders reproduced after the ggplot2 world database (H. Wickham, 2016) are indicated by black lines.

Plant diversity indicators and ecosystem services

For all Guiana Shield dataset plots, we calculated woody species richness (species ha^{-1}) and the stock component of three ecosystem services: carbon storage, timber provisioning and non-timber forest product (NTFP) provisioning. Carbon storage was indicated by the aboveground carbon stock (in Mg ha^{-1}), timber provisioning was indicated by the commercially relevant timber stock (m^{3} ha^{-1}), and non-timber forest product (NTFP) provisioning was indicated by the number of stems of commercially relevant non-timber forest product-producing woody plant species, or 'NTFP abundance' (stems ha^{-1}). Carbon stock on itself is considered an ecosystem service, whereas timber stock and NTFP stock represent the potential of their services. Although not all timber stock and NTFP stock will be ultimately used, it is generally assumed that timber stock and NTFP stock will be positively related to their use. Therefore, in this paper all three services stocks are used as representatives for their ecosystem services.

Aboveground carbon stock per plot was estimated following Sullivan et al. (2017). Here, first tree aboveground biomass was estimated on the basis of stem diameter, height, and wood density by using the pantropical allometric equation of Chave et al. (2014). Tree height was estimated on the basis of tree diameter by using biogeographical region specific 'Weibull' equations developed by Feldpausch et al. (2012). Wood density was retrieved from an appended version of the Chave et al. (2009) global wood density database, specifically for Amazonian woody species (ter Steege et al., in prep.; version 20200401). Second, tree biomass was converted to carbon stock by applying a conversion factor of 0.471.

We considered using a single allometric equation that was calibrated for the neotropics specifically and does not use height as input instead of the approach of Sullivan et al. (2017), but we found that using such an equation did not lead to significant different estimates. Ultimately, we wanted to keep the method of calculating carbon stock consistent across datasets, and we therefore choose to use the approach of Sullivan et al. (2017). For more details, see the section comparing the Guiana Shield and Amazonia datasets, below.

Commercially relevant timber stock per plot was estimated similar to Piponiot et al. (2019). First, a list of recently commercially traded timber tree species was compiled on the basis of the tree species that were reportedly traded for timber in at least one of the relevant countries or country states for the last 25 years (1995-2020). Relevant countries or country states included: Brazil with the states of Pará and Amapá, Venezuela with the states of Bolivar and Amazonas, Guyana, Suriname, and French Guiana. For these relevant countries and country states we compiled a list of 1184 reported timber tree species, 727 of which were present in our plots. See Table S1.1 (below) for an overview of the morphospecies included and used sources. Second, for each plot the stem volume was calculated for individuals of the relevant tree species with DBH ≥ 50 cm, in accordance to local forestry laws. Stem volume was calculated by using the neotropical moist-forest allometric equation of Chave et al. (2005).

Following Steur et al. (2021), the number of tree and arborescent palm individuals that produce commercially relevant NTFPs, hereafter referred to as 'NTFP abundance', was counted per plot (stems ha^{-1}) as a proxy for NTFP stock. Similar to the approach for timber stock, a list was compiled of tree and arborescent palm species that were reported to have produced commercially traded non-timber forest products in at least one of the relevant countries or country states for the last 25 years (1995-2020). For the relevant countries and country states we compiled a list of 216 woody NTFP species and 7 woody NTFP genera, of which 295 morphospecies were present in our plots. See Table S1.2 (below) for an overview of the morphospecies included and used sources.

Amazonia dataset

We combined the Guiana Shield data with data from 132 1-ha tropical forest plots published by Sullivan et al. (2017) to create a dataset of 283 plot measurements of woody species richness and carbon stock across Amazonia (Figure 3-1; Table 3-1; references provided in Table S3.1.3). Taxonomic precision and the minimum DBH used by Sullivan et al. (2017) was comparable to our Guiana Shield dataset data. The data taken from Sullivan et al. (2017) also included 14 additional plot measurements on the Guiana Shield that were not included in the Guiana Shield dataset.

Environmental covariables

To investigate how relationships with woody species richness changed according to environmental heterogeneity, we used forest type and biogeographical strata as categorical environmental covariables.

For the entire Amazonia dataset (including the Guiana Shield dataset), we classified all available plots into two main non-flooded forest types, recognized after ter Steege et al., (2013; 2019a): forests on brown soils, hereafter referred to as 'terra firme forests' (TF; n = 130 for Guiana Shield dataset, n = 257 for Amazonia dataset) and forests on white sands, hereafter referred to as 'white sand forests' (PZ; n = 21 for Guiana Shield dataset, n = 26 for Amazonia dataset). These forest types mainly differ in physiognomy, species composition, and substrate origin, and their sample sizes reflect the geographical coverage of these forest types, where terra firme forests cover more than 50% of Amazonia and white sand forests just under 5% (ter Steege et al., 2019a). Both forest types represent forests that occur on well-drained, never inundated soils, but white sands forests occur on bleached and leached, nutrient-poor sandy soils (Albic Arenosols), while the terra firme forests on brown soils include brown sands (sand, loam, clay) and Leptosols. Previous research has found that terra firme forests on brown soils are generally relatively tree species rich (Stropp, 2011; ter Steege et al., 2019a; ter Steege & Zondervan, 2000), while white sand forests are generally relatively species poor (Stropp, 2011; ter Steege et al., 2013; 2019a).

For the entire Amazonia dataset (including the Guiana Shield dataset), we classified all available plots into six biogeographical regions (Figure 1), recognized after ter Steege et al., (2013; 2019a): the Guiana Shield (GS; n = 165), the Brazilian Shield (BS; n = 9), north-western Amazonia (WAN; n = 21), south-western Amazonia (WAS; n = 51), central Amazonia (CA; n = 22) and eastern Amazonia (EA; n = 15). These biogeographical regions have been identified according to differences in substrate history, geological age and floristic composition. Here, both GS and BS dominated by relatively nutrient poor igneous and metamorphic rocks but are spatially separated from each other, forming distinct floristic clusters. Both WAN and WAS are both dominated by relatively nutrient rich Andean sediments but differ in mean annual precipitation, where WAN is wetter than WAS, forming two different floristic clusters. Last, both CA en EA are different mixtures of nutrient poor sediments originating from GS, BS, WAN and WAS, forming two different floristic clusters.

For the Guiana Shield dataset, we classified the plots into four subregions of the Guiana Shield biogeographical region (Figure S3.1.1), recognized after the 'forest regions' identified by ter Steege & Zondervan (2000) and revised after the floristic analyses between West and East terra firme forests of the Guiana Shield region carried out by Stropp (2011). On the basis of differences in substrate history and age, and by differences in floristic composition, we recognized the following subregions: forests of the northern Pleistocene sands (NPS, n = 56), forests of the south-western Pleistocene sands in the upper Rio Negro region (SWPS, n = 11), forests of the southern Guiana Shield (SGS, n = 63) and forests of the north-western Guiana Shield (NWGS, n = 21). SGS and NWGS lie on the actual Guiana Shield formation and consist of soils that have developed from the relatively ancient Pre-Cambrian crystalline substrates. By contrast, NPS and SWPS lie on the periphery of the Guiana Shield formation and consist of varied weathered soils that have been deposited during the relatively younger Tertiary-Pleistocene (ter Steege & Zondervan, 2000). In general, the forests on the Guiana Shield formation have a higher fisher's alpha (are more diverse) than the forests on the Pleistocene sands. However, there are also floristic differences between the forests on the Guiana Shield formation and between the forests on the Pleistocene sands. The forests of SGS (the 'Guiana peneplain') have a relatively higher fisher's alpha than the forest of NWGS and different genera tend to dominate the forest (Stropp et al., 2009; ter Steege & Zondervan, 2000). In addition, the forests of SWPS have a higher alpha diversity than the forests of the NPS (Stropp, 2011).

Last, originally, we had also data available on the soil type of the Guiana Shield dataset plots. However, as we found that soil class was highly collinear to both biogeographical subregions and forest types, we therefore excluded it from our analyses. For reference, the classification of the soils is given below.

For the plots in the Guiana Shield dataset the main soil type was noted. We classified these soil types into three soil classes based on the description Amazonian soils and their putative relationships to forest productivity and species composition (Hawes et al., 2012; Quesada et al., 2012; Saatchi et al., 2008): brown sands (n = 64), Leptosols (n = 67) and Albic Arenosols (n = 21). Here, the class brown sands include fine textured, strongly weathered, brownish, sandy, loamy or clayey soils (i.e. Ferralic Arenosols, Haplic Ferralsols and Xanthic Ferralsols; Plinthosols; Haplic Acrisols and Humic Acrisols). They have a high water-permeability and due to the presence of organic material they are moderately fertile and have a moderate water-holding capacity. Brown sands can be either acidic (Acrisols) or neutral (Ferrasols), which potentially impacts the species composition. However, as Acrisols are rare on the Guiana Shield and are most similar to Ferrasols, we combined them into one class. The class Leptosols include shallow clayey to stony soils on weather-resistant rock, for example in the Guiana Shield on lateritic caps. They have a low water-permeability and can be relatively fertile but in general inhibit plant growth with their limited depth. Last, the class Albic Arenosols includes fine-textured, extremely weathered, white-bleached, sandy soils. These have a high water-permeability but due to little organic material, they have a low water-holding capacity and are one of the most infertile soils in the Guiana Shield.

Table S3.1.4. Overview of the number of forest types per biogeographical stratum for the Guiana Shield dataset (n = 151) and the Amazonia dataset (n = 284). Forest types are TF = terra firme forests and PZ = white sand forests. Biogeographical subregions of the Guiana Shield are SGS = Forests of the Southern Guiana Shield, NWGS = Forests of the North-Western Guiana Shield, NPS = Forests of the Northern Pleistocene sands, and SWPS = Forests of the South-Western Pleistocene sands. Biogeographical regions of Amazonia are GS = Guiana Shield, BS = Brazilian Shield, WAN = North-West Amazonia, WAS = South-West Amazonia, CA = Central Amazonia, and EA = Eastern Amazonia.

Guiana Shield dataset	**SGS**	**NWGS**	**NPS**	**SWPS**			**Totals**
TF	63	21	40	6			
PZ	0	0	16	5			21
Totals	63	21	56	11			151
Amazonia dataset	**GS**	**BS**	**WAN**	**WAS**	**CA**	**EA**	
TF	141	9	19	51	22	15	257
PZ	24	0	2	0	0	0	26
Totals	165	9	21	51	22	15	283

Review of aboveground carbon stock estimation methods

When reviewing the methodology of Sullivan et al. (2017) we noticed that they used a tree volume allometric equation based on stem diameter and stem height while the stem height measurements were not available. They used the stem diameter to also estimate the stem height using a separate region-specific tree height allometric equation. However, this presented approach does not follow proper error propagation as the error of the height estimate is not inputted into the tree volume allometric equation. In addition, Sullivan et al. (2017) for their pantropical analyses used a tree volume allometric equation calibrated with trees from across the tropics, while for our analyses we focus on the Neotropics only. Using a pantropical tree volume allometric equation might lead to a bias for neotropical trees. Both issues could potentially reduce the amount of variation that can be explained by plant diversity or environmental covariables. Therefore, we investigated the impact of these two issues by calculating the aboveground biomass for the Guiana Shield dataset using two approaches: the 'Sullivan et al. (2017) approach' sensu Sullivan et al. (2017) and a second, 'alternative approach', using a neotropical tree volume allometric equation that uses only tree diameter instead of also tree height.

For the alternative approach we used the moist forest tree diameter allometric equation by Chave et al. (2005). This equation was calibrated for south-American tropical forests and does not require height measurements. We did not use the different dry, moist and wet forest equations by Chave et al. (2005) because this would artificially introduce differences in our estimates on the basis of a hard climatic threshold. In addition, we did not use a separate allometric equation for palm biomass, as the comparison by Selaya et al. (2017) showed that using a palm-specific allometric equation does not necessarily improve the accuracy of biomass estimates. The aboveground biomass was converted to aboveground carbon stock by multiplying with the conversion factor 0.474.

Mean aboveground carbon stock estimated by the alternative approach was not significantly different from the mean aboveground carbon stock estimated by the Sullivan et al. (2017) approach (t-value = 0.72264, df = 301.64, p-value = 0.4705; Table S3.1.5). In addition, a linear regression model explaining the aboveground carbon stock estimated by the Sullivan et al. (2017) approach by the estimates by the Alternative approach showed that both estimates were highly related (R = 99.3%; Table S1.6, Figure S3.1.1). We therefore concluded that the impact of using the Sullivan et al. (2017) is likely to be minor.

Table S3.1.5. Estimated aboveground carbon stock across the 151 1 ha plots of the Guiana Shield dataset, using the method of Sullivan et al. (2017) and the alternative method (see text). Showing the mean with standard deviation, the minimum and the maximum.

Aboveground carbon stock (Mg ha-1) across 151 1 ha Guiana Shield plots	**Mean ± SD**	**min - max**
Method Sullivan et al. 2017	212.20 ± 49.48	76.30 - 350.60
Alternative method	207.90 ± 51.37	70.49 - 360.79

Table S3.1.6. Detailed results for the bivariate linear model of aboveground carbon stock values across the Guiana Shield dataset (n = 151) estimated by the Sullivan et al. (2017) approach predicted by the estimates by the alternative approach (see text). Showing model coefficients with its standard error (SE), the t-test value, the p -value of the t-test (H_0: b = 0), and the R^2 of the total model.

Model	Coefficient	SE	t-value	p-value	R^2
Model $AGC_{Sullivan} \sim AGC_{Alternative}$					
Intercept	12.684816	1.457244	8.705	5.53E-15	
$AGC_{Alternative}$	0.959644	0.006806	141.002	< 2e-16	
					0.9926

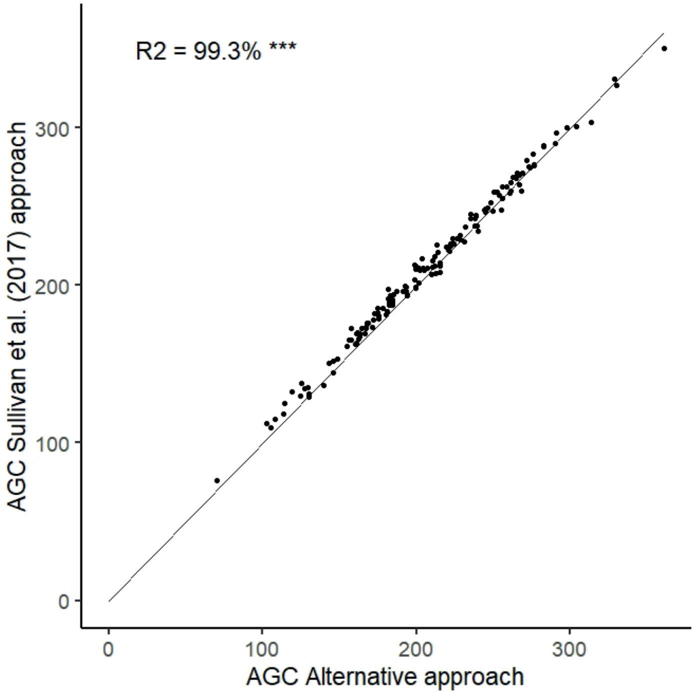

Figure S3.1.2. Comparison of aboveground carbon stock (AGC, in Mg ha^{-1}) for the 151 1-ha Guiana Shield plots estimated by the Sullivan et al (2017) approach (y-axis) and the Alternative approach (x-axis). A perfect relationship between both estimation approaches is indicated by the black line.

Statistical analyses

We used standard linear models to analyse relationships between species richness and ecosystem service stock components and to explore how the environmental covariables influenced these relationships. To test for direct and indirect effects of species richness and also test the extent to which species richness and environmental covariables independently contributed to explaining variation in ecosystem services, we used multiple linear regression models that were optimised using a backward model selection procedure proposed by Crawley (2015). In this procedure, a full model containing all relevant and non-collinear variables is optimized by excluding one variable at a time, and testing with a Log-Likelihood Ratio test whether this does not lead to a significant difference in the amount of variation explained. This is repeated until no variable can be removed without the model explaining a significantly different amount of variation.

Regarding linear model assumptions, all dependent variables, here all three ecosystem services, followed an approximate normal distribution (Figure S3.1.4-S3.1.5). Log transformation did not seem to significantly improve distributions. Multicollinearity between explanatory variables might lead to erroneous exclusion of explanatory variables under model optimization. Therefore, we checked for multicollinearity between the explanatory variables in the full model by omitting any variables with a Variance Inflation Factor (VIF) larger than 3 (after Zuur et al., 2010). The sample sizes of our covariables were unequal (forest type, biogeographical region, biogeographical subregion), which could have potentially led to heterogenous model variances and therefore erroneous exclusion of the covariables under model optimization. However, we checked the residuals vs the fitted values of all of our full and optimized models and did not detect clear heterogeneity for our models. Last, low sample sizes could lead to a low power to detecting relationships and could lead to potential model overfitting. Generally, a conservative value of at least 10 samples per parameter is advocated for linear regression (Crawley, 2015). Although in one case the number of samples per parameter was lower than 10 (i.e. for the region of the Brazilian Shield, n = 9), all other parameters in our models were above the conservative number. In addition, to check for effects of overfitting, we also carried out a regression analysis for each covariable parameter separately.

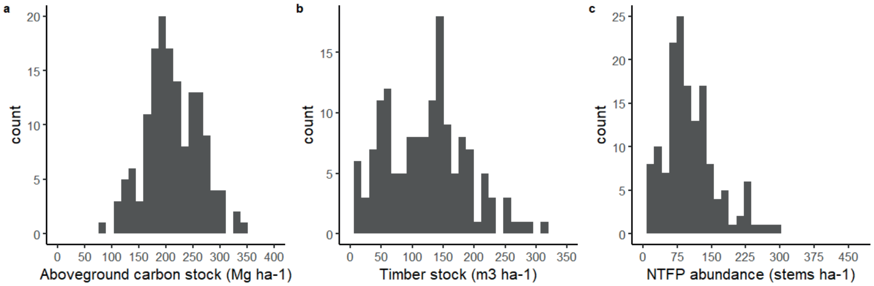

Figure S3.1.4 Histograms of aboveground carbon stock (Mg ha^{-1}; panel a), timber stock (m^{3} ha^{-1}; panel b) and NTFP abundance (stems ha^{-1}; panel c) in the Guiana Shield dataset (n = 151).

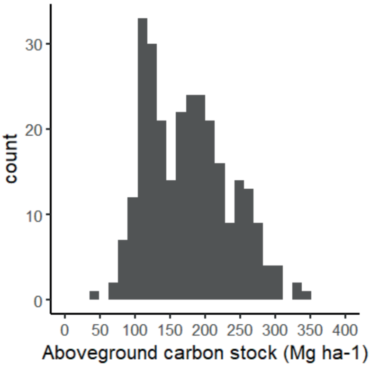

Figure S3.1.5 Histogram of aboveground carbon stock (Mg ha^{-1}) in the Amazonia dataset (n = 283).

We used the relative contribution to the total amount of variation explained (R^2; after Lindeman et al., 1980) as a measure of relative importance of variables because it can be calculated for both continuous as categorial variables. The relative contribution of each variable is calculated according to the amount of explained variation that is added when a variable is included, and taking the average of this amount across all possible variable orders in the model. In this way, the relative contribution of the variable to R^2 is compensated for the amount of variation already explained by other variables in the model.

We tested if there was significant variation in ecosystem services and/or plant diversity indicators across soil classes, forest types and biogeographical regions, by using analysis of variance F-tests. If significant variation across groups was detected, we applied post-hoc Tukey tests to assess the differences among the groups. The Tukey Post-hoc test adjusts the p-value for multiple testing, controlling for the increased chance of obtaining a false positive when multiple tests are carried out in sequence (Type I error).

As stem density, basal area and wood density had been used to estimate aboveground carbon stock, these variables are structurally collinear. Therefore, these variables were not used for model optimization of aboveground carbon stock models. The structural collinearity of stem density, basal area and wood density with timber stock and NTFP abundance was expected to be less problematic: for estimates of timber stock and NTFP abundance only a subset of all woody species had been used.

Software

All statistical analyses were carried out in R (R Core Team, 2020). In addition, we used the following R packages: ‘**stringr**' (Hadley Wickham, 2019) for general coding support; '**vegan**' (Oksanen et al., 2019) for calculation of all plant diversity indicators except for the

Camargo evenness for which own code was used; ‘**Hmisc**’ (Harrell Jr, 2020) for calculation of correlation matrices; ‘**pastecs**' (Grosjean & Ibanez, 2018) for standard variable statistics; ‘**car**’ (Fox & Weisberg, 2019) to calculate variance inflation factors; ‘**relaimpo**’ (Grömping, 2006) to calculate the relative contribution to R^2; ‘**multcomp**’ (Hothorn et al., 2008) to carry out post-hoc Tukey tests; and ‘**ggplot2**’, ‘**ggrepel**', ‘**raster**’ and ‘**ggpubr**' (Hijmans, 2020; Kassambara, 2019; Slowikowski, 2019; H. Wickham, 2016) for graphical output.

Table S3.1.1. List of commercially relevant timber tree species in the Guiana Shield region

Timber tree species	References
Abarema jupunba	1, 3, 5, 6, 7, 8
Acioa longipendula	5, 8
Acosmium cardenasii	5
Acrocomia aculeata	5, 8
Agonandra brasiliensis	5, 8
Aiouea montana	5, 8
Albizia niopoides	5, 8
Alchornea triplinervia	5
Alchorneopsis floribunda	5, 7
Aldina insignis	5
Alexa imperatricis	3, 5, 8
Alexa wachenheimii	5, 7
Allantoma decandra	2, 5
Amanoa guianensis	5
Ampelocera ruizii	5
Amphiodon effusus	5, 8
Anacardium giganteum	5, 8
Anacardium parvifolium	5, 8
Anacardium spruceanum	1, 2, 5, 6, 8
Anadenanthera colubrina	2, 5, 8
Anadenanthera peregrina	5, 8
Andira coriacea	5, 7, 8
Andira fraxinifolia	5, 8
Andira inermis	1, 3, 5, 6, 7, 8
Andira parviflora	5, 8
Andira surinamensis	1, 3, 5, 6, 7, 8
Aniba canelilla	5, 8
Aniba citrifolia	5, 8
Aniba guianensis	5, 8
Aniba hostmanniana	5, 7, 8
Aniba hypoglauca	3, 5
Aniba kappleri	5, 7, 8
Aniba megaphylla	5, 8
Aniba panurensis	1, 5, 6, 8
Aniba parviflora	5, 8
Aniba rosiodora	1, 5, 6, 8
Aniba terminalis	5, 8
Aniba williamsii	5, 8
Antonia ovata	1, 3, 5, 6
Apeiba albiflora	5, 8
Apeiba glabra	5, 8
Apeiba petoumo	2, 5, 8
Apuleia leiocarpa	2, 5, 8
Aspidosperma album	1, 3, 5, 6, 7, 8
Aspidosperma carapanauba	5, 8
Aspidosperma cylindrocarpon	5
Aspidosperma desmanthum	2, 3, 5, 7, 8
Aspidosperma discolor	5, 8
Aspidosperma excelsum	5, 7, 8
Aspidosperma helstonei	5, 7
Aspidosperma megalocarpon	5, 8
Aspidosperma parvifolium	3, 5
Aspidosperma sandwithianum	5, 7, 8
Aspidosperma spruceanum	5, 8
Aspidosperma tomentosum	5
Astronium graveolens	2, 5, 8
Astronium lecointei	2, 5, 7, 8
Astronium ulei	2, 3, 5, 8
Bagassa guianensis	1, 2, 3, 4, 5, 6, 7, 8
Balizia pedicellaris	2, 4, 5, 8
Barnebydendron riedelii	5
Batesia floribunda	5
Batocarpus amazonicus	5
Bocoa prouacensis	1, 4, 5, 6, 7
Bowdichia virgilioides	2, 5, 8
Brosimum acutifolium	2, 4, 5, 7, 8
Brosimum alicastrum	5
Brosimum guianense	1, 4, 5, 6, 7, 8
Brosimum lactescens	5, 8
Brosimum parinarioides	2, 4, 5, 7, 8
Brosimum potabile	2, 5, 8
Brosimum rubescens	1, 2, 4, 5, 6, 7, 8
Brosimum utile	4, 5, 8
Byrsonima aerugo	5, 8
Byrsonima crassifolia	5, 8
Byrsonima crispa	5, 8
Byrsonima densa	5, 8
Byrsonima laevigata	5
Byrsonima stipulacea	5, 8
Calatola costaricensis	5
Calliandra laxa	5, 8
Calophyllum brasiliense	2, 3, 5, 7, 8
Calycophyllum megistocaulum	5, 8
Candolleodendron brachystachyum	5
Capirona decorticans	5

Timber tree species	References	Timber tree species	References
Caraipa densifolia	2, 5, 7, 8	*Chrysophyllum gonocarpum*	5
Caraipa punctulata	5, 8	*Chrysophyllum lucentifolium*	2, 5
Caraipa racemosa	5	*Chrysophyllum pomiferum*	3, 4, 5, 7, 8
Caraipa richardiana	5, 7, 8	*Chrysophyllum prieurii*	5, 8
Carapa guianensis	1, 2, 3, 4, 5, 6, 7, 8	*Chrysophyllum sanguinolentum*	4, 5, 8
Carapa surinamensis	1, 3, 4, 5, 6	*Chrysophyllum sparsiflorum*	5, 8
Cariniana estrellensis	5	*Chrysophyllum venezuelanense*	5, 8
Cariniana ianeirensis	5	*Citharexylum spinosum*	5, 8
Cariniana micrantha	2, 5, 8	*Clarisia racemosa*	2, 5, 8
Caryocar glabrum	2, 4, 5, 8	*Clathrotropis brachypetala*	3, 5
Caryocar microcarpum	4, 5, 8	*Clathrotropis macrocarpa*	3, 5, 8
Caryocar nuciferum	1, 5, 6	*Copaifera guyanensis*	1, 5, 6, 8
Caryocar villosum	2, 5, 8	*Copaifera martii*	5, 8
Casearia arborea	5, 8	*Cordia alliodora*	1, 5, 6, 8
Casearia commersoniana	5, 8	*Cordia bicolor*	2, 5, 8
Casearia decandra	5, 8	*Cordia exaltata*	5, 8
Casearia grandiflora	5, 8	*Cordia fallax*	5, 8
Casearia javitensis	5, 8	*Cordia goeldiana*	2, 5, 8
Casearia negrensis	5, 8	*Cordia laevifrons*	5, 8
Casearia pitumba	5, 8	*Cordia nodosa*	5, 8
Casearia spinescens	5, 8	*Cordia panicularis*	5, 8
Casearia sylvestris	5, 8	*Cordia sagotii*	2, 5, 8
Cassia spruceana	5	*Cordia tetrandra*	5, 8
Catostemma altsonii	3, 5	*Couepia bracteosa*	5, 8
Catostemma commune	3, 5	*Couepia caryophylloides*	1, 5, 6
Catostemma fragrans	3, 5	*Couepia guianensis*	5, 8
Cecropia sciadophylla	5	*Couepia joaquinae*	5, 8
Cedrela fissilis	2, 5, 8	*Couepia magnoliifolia*	5, 8
Cedrela odorata	1, 2, 3, 4, 5, 6, 7, 8	*Couepia robusta*	5, 8
Cedrelinga cateniformis	1, 2, 5, 6, 7, 8	*Couma guianensis*	4, 5, 7, 8
Ceiba pentandra	2, 5, 8	*Couma macrocarpa*	5, 8
Ceiba samauma	5	*Couma utilis*	5, 8
Centrolobium microchaete	5	*Couratari gloriosa*	3, 5
Chaetocarpus schomburgkianus	5, 7	*Couratari guianensis*	1, 2, 3, 5, 6, 8
Chamaecrista adiantifolia	5, 8	*Couratari multiflora*	2, 3, 5, 8
Chamaecrista apoucouita	5	*Couratari oblongifolia*	2, 5, 7, 8
Chaunochiton kappleri	5, 7	*Couratari oligantha*	5, 8
Chimarrhis barbata	5, 8	*Couratari stellata*	2, 5, 7, 8
Chimarrhis turbinata	5, 8	*Crudia bracteata*	5, 8
Chlorocardium rodiei	3, 5	*Crudia glaberrima*	5, 8
Chromolucuma rubriflora	5, 8	*Cupania diphylla*	5, 8
Chrysophyllum argenteum	5, 8	*Cupania hirsuta*	5, 8
Chrysophyllum cuneifolium	5, 7, 8	*Cupania scrobiculata*	5, 8
Chrysophyllum eximium	5, 8	*Cyclolobium brasiliense*	5

Timber tree species	References	Timber tree species	References
Dacryodes nitens	5	*Eschweilera collina*	5, 8
Dalbergia ecastaphyllum	5, 8	*Eschweilera coriacea*	1, 2, 3, 5, 6, 8
Dendrobangia boliviana	4, 5	*Eschweilera decolorans*	3, 5
Dendropanax arboreus	5	*Eschweilera grandiflora*	5, 8
Dialium guianense	5, 8	*Eschweilera micrantha*	5, 8
Dicorynia guianensis	1, 4, 5, 6, 7	*Eschweilera ovata*	5, 8
Didymopanax decaphyllus	3, 5, 7, 8	*Eschweilera parviflora*	3, 5, 8
Didymopanax morototoni	1, 2, 3, 5, 6, 7, 8	*Eschweilera pedicellata*	3, 5, 7, 8
Dimorphandra polyandra	3, 5, 8	*Eschweilera rhododendrifolia*	5, 8
Dinizia excelsa	2, 5, 8	*Eschweilera sagotiana*	3, 5, 8
Diospyros capreifolia	5, 8	*Eschweilera subglandulosa*	3, 5, 7, 8
Diospyros carbonaria	5, 8	*Eschweilera truncata*	5, 8
Diospyros cayennensis	5, 8	*Eschweilera wachenheimii*	3, 5
Diploon cuspidatum	5, 8	*Eugenia coffeifolia*	5, 8
Diplotropis purpurea	1, 2, 3, 4, 5, 6, 7, 8	*Eugenia cupulata*	5, 8
Diplotropis triloba	5	*Eugenia florida*	5, 8
Dipteryx magnifica	2, 5, 8	*Eugenia lambertiana*	5, 8
Dipteryx odorata	1, 2, 3, 4, 5, 6, 7, 8	*Eugenia moschata*	5, 8
Dipteryx punctata	1, 4, 5, 6, 7, 8	*Eugenia patrisii*	5, 8
Drypetes variabilis	1, 5, 6, 7, 8	*Eugenia protenta*	5, 8
Duroia eriopila	5	*Eugenia punicifolia*	5, 8
Duroia longiflora	5	*Eugenia stictopetala*	5, 8
Ecclinusa guianensis	5	*Eugenia wentii*	5, 8
Ecclinusa lanceolata	5, 8	*Eugenia wullschlaegeliana*	5, 8
Ecclinusa ramiflora	5, 8	*Euplassa pinnata*	5, 8
Emmotum fagifolium	5, 8	*Exellodendron barbatum*	5, 8
Emmotum nitens	5, 8	*Ficus americana*	5, 8
Endopleura uchi	5, 8	*Ficus boliviana*	5
Enterolobium oldemanii	4, 5	*Ficus coerulescens*	5
Enterolobium schomburgkii	2, 4, 5, 7, 8	*Ficus gomelleira*	5, 8
Eperua falcata	1, 3, 4, 5, 6, 7, 8	*Ficus insipida*	5, 8
Eperua grandiflora	1, 3, 4, 5, 6	*Ficus maxima*	5, 8
Eperua jenmanii	3, 5	*Ficus nymphaeifolia*	5, 8
Eperua rubiginosa	1, 3, 4, 5, 6	*Ficus paraensis*	5, 8
Eriotheca crassa	5, 7, 8	*Ficus pertusa*	5, 8
Eriotheca globosa	5, 8	*Garcinia benthamiana*	1, 5, 6
Eriotheca longitubulosa	5	*Garcinia macrophylla*	1, 5, 6
Eriotheca surinamensis	5, 8	*Garcinia madruno*	1, 5, 6
Erisma calcaratum	5, 8	*Gaulettia elata*	5, 8
Erisma uncinatum	1, 2, 5, 6, 7, 8	*Geissospermum laeve*	5, 8
Eschweilera alata	3, 5	*Geissospermum sericeum*	5, 8
Eschweilera albiflora	5, 8	*Genipa americana*	5
Eschweilera apiculata	5, 8	*Glycydendron amazonicum*	4, 5
Eschweilera atropetiolata	5, 8	*Goupia glabra*	1, 2, 3, 4, 5, 6, 7, 8

Timber tree species	References
Guarea gomma	5, 8
Guarea guidonia	5, 8
Guarea kunthiana	5, 8
Guarea macrophylla	5, 8
Guarea pubescens	5, 8
Guarea scabra	5, 8
Guarea silvatica	5, 8
Guarea trunciflora	5, 8
Guatteria megalophylla	5, 8
Guatteria punctata	5, 8
Guatteria schomburgkiana	5, 8
Guazuma ulmifolia	5, 8
Guianodendron praeclarum	3, 5
Gustavia augusta	5, 8
Gustavia hexapetala	5, 8
Gustavia poeppigiana	5, 8
Handroanthus capitatus	1, 5, 6, 7, 8
Handroanthus impetiginosus	2, 4, 5, 8
Handroanthus incanus	2, 5
Handroanthus ochraceus	2, 5, 8
Handroanthus serratifolius	1, 2, 3, 4, 5, 6, 7, 8
Hebepetalum humiriifolium	5
Heisteria ovata	5
Helicostylis pedunculata	5, 8
Helicostylis scabra	5, 8
Helicostylis tomentosa	5, 8
Heliocarpus americanus	5
Hernandia guianensis	5, 8
Hevea benthamiana	5, 8
Hevea guianensis	5, 8
Hevea pauciflora	5, 8
Hieronyma alchorneoides	3, 5, 7, 8
Himatanthus articulatus	5, 8
Himatanthus bracteatus	5
Himatanthus sucuuba	5, 8
Hirtella bicornis	5, 8
Hirtella glandulosa	5, 8
Hirtella macrosepala	5, 7
Hirtella obidensis	5, 8
Hirtella triandra	5, 8
Homalolepis cedron	5, 8
Homalolepis morettii	5
Huberodendron swietenioides	5
Humiria balsamifera	1, 3, 4, 5, 6, 7
Humiriastrum cuspidatum	5, 8
Humiriastrum obovatum	5
Humiriastrum subcrenatum	5
Hura crepitans	2, 5, 8
Hydrochorea corymbosa	1, 5, 6, 7, 8
Hydrochorea gonggrijpii	5, 7
Hymenaea courbaril	1, 2, 3, 4, 5, 6, 7, 8
Hymenaea intermedia	5, 8
Hymenolobium excelsum	2, 5, 8
Hymenolobium flavum	1, 3, 5, 6, 7, 8
Hymenolobium heterocarpum	2, 5, 8
Hymenolobium modestum	2, 5, 8
Hymenolobium petraeum	2, 5, 8
Hymenolobium pulcherrimum	2, 5, 8
Hymenolobium sericeum	2, 5, 8
Hymenopus heteromorphus	1, 5, 6, 8
Hymenopus laevigatus	5, 8
Hymenopus latifolius	5, 8
Hymenopus macrophyllus	5, 8
Ilex inundata	5
Inga acrocephala	5, 8
Inga alba	1, 3, 4, 5, 6, 7, 8
Inga auristellae	5, 8
Inga bourgonii	5
Inga brachystachys	5, 8
Inga capitata	5, 8
Inga cayennensis	5, 8
Inga cinnamomea	5, 8
Inga cordatoalata	5, 8
Inga cylindrica	5, 8
Inga disticha	5, 8
Inga edulis	5, 8
Inga flagelliformis	5, 8
Inga gracilifolia	5, 8
Inga heterophylla	5, 8
Inga huberi	5, 8
Inga ingoides	5, 8
Inga lateriflora	5, 8
Inga laurina	5, 8
Inga leiocalycina	5, 8
Inga longiflora	5, 8
Inga macrophylla	5, 8
Inga marginata	5, 8
Inga obidensis	5, 8

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Inga paraensis	5, 8
Inga pezizifera	5, 8
Inga rubiginosa	5, 8
Inga sertulifera	5, 8
Inga splendens	5, 8
Inga stipularis	5, 8
Inga thibaudiana	5, 8
Inga umbellifera	5, 8
Inga umbratica	5, 8
Inga vera	5, 8
Iryanthera crassifolia	5, 8
Iryanthera elliptica	5, 8
Iryanthera hostmannii	5, 8
Iryanthera juruensis	5, 8
Iryanthera laevis	5, 8
Iryanthera lancifolia	3, 5, 8
Iryanthera olacoides	5, 8
Iryanthera paradoxa	5, 8
Iryanthera paraensis	5, 8
Iryanthera sagotiana	5, 8
Jacaranda copaia	1, 2, 3, 4, 5, 6, 7, 8
Jacaratia spinosa	5
Kubitzkia mezii	5, 7, 8
Lacmellea aculeata	5
Lacunaria jenmanii	5
Laetia procera	1, 2, 3, 4, 5, 6, 7, 8
Laplacea fruticosa	5, 7
Lecointea amazonica	5, 8
Lecythis chartacea	5, 8
Lecythis confertiflora	3, 5
Lecythis congestiflora	5, 7
Lecythis corrugata	1, 3, 5, 6, 8
Lecythis holcogyne	5
Lecythis idatimon	1, 5, 6, 8
Lecythis persistens	5
Lecythis poiteaui	5, 7, 8
Lecythis prancei	5
Lecythis retusa	5, 8
Lecythis zabucajo	3, 5, 7, 8
Leptobalanus apetalus	5, 7, 8
Leptobalanus longistylus	5, 8
Leptobalanus octandrus	5, 8
Leptobalanus sclerophyllus	5, 8
Leptolobium nitens	5, 8
Licania affinis	5, 8
Licania alba	3, 5, 8
Licania bracteata	5, 8
Licania buxifolia	5
Licania canescens	5, 8
Licania cuprea	5
Licania densiflora	5, 7, 8
Licania hypoleuca	5, 8
Licania incana	5, 8
Licania kunthiana	5, 8
Licania laxiflora	3, 5, 7
Licania leptostachya	5, 8
Licania majuscula	1, 3, 5, 6
Licania membranacea	5, 8
Licania micrantha	5, 8
Licania pallida	5, 8
Licania robusta	5, 8
Licaria canella	1, 5, 6, 8
Licaria cannella	1, 3, 5, 6, 7, 8
Licaria chrysophylla	5, 8
Licaria crassifolia	5
Licaria guianensis	5, 8
Licaria martiniana	5
Licaria pachycarpa	5, 8
Licaria triandra	5
Lindackeria paludosa	5, 8
Lonchocarpus nicou	5, 7
Lonchocarpus sericeus	5, 8
Loxopterygium sagotii	1, 3, 5, 6, 7
Luehea grandiflora	5
Luehea speciosa	5, 8
Lueheopsis rosea	1, 5, 6
Lueheopsis rugosa	5
Mabea piriri	5
Machaerium nyctitans	5
Machaerium villosum	5
Maclura tinctoria	5, 8
Macoubea guianensis	5, 7, 8
Macrolobium acaciifolium	5, 8
Macrolobium angustifolium	5, 8
Macrolobium bifolium	5, 8
Macrolobium campestre	5, 8
Macrolobium multijugum	5, 8
Macrolobium pendulum	5, 8

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Mahurea palustris	5
Malouetia tamaquarina	5, 8
Manilkara bidentata	1, 2, 3, 4, 5, 6, 7, 8
Manilkara elata	2, 4, 5, 7, 8
Manilkara paraensis	5, 8
Maprounea guianensis	5
Maquira calophylla	5, 8
Maquira guianensis	5, 8
Maquira sclerophylla	2, 5, 8
Martiodendron parviflorum	1, 5, 6, 7, 8
Matayba opaca	5
Maytenus guyanensis	5, 8
Melicoccus pedicellaris	5, 7
Mezilaurus itauba	2, 5, 8
Mezilaurus synandra	5
Miconia mirabilis	5
Miconia tschudyoides	5
Micrandra elata	5, 8
Micrandra rossiana	5, 8
Micropholis acutangula	5, 8
Micropholis egensis	4, 5, 7, 8
Micropholis guyanensis	1, 5, 6, 8
Micropholis melinoniana	2, 4, 5, 8
Micropholis mensalis	5, 8
Micropholis obscura	5
Micropholis trunciflora	5, 8
Micropholis venulosa	5, 7, 8
Micropholis williamii	5, 8
Minquartia guianensis	5, 7, 8
Monopteryx inpae	4, 5
Monteverdia myrsinoides	5, 8
Monteverdia pruinosa	5, 8
Moquilea egleri	5, 8
Moquilea guianensis	5, 8
Moquilea minutiflora	5, 8
Moquilea unguiculata	5, 8
Mora excelsa	1, 3, 5, 6, 7
Mora gonggrijpii	3, 5, 7, 8
Moronobea coccinea	3, 4, 5, 8
Mouriri collocarpa	5, 8
Mouriri crassifolia	5, 8
Mouriri duckeana	5, 8
Mouriri francavillana	5, 8
Mouriri grandiflora	5, 8
Mouriri huberi	5, 8
Mouriri sagotiana	5, 8
Myrcia guianensis	5, 8
Myrciaria floribunda	5, 8
Myroxylon balsamum	5
Naucleopsis oblongifolia	5, 8
Nectandra cissiflora	5, 8
Nectandra cuspidata	5, 8
Nectandra globosa	5, 8
Nectandra lanceolata	5, 8
Neea floribunda	5
Ocotea aciphylla	5, 8
Ocotea amazonica	5, 8
Ocotea argyrophylla	5
Ocotea aurantiodora	5, 8
Ocotea canaliculata	3, 5, 8
Ocotea cernua	5, 8
Ocotea cujumary	5, 8
Ocotea douradensis	5, 8
Ocotea floribunda	3, 5, 7
Ocotea glomerata	1, 3, 5, 6, 7, 8
Ocotea guianensis	1, 5, 6, 7, 8
Ocotea leucoxylon	5, 8
Ocotea oblonga	3, 5
Ocotea percurrens	1, 5, 6
Ocotea petalanthera	5, 7, 8
Ocotea puberula	5, 7, 8
Ocotea splendens	5, 7, 8
Ocotea tomentella	3, 5, 8
Ormosia arborea	5
Ormosia coarctata	5
Ormosia coccinea	1, 3, 5, 6, 7, 8
Ormosia coutinhoi	3, 5, 8
Ormosia discolor	5, 8
Ormosia flava	5, 8
Ormosia nobilis	5, 8
Ormosia paraensis	5, 7, 8
Osteophloeum platyspermum	2, 5, 8
Otoba parvifolia	5
Oxandra asbeckii	5
Pachira aquatica	5, 8
Pachira coriacea	5, 8
Pachira dolichocalyx	5
Pachira flaviflora	5

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Pachira insignis	5, 8
Pachira nervosa	5, 7
Panopsis sessilifolia	5, 8
Parahancornia fasciculata	2, 3, 5, 8
Paramachaerium ormosioides	4, 5
Parinari campestris	1, 3, 5, 6, 7, 8
Parinari excelsa	5, 8
Parinari montana	5, 8
Parinari parvifolia	5
Parinari rodolphii	3, 5, 8
Parinariopsis licaniiflora	5, 8
Parkia decussata	5, 8
Parkia igneiflora	5, 8
Parkia multijuga	2, 5, 8
Parkia nitida	1, 5, 6, 7, 8
Parkia pendula	1, 2, 4, 5, 6, 7, 8
Parkia reticulata	5, 8
Parkia ulei	5, 7, 8
Parkia velutina	5, 8
Peltogyne catingae	5, 8
Peltogyne floribunda	5, 8
Peltogyne lecointei	5, 8
Peltogyne paniculata	1, 5, 6, 8
Peltogyne venosa	1, 3, 5, 6, 7, 8
Pentaclethra macroloba	5, 8
Pera glabrata	5
Perebea guianensis	5, 8
Perebea mollis	5, 8
Perebea rubra	5, 8
Phyllostylon rhamnoides	5
Platonia insignis	1, 3, 4, 5, 6, 7, 8
Platymiscium pinnatum	1, 5, 6, 7, 8
Platymiscium trinitatis	2, 5, 8
Pogonophora schomburgkiana	5, 8
Poraqueiba guianensis	5, 8
Pourouma bicolor	5, 8
Pourouma cecropiifolia	5, 8
Pourouma guianensis	5, 8
Pourouma melinonii	5, 8
Pourouma mollis	5, 8
Pourouma velutina	5, 8
Pouteria ambelaniifolia	5, 8
Pouteria anomala	5, 8
Pouteria bangii	5, 8
Pouteria bilocularis	5, 8
Pouteria caimito	5, 8
Pouteria campanulata	5, 8
Pouteria cladantha	5, 8
Pouteria coriacea	5, 8
Pouteria cuspidata	1, 3, 5, 6, 8
Pouteria decorticans	5, 8
Pouteria egregia	5, 8
Pouteria elegans	5, 8
Pouteria engleri	5, 8
Pouteria eugeniifolia	5, 8
Pouteria flavilatex	5
Pouteria glomerata	5, 8
Pouteria gongrijpii	5, 8
Pouteria guianensis	3, 5, 8
Pouteria hispida	5, 8
Pouteria jariensis	5, 8
Pouteria laevigata	4, 5
Pouteria macrocarpa	5, 8
Pouteria manaosensis	5, 8
Pouteria melanopoda	5, 8
Pouteria nemorosa	5
Pouteria opposita	5
Pouteria platyphylla	5
Pouteria reticulata	5, 8
Pouteria retinervis	5, 8
Pouteria rodriguesiana	4, 5
Pouteria sagotiana	5, 8
Pouteria singularis	5
Pouteria speciosa	3, 5, 8
Pouteria torta	5
Pouteria venosa	5, 8
Pouteria virescens	5, 8
Pradosia cochlearia	5, 8
Pradosia ptychandra	1, 5, 6, 7
Pradosia schomburgkiana	5
Pradosia surinamensis	1, 5, 6, 7, 8
Pradosia verticillata	5, 8
Protium altissimum	1, 3, 5, 6, 8
Protium altsonii	5, 8
Protium apiculatum	5, 8
Protium aracouchini	5, 8
Protium crenatum	5, 8
Protium cuneatum	5, 8

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Protium decandrum	1, 3, 5, 6, 8
Protium giganteum	5, 8
Protium guianense	5, 8
Protium hebetatum	5, 8
Protium heptaphyllum	2, 5, 8
Protium morii	5, 8
Protium nitidifolium	5, 8
Protium opacum	5, 8
Protium pallidum	5, 8
Protium paniculatum	5, 8
Protium pilosum	5, 8
Protium polybotryum	1, 5, 6, 8
Protium robustum	5, 8
Protium sagotianum	5, 7, 8
Protium spruceanum	5, 8
Protium stevensonii	5, 7, 8
Protium strumosum	5, 8
Protium subserratum	5, 8
Protium surinamense	1, 5, 6, 8
Protium tenuifolium	1, 5, 6, 8
Protium trifoliolatum	5, 8
Protium unifoliolatum	5, 8
Pseudolmedia laevis	5
Pseudopiptadenia psilostachya	4, 5, 8
Pseudopiptadenia suaveolens	1, 2, 4, 5, 6, 7
Pterocarpus officinalis	5, 8
Pterocarpus rohrii	2, 3, 5, 8
Pterocarpus santalinoides	5, 8
Qualea coerulea	1, 5, 6, 7, 8
Qualea dinizii	1, 2, 5, 6, 7, 8
Qualea paraensis	2, 5, 8
Qualea rosea	1, 4, 5, 6, 7
Qualea tessmannii	5
Rauvolfia paraensis	5, 8
Rauvolfia pentaphylla	5, 8
Recordoxylon speciosum	4, 5
Rhodostemonodaphne grandis	1, 5, 6
Rhodostemonodaphne morii	5
Roupala montana	2, 5, 8
Ruizterania albiflora	1, 4, 5, 6, 7, 8
Ruizterania cassiquiarensis	5, 8
Sacoglottis cydonioides	5, 7
Sacoglottis guianensis	1, 3, 5, 6, 7, 8
Samanea saman	5, 8
Sapindus saponaria	5
Sapium ciliatum	5, 8
Sapium glandulosum	5, 8
Scleronema micranthum	5, 8
Senegalia bonariensis	5
Senna multijuga	5, 8
Sextonia rubra	1, 2, 3, 4, 5, 6, 7, 8
Simaba guianensis	5, 8
Simaba orinocensis	5, 8
Simarouba amara	1, 2, 3, 4, 5, 6, 7, 8
Sloanea brevipes	5, 8
Sloanea eichleri	5, 8
Sloanea fendleriana	5, 8
Sloanea floribunda	5, 8
Sloanea garckeana	5, 8
Sloanea grandiflora	5, 8
Sloanea guianensis	5, 8
Sloanea laurifolia	5, 8
Sloanea nitida	5, 8
Sloanea obtusifolia	5, 8
Spondias mombin	2, 5, 8
Stenostomum acreanum	5
Sterculia excelsa	2, 5, 8
Sterculia multiovula	5
Sterculia pruriens	1, 3, 5, 6, 7, 8
Sterculia rugosa	3, 5
Sterculia villifera	5, 7
Stryphnodendron adstringens	5
Stryphnodendron guianense	5, 8
Stryphnodendron paniculatum	5, 8
Stryphnodendron polystachyum	5, 7, 8
Stryphnodendron pulcherrimum	5, 8
Swartzia aptera	5, 8
Swartzia arborescens	5, 8
Swartzia benthamiana	3, 5
Swartzia brachyrachis	5, 8
Swartzia cardiosperma	5, 8
Swartzia corrugata	5, 8
Swartzia grandifolia	5, 8
Swartzia guianensis	5, 7
Swartzia laevicarpa	5, 8
Swartzia leiocalycina	3, 5
Swartzia oblanceolata	5
Swartzia panacoco	4, 5

Timber tree species	**References**
Swartzia polyphylla	5, 8
Swartzia recurva	5, 8
Swartzia schomburgkii	5
Swartzia sprucei	3, 5
Swartzia ulei	5, 8
Symphonia globulifera	1, 2, 3, 4, 5, 6, 7, 8
Tabebuia insignis	3, 5, 8
Tachigali chrysophylla	5, 8
Tachigali glauca	2, 5, 8
Tachigali guianensis	3, 5, 7, 8
Tachigali melanocarpa	5, 8
Tachigali melinonii	4, 5, 7, 8
Tachigali micropetala	3, 5, 8
Tachigali paniculata	5, 8
Tachigali paraensis	5, 7, 8
Tachigali richardiana	5
Tachigali vulgaris	5, 8
Talisia carinata	5, 8
Talisia furfuracea	5
Talisia guianensis	5, 8
Talisia longifolia	5, 8
Talisia megaphylla	5, 8
Talisia retusa	5, 8
Talisia squarrosa	3, 5
Tapirira guianensis	1, 2, 5, 6, 8
Tapirira obtusa	5, 8
Tapirira retusa	5, 8
Taralea oppositifolia	5, 8
Terminalia amazonia	1, 2, 3, 5, 6, 8
Terminalia aubletii	5
Terminalia congesta	5, 8
Terminalia dichotoma	1, 3, 5, 6, 7, 8
Terminalia fanshawei	3, 5
Terminalia grandis	2, 5, 8
Terminalia guyanensis	1, 5, 6, 7, 8
Terminalia nitidissima	5
Terminalia oblonga	5
Terminalia oxycarpa	5, 8
Terminalia parvifolia	5, 8
Terminalia tetraphylla	1, 5, 6, 7, 8
Theobroma obovatum	5
Thyrsodium guianense	5, 8
Thyrsodium puberulum	5
Thyrsodium spruceanum	5, 8
Tovomita obovata	5
Trattinnickia burserifolia	1, 2, 5, 6, 7, 8
Trattinnickia demerarae	3, 5, 7, 8
Trattinnickia glaziovii	5, 8
Trattinnickia rhoifolia	1, 3, 5, 6, 7, 8
Trichilia cipo	5, 8
Trichilia elegans	5, 8
Trichilia martiana	5, 8
Trichilia micrantha	5, 8
Trichilia pallida	5, 8
Trichilia pleeana	5, 8
Trichilia quadrijuga	5, 8
Trichilia rubra	5, 8
Trichilia schomburgkii	5, 8
Trichilia septentrionalis	5, 8
Trichilia surinamensis	5, 7
Triplaris weigeltiana	5, 8
Trymatococcus amazonicus	5
Vantanea guianensis	5, 8
Vantanea parviflora	5, 8
Vatairea erythrocarpa	4, 5, 8
Vatairea guianensis	1, 3, 5, 6, 7, 8
Vatairea paraensis	5, 8
Vatairea sericea	5, 8
Vataireopsis speciosa	5, 7, 8
Vataireopsis surinamensis	1, 5, 6
Virola caducifolia	5, 8
Virola calophylla	5, 8
Virola elongata	5, 8
Virola kwatae	4, 5
Virola michelii	1, 3, 4, 5, 6, 7, 8
Virola minutiflora	5, 8
Virola mollissima	5, 8
Virola multicostata	5, 8
Virola multinervia	5, 8
Virola pavonis	5, 8
Virola sebifera	5, 7, 8
Virola surinamensis	1, 2, 3, 4, 5, 6, 7, 8
Virola theiodora	5, 8
Vitex guianensis	5
Vitex stahelii	3, 5
Vitex triflora	5
Vochysia densiflora	5, 7
Vochysia divergens	5, 8

Timber tree species	References
Vochysia guianensis	1, 4, 5, 6, 7, 8
Vochysia lanceolata	5
Vochysia neyratii	4, 5
Vochysia surinamensis	3, 4, 5, 8
Vochysia tetraphylla	3, 5
Vochysia tomentosa	1, 4, 5, 6, 7
Vochysia vismiifolia	5, 8
Vouacapoua americana	1, 4, 5, 6, 7, 8
Xylopia amazonica	5, 8
Xylopia aromatica	5, 8
Xylopia benthamii	5, 8
Xylopia emarginata	5, 8
Xylopia nitida	5, 8
Xylopia pulcherrima	5
Xylopia sericea	5, 8
Zanthoxylum acuminatum	5, 8
Zanthoxylum rhoifolium	5, 8
Zygia cataractae	5, 8
Zygia cauliflora	5, 8
Zygia latifolia	5, 8
Zygia racemosa	4, 5, 7, 8

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Table S1.2. List of commercially relevant NTFP taxa in the Guiana Shield region

NTFP taxon	Main use	References
Ambelania acida	Food	9
Anacardium giganteum	Food	9
Aniba rosiodora	Medicinal	6, 8,
Annona sericea	Food, Medicinal	9
Aspidosperma album	Crafts	6, 9
Aspidosperma araracanga	Crafts	6, 9
Aspidosperma carapanauba	Crafts	6, 9
Aspidosperma cuspa	Crafts	6, 9
Aspidosperma desmanthum	Crafts	6, 9
Aspidosperma discolor	Crafts	6, 9
Aspidosperma excelsum	Crafts	6, 9
Aspidosperma helstonei	Crafts	6, 9
Aspidosperma megalocarpon	Crafts	6, 9
Aspidosperma parvifolium	Crafts	6, 9
Aspidosperma sandwithianum	Crafts	6, 9
Aspidosperma schultesii	Crafts	6, 9
Aspidosperma spp. (84 morphospecies)	Crafts	6, 9
Astrocaryum sciophilum	Food, Medicinal, Crafts	9
Attalea maripa	Food, Medicinal, Crafts	6, 3, 8, 9
Bagassa guianensis	Crafts	9
Bellucia grossularioides	Food, Medicinal	9
Bixa orellana	Paint, Rituals	9
Brosimum guianense	Crafts	9
Brosimum parinarioides	Crafts	8
Brosimum potabile	Crafts	8
Brosimum rubescens	Crafts	6, 8, 9
Brosimum utile	Crafts	6
Byrsonima crassifolia	Medicinal	9
Campomanesia aromatica	Bathing, Medicinal	9
Carapa guianensis	Medicinal	6, 8, 5, 9
Carapa spp. (4 morphospecies)	Medicinal	9
Carapa surinamensis	Medicinal	9
Caryocar nuciferum	Food	6
Caryocar villosum	Food, Crafts	8
Caryodendron amazonicum	Food	8
Casearia arborea	Medicinal, Rituals	9
Cecropia obtusa	Rituals	9
Cecropia peltata	Medicinal, Rituals	9
Cecropia sciadophylla	Rituals	9
Cedrela odorata	Crafts, Medicinal	6, 9
Clathrotropis brachypetala	Medicinal	9
Clusia grandiflora	Crafts	6
Clusia hoffmannseggiana	Crafts	6
Copaifera epunctata	Medicinal	6, 1, 4, 7, 8, 9

NTFP taxon	Main use	References
Copaifera guyanensis	Medicinal	6, 1, 4, 7, 8, 9
Copaifera martii	Medicinal	6, 1, 4, 7, 8, 9
Copaifera pubiflora	Medicinal	6, 1, 4, 7, 8, 9
Copaifera spp. (4 morphospecies)	Medicinal	6, 1, 4, 7, 8, 9
Cordia tetrandra	Food, Medicinal	9
Couma guianensis	Crafts	6, 8,
Couma macrocarpa	Crafts	6
Couratari stellata	Crafts, Rituals	9
Dicorynia guianensis	Crafts	9
Didymopanax morototoni	Crafts, Medicinal	9
Dipteryx odorata	Food, Medicinal, Hair product	6, 8, 9
Duguetia pycnastera	Crafts	5
Endopleura uchi	Food, Medicinal	8
Eperua falcata	Crafts, Rituals	9
Eugenia moschata	Food	8
Eugenia patrisii	Food	9
Euterpe oleracea	Food, Crafts, Rituals	6, 2, 8, 5, 9
Euterpe precatoria	Food, Crafts, Rituals	6, 1, 8, 9
Euterpe spp.	Food, Crafts	9
Ficus insipida	Crafts	6, 9
Ficus nymphaeifolia	Rituals	9
Garcinia macrophylla	Food	8, 9
Garcinia madruno	Food	8
Geissospermum sericeum	Medicinal	9
Genipa americana	Food	6
Goupia glabra	Medicinal	9
Guarea gomma	Medicinal, Rituals	9
Guatteria schomburgkiana	Food, Bathing, Medicinal	9
Gustavia augusta	Medicinal	9
Handroanthus impetiginosus	Medicinal	8
Handroanthus serratifolius	Medicinal	8
Hevea benthamiana	Crafts	6
Hevea guianensis	Crafts	6
Hevea pauciflora	Crafts	6
Hevea spp. (5 morphospecies)	Crafts	6, 8
Himatanthus sucuuba	Medicinal	8
Hirtella paniculata	Bathing, Medicinal	9
Hymenaea courbaril	Food, Medicinal	6, 8
Inga alba	Crafts, Medicinal	8, 9
Inga capitata	Food	8
Inga cayennensis	Food	8
Inga cinnamomea	Food	8
Inga edulis	Food	8
Inga heterophylla	Food	9

NTFP taxon	Main use	References
Inga ingoides	Food	8
Inga laurina	Food	8
Inga macrophylla	Food	8
Inga stipularis	Food	8
Inga virgultosa	Food	9
Jacaranda copaia	Medicinal, Crafts	9
Leonia cymosa	Medicinal	9
Licania membranacea	Medicinal, Rituals	9
Lueheopsis rosea	Rituals	9
Lueheopsis rugosa	Medicinal, Rituals	9
Manicaria saccifera	Crafts	6, 5
Manilkara bidentata	Crafts	6
Manilkara elata	Crafts	6, 8
Maprounea guianensis	Medicinal	9
Mauritia flexuosa	Food, Crafts	6, 3, 8, 5, 9
Miconia lepidota	Bathing, Medicinal	9
Miconia prasina	Bathing, Medicinal	9
Myrciaria dubia	Food	6, 8
Myrciaria floribunda	Bathing, Medicinal	9
Ocotea guianensis	Hair product, Crafts, Medicinal	9
Oenocarpus bacaba	Food	6, 3, 9
Oenocarpus bataua	Food	6, 8
Ormosia amazonica	Crafts	8, 9
Ormosia bolivarensis	Crafts	8, 9
Ormosia coarctata	Crafts	8, 9
Ormosia coccinea	Crafts	8, 9
Ormosia costulata	Crafts	8, 9
Ormosia coutinhoi	Crafts	8, 9
Ormosia discolor	Crafts	8, 9
Ormosia flava	Crafts	8, 9
Ormosia grossa	Crafts	8, 9
Ormosia lignivalvis	Crafts	8, 9
Ormosia macrophylla	Crafts	8, 9
Ormosia melanocarpa	Crafts	8, 9
Ormosia nobilis	Crafts	8, 9
Ormosia paraensis	Crafts	8, 9
Ormosia spp. (38 morphospecies)	Crafts	8, 9
Ormosia stipularis	Crafts	8, 9
Palicourea guianensis	Medicinal, Rituals	8, 9
Parahancornia fasciculata	Food	8
Parinari campestris	Food, Crafts, Rituals	9
Parkia pendula	Medicinal, Rituals	9
Parkia ulei	Crafts	9
Platonia insignis	Food, Crafts, Rituals	8

NTFP taxon	**Main use**	**References**
Poraqueiba guianensis	Food	8
Poraqueiba sericea	Food	6, 8
Pouteria caimito	Food	8
Pouteria glomerata	Food	8
Protium altissimum	Crafts, Rituals	9
Protium heptaphyllum	Crafts, Rituals	9
Protium stevensonii	Crafts, Rituals	9
Pseudopiptadenia suaveolens	Medicinal, Rituals	9
Ptychopetalum olacoides	Medicinal	8
Quararibea guianensis	Crafts, Rituals	9
Quiina guianensis	Crafts	5
Simaba orinocensis	Rituals	9
Siparuna guianensis	Medicinal, Rituals	9
Sloanea grandiflora	Rituals	9
Spondias mombin	Food	6, 8
Spondias spp.	Food	8
Symphonia globulifera	Crafts, Medicinal, Rituals	9
Tabebuia insignis	Medicinal	5
Tabernaemontana siphilitica	Medicinal, Rituals	9
Tabernaemontana undulata	Medicinal, Rituals	9
Tachigali melinonii	Medicinal	9
Terminalia amazonia	Bathing, Medicinal	9
Theobroma cacao	Food, Rituals	8
Virola michelii	Medicinal	8
Virola sebifera	Medicinal	6
Virola surinamensis	Medicinal	6
Vismia cayennensis	Bathing, Medicinal	9
Vismia guianensis	Medicinal	9
Vismia japurensis	Medicinal	9
Vismia latifolia	Medicinal	9
Vismia macrophylla	Medicinal	9
Vouarana guianensis	Rituals	9
Zygia latifolia	Medicinal, Rituals	9
Zygia racemosa	Medicinal	9

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Table S3.1.3. Summary of the 283 1-ha plots used in this paper. AGC = Aboveground carbon stock estimates sensu method Sullivan et al. (2017) (Mg ha^{-1}), Timber = commercially relevant timber stock (m^3 ha^{-1}), NTFPs = commercially relevant NTFP species abundance (# stems ha^{-1}), Spp = woody species richness (# species ha^{-1}). For visualization, all numbers have been truncated to two decimal points.

Table S3.1.3. has been omitted to save paper. It can be accessed at the published version of this chapter (see the beginning of this chapter for a DOI and QR code).

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Annex S3.2: Supplementary results

Guiana Shield linear relationships across environmental covariables

Table S3.2.1. Detailed results for the bivariate linear models of the three ecosystem services of aboveground carbon stock, timber stock and NTFP abundance predicted by woody species richness across the Guiana Shield dataset (n = 151). Showing model coefficients with its standard error (SE), the t-test value, the p -value of the t-test (H_0: b = 0), and the R^2 of the total model.

Model	Coefficient	SE	t-value	p-value	R^2
Model AGC ~ Spp					
Intercept	163.68276	9.86965	16.584	<2.00E-16	
Species richness	0.39147	0.07381	5.304	4.03E-07	
					0.1588
Model Timber ~ Spp					
Intercept	48.58106	13.33746	3.642	0.000372	
Species richness	0.57467	0.09974	5.761	4.62E-08	
					0.1822
Model NTFP ~ Spp					
Intercept	104.80933	12.59899	8.319	5.19E-14	
Species richness	-0.01695	0.09422	-0.18	0.857	
					0.0002172

Table S3.2.2. Detailed results for the multivariate linear models of the three ecosystem services of aboveground carbon stock, timber stock and NTFP abundance predicted by woody species richness and either biogeographical subregion or forest types across the Guiana Shield dataset (n = 151, 1-ha plots). Showing model coefficients with its standard error (SE), the t-test value, the p -value of the t-test (H_0: b = 0), and the R^2 of the total model. Forest types included were: TF = terra firme forests (n = 130) and PZ = white sand forests (n = 21). Biogeographical subregions included were: SGS = forests of the Southern Guiana Shield (n = 63), NWGS = forests of the North-Western Guiana Shield (n = 21), NPS = forests of the Northern Pleistocene sands (n = 56) and SWPS = forests of the South-Western Pleistocene sands in the upper Rio Negro region (n = 11).

Model	Coefficient estimate	Coefficient SE	t-value	t-test p-value	Rel. contr. R^2	R^2
Carbon stock						
Species richness	0.34971	0.07527	4.646	7.48E-06	0.1286891	
Biogeographical subregion					0.2046719	
SGS (intercept)	163.91438	12.16237	13.477	<2.00E-16		
NWGS	-23.26744	11.63995	-1.999	0.047472		
NPS	28.46651	7.81838	3.641	0.000376		
SWPS	-32.6318	13.52743	-2.412	0.017095		

Model	Coefficient estimate	Coefficient SE	t-value	t-test p-value	Rel. contr. R^2	R^2
						0.3334
Carbon stock						
Species richness	0.54094	0.08191	6.604	6.74E-10	0.19310891	
Forest type					0.03514065	
TF (Intercept)	139.12729	11.62969	11.963	<2.00E-16		
PZ	43.36936	11.88436	3.649	0.000364		
						0.2282
Timber stock						
Species richness	0.4159	0.1041	3.995	1.02E-04	0.1282011	
Biogeographical subregion					0.1930405	
SGS (intercept)	89.6015	16.8199	5.327	3.70E-07		
NWGS	-47.7668	16.0974	-2.967	0.003511		
NPS	-20.6756	10.8124	-1.912	0.057807		
SWPS	-96.5015	18.7077	-5.158	7.99E-07		
						0.3212
Timber stock						
Species richness	0.4474	0.1137	3.936	0.000127	0.13250222	
Forest type					0.07649242	
TF (Intercept)	69.4906	16.1366	4.306	3.01E-05		
PZ	-36.93	16.49	-2.24	0.026612		
						0.209
NTFP abundance						
Species richness	-0.10557	0.09929	-1.063	0.2894	0.003384304	
Biogeographical subregion					0.150451398	
SGS (intercept)	125.51139	16.04461	7.82E+00	9.54E-13		
NWGS	-29.57142	15.35544	-1.926	0.0561		
NPS	1.22552	10.31402	1.19E-01	0.9056		
SWPS	-83.20705	17.84541	-4.663	6.98E-06		
						0.1538
NTFP abundance						
Species richness	-0.06197	0.10892	-0.569	0.57	0.001196909	
Forest type					0.003614758	
TF (Intercept)	112.20508	15.46363	7.256	2.08E-11		
PZ	-13.06222	15.80226	-0.827	0.41		
						0.004812

Table S3.2.3. Detailed results for the optimized linear models of the three ecosystem services of carbon stock, timber stock and NTFP abundance predicted by species richness and environmental covariables across the Guiana Shield dataset (n = 151, 1-ha plots). Originally included predictors were species richness, forest type, biogeographical subregion, latitude and longitude. Forest types included were: TF = terra firme forests (n = 130) and PZ = white sand forests (n = 21). Biogeographical subregions included were: SGS = forests of the Southern Guiana Shield (n = 63), NWGS = forests of the North-Western Guiana Shield (n = 21), NPS = forests of the Northern Pleistocene sands (n = 56) and SWPS = forests of the South-Western Pleistocene sands in the upper Rio Negro region (n = 11). Showing model coefficients (b) with their standard error (SE), t-test value, p -value of the t-test (H_0: b = 0) and relative contribution to total R^2; and total model R^2.

Model	Coefficient b	Coefficient SE	t-value	t-test p-value	Rel. contr. R^2	R^2
Carbon stock						
Intercept (TF & SGS)	142.04436	14.18498	10.014	<2.00E-16		
Species richness	0.49916	0.09061	5.509	1.60E-07	0.15135157	
Forest type					0.02360114	
PZ	36.98588	13.10284	2.823	0.00543		
Biogeographical subregion					0.1931324	
NWGS	-12.57085	11.98652	-1.049	2.96E-01		
NPS	22.14163	7.96011	2.782	0.00613		
SWPS	-45.50795	13.98085	-3.255	0.00141		
						0.3681
Timber stock						
Intercept (TF & SGS)	111.4114	19.8741	5.606	1.01E-07		
Species richness	0.2668	0.127	2.102	0.037294	0.09360782	
Forest type					0.06473521	
PZ	-36.8843	18.3579	-2.009	0.046375		
Biogeographical subregion					0.18128327	
NWGS	-58.434	16.7939	-3.479	0.000664		
NPS	-14.3681	11.1526	-1.288	0.199687		
SWPS	-83.6607	19.5881	-4.271	3.50E-05		
						0.3396
NTFP abundance						
Biogeographical subregion					0.1473	
SGS (intercept)	110.063	6.809	16.164	<2.00E-16		
NWGS	-22.016	13.618	-1.617	0.108		
NPS	4.222	9.926	0.425	6.71E-01		
SWPS	-80.427	17.661	-4.554	1.10E-05		
						0.1473

Table S3.2.4. Detailed results for the bivariate linear models of the three ecosystem services of aboveground carbon stock (AGB), timber stock (timber) and NTFP abundance (NTFP) predicted by woody species richness, aggregated and separate per biogeographical subregion, across the Guiana Shield dataset (n = 151). Showing model coefficients with its standard error (SE), the t-test value, the p -value of the t-test (H_0: b = 0), and the R^2 of the total model.

Model - subset	Coefficient	SE	t-value	p-value	R^2
Model AGC ~ Spp					
Aggregated (n = 151)					
Intercept	163.68276	9.86965	16.584	<2.00E-16	
Species richness	0.39147	0.07381	5.304	4.03E-07	
					0.1588
SGS (n = 63)					
Intercept	135.3323	18.7655	7.212	1.00E-09	
Species richness	0.545	0.1246	4.375	4.82E-05	
					0.2389
NWGS (n = 21)					
Intercept	33.5981	48.7157	0.69	0.4987	
Species richness	1.7816	0.6427	2.772	1.21E-02	
					0.2879
NPS (n = 56)					
	202.9563	14.1427	14.351	<2e-16	
	0.26	0.1071	2.427	0.0186	
					0.09835
SWPS (n = 11)					
	153.2535	32.0558	4.781	0.001	
	0.1666	0.255	0.653	0.53	
					0.04528
Model Timber ~ Spp					
Aggregated (n = 151)					
Intercept	48.58106	13.33746	3.642	0.000372	
Species richness	0.57467	0.09974	5.761	4.62E-08	
					0.1822
SGS (n = 63)					
Intercept	107.871	34.4695	3.129	0.00269	
Species richness	0.291	0.2288	1.272	0.20822	
					0.02584
NWGS (n = 21)					
Intercept	22.0379	62.3417	0.354	0.728	
Species richness	0.6807	0.8225	0.828	0.418	
					0.03479
NPS (n = 56)					
	56.876	15.182	3.746	0.000438	
	0.518	0.115	4.504	3.61E-05	
					0.2731

Model - subset	Coefficient	SE	t-value	p-value	R^2
SWPS (n = 11)					
	77.8414	43.6885	1.782	0.108	
	-0.2903	0.3476	-0.835	0.425	
					0.07194
Model NTFP ~ Spp					
Aggregated (n = 151)					
Intercept	104.80933	12.59899	8.319	5.19E-14	
Species richness	-0.01695	0.09422	-0.18	0.857	
					0.0002172
SGS (n = 63)					
Intercept	102.62274	24.51845	4.186	9.28E-05	
Species richness	0.05085	0.16275	0.312	0.756	
					0.001598
NWGS (n = 21)					
Intercept	82.43355	42.10075	1.958	0.0651	
Species richness	0.07509	0.55546	0.135	0.8939	
					0.000961
NPS (n = 56)					
	136.5336	21.0638	6.482	2.85E-08	
	-0.1886	0.1596	-1.182	0.242	
					0.02522
SWPS (n = 11)					
	18.05263	15.1741	1.19	0.265	
	0.09653	0.12072	0.8	0.445	
					0.06633

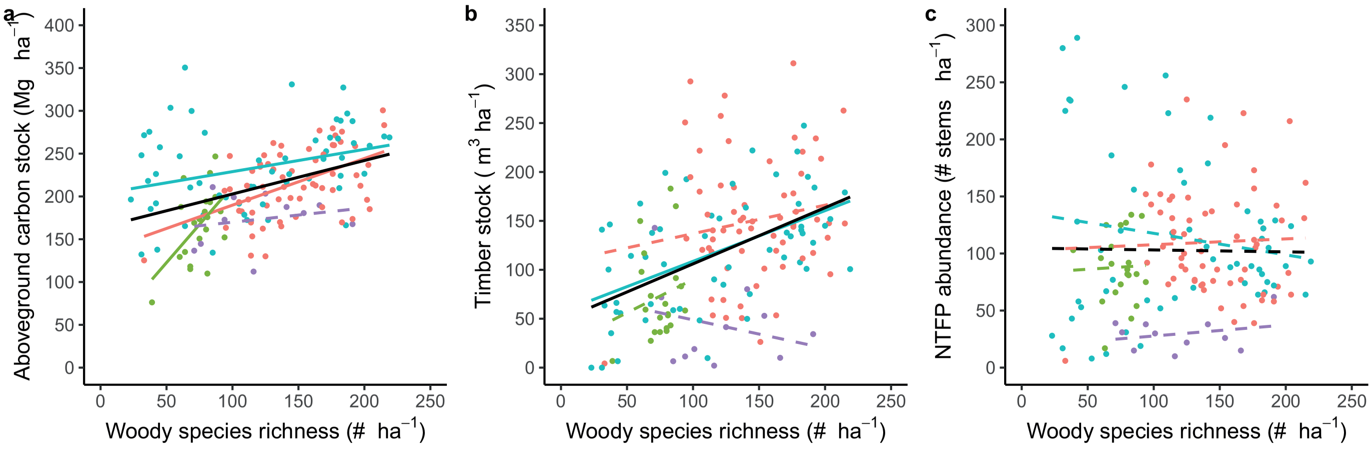

Figure S3.2.1. Visualisation of linear bivariate relationships between carbon stock and species richness (panel a), between timber stock and species richness (panel b) and between NTFP abundance and species richness (panel c) for each of the four subregions of the Guiana Shield separately (different colours), and aggregated across all subregions (black line). Colours according to the subregion of the Guiana Shield: Forests of the Southern Guiana Shield (SGS, red, n = 63), Forests of the North-Western Guiana Shield (NWGS, green, n = 21), Forests of the Northern Pleistocene sands (NPS, turquoise, n = 56) and Forests of the South-Western Pleistocene sands in the upper Rio Negro region (SWPS, purple, n = 11). Solid lines indicate significant relationships, $p < 0.05$, and dashed lines non-significant relationships. Model details included in Table S3.2.4.

Table S3.2.5. Analysis of variance F-tests for aboveground carbon stock, timber stock, NTFP abundance and woody species richness across ~ biogeographical subregions in the Guiana Shield dataset (4 subregions, n = 151).

Model	F-statistic	Df1	Df2	p-value	Multiple R-squared
Carbon stock ~ Biogeographical subregion	15.03	3	147	1.38E-08	0.2348
Timber stock ~ Biogeographical subregion	16.08	3	147	4.326e-09	0.247
NTFP abundance ~ Biogeographical subregion	8.463	3	147	3.177e-05	0.1473
Species richness ~ Biogeographical subregion	14.0	3	147	4.467e-08	0.2222

Table S3.2.6. Summary of post-hoc Tukey contrasts of aboveground carbon stock, timber stock, NTFP abundance and woody species richness across biogeographical subregions in the Guiana Shield dataset (4 subregions, n = 151). Simultaneous Tests for General Linear Hypotheses. Showing adjusted p values of single-step method.

Linear Hypothesis	Estimate	SE	t-value	Adjusted p-value
Carbon stock ~ Biogeographical subregion				
H_0: NWGS - SGS = 0	-48.296	11.017	-4.384	<0.001
H_0: NPS - SGS = 0	18.539	8.03	2.309	0.095
H_0: SWPS - SGS = 0	-41.841	14.288	-2.928	0.0192
H_0: NPS - NWGS = 0	66.836	11.188	5.974	<0.001
H_0: SWPS - NWGS = 0	6.456	16.274	0.397	0.9777
H_0: SWPS - NPS= 0	-60.38	14.42	-4.187	<0.001
Timber stock ~ Biogeographical subregion				
H_0: NWGS - SGS = 0	-77.53	14.98	-5.176	<0.001
H_0: NPS - SGS = 0	-32.48	10.92	-2.975	0.01696
H_0: SWPS - SGS = 0	-107.45	19.42	-5.532	<0.001
H_0: NPS - NWGS = 0	45.05	15.21	2.962	0.01698
H_0: SWPS - NWGS = 0	-29.92	22.12	-1.352	0.51838
NTFP abundance ~ Biogeographical subregion				
H_0: NWGS - SGS = 0	-22.016	13.618	-1.617	0.3598
H_0: NPS - SGS = 0	4.222	9.926	0.425	0.9727
H_0: SWPS - SGS = 0	-80.427	17.661	-4.554	<0.001
H_0: NPS - NWGS = 0	26.238	13.829	1.897	0.2232
H_0: SWPS - NWGS = 0	-58.411	20.115	-2.904	0.0201
Species richness ~ Biogeographical subregion				
H_0: NWGS - SGS = 0	-71.571	11.307	-6.33	<0.001
H_0: NPS - SGS = 0	-28.387	8.242	-3.444	0.00392
H_0: SWPS - SGS = 0	-26.333	14.664	-1.796	0.26819
H_0: NPS - NWGS = 0	43.185	11.483	3.761	0.00118
H_0: SWPS - NWGS = 0	45.238	16.702	2.709	0.03503

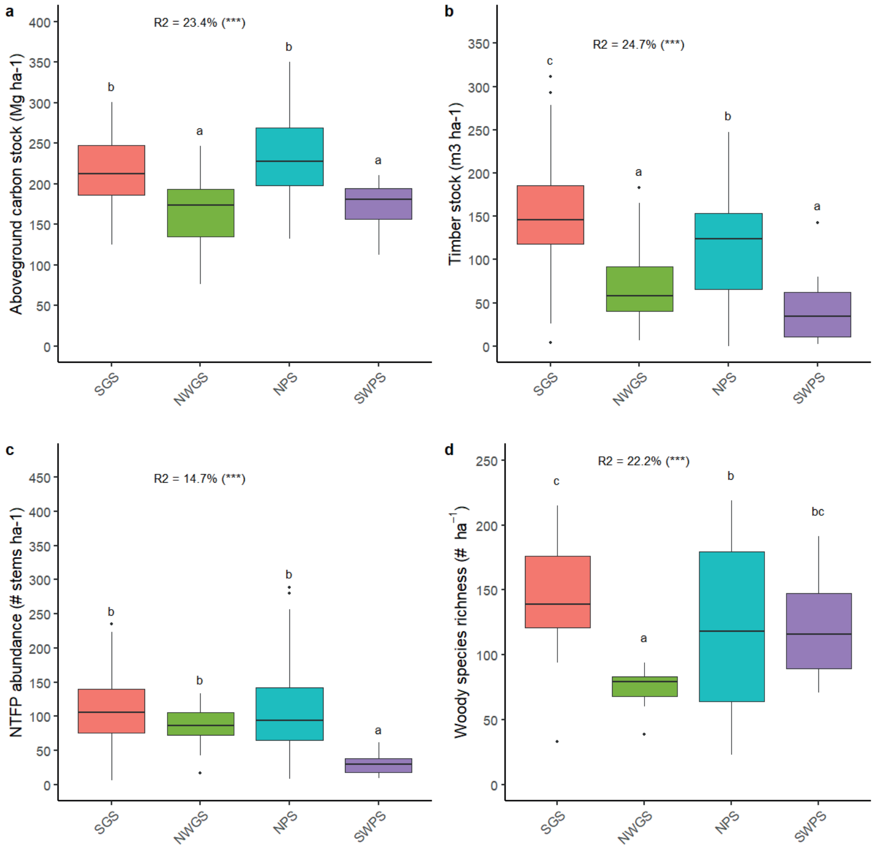

Figure S3.2.2. Box plots of mean aboveground carbon stock (Panel a), timber stock (Panel b), NTFP abundance (Panel c) and species richness (Panel d), across four subregions of the Guiana Shield. R2 is given, and the p-value rank of the F-test is given between parentheses. P-value ranks: $p < 0.001$ (***), $p < 0.01$ (**), $p < 0.05$ (*), $p \geq 0.05$ (ns). Significance differences between the means on the basis of Post-hoc Tukey Contrasts are indicated by unique letter combinations. Subregion: Forests of the Southern Guiana Shield (SGS, red, n = 63), Forests of the North-Western Guiana Shield (NWGS, green, n = 21), Forests of the Northern Pleistocene sands (NPS, turquoise, n = 56) and Forests of the South-Western Pleistocene sands (SWPS, purple, n = 11). F-test values and Tukey contrasts are included in Tables S3.2.5-S3.2.6.

Table S3.2.7. Detailed results for the bivariate linear models of the three ecosystem services of aboveground carbon stock, timber stock and NTFP abundance predicted by woody species richness, aggregated and separate per forest type, across the Guiana Shield dataset (n = 151). Showing model coefficients with its standard error (SE), the t-test value, the p -value of the t-test (H_0: b = 0), and the R^2 of the total model.

Model - subset	Coefficient	SE	t-value	p-value	R^2
Model AGC ~ Spp					
Aggregated (n = 151)					
Intercept	163.68276	9.86965	16.584	<2.00E-16	
Species richness	0.39147	0.07381	5.304	4.03E-07	
					0.1588
TF (n = 130)					
Intercept	127.51249	10.78668	11.821	<2.00E-16	
Species richness	0.6276	0.07634	8.221	1.94E-13	
					0.3456
PZ (n = 21)					
Intercept	238.4232	26.4577	9.011	2.74E-08	
Species richness	-0.3688	0.3756	-0.982	0.339	
					0.04829
Model Timber ~ Spp					
Aggregated (n = 151)					
Intercept	48.58106	13.33746	3.642	0.000372	
Species richness	0.57467	0.09974	5.761	4.62E-08	
					0.1822
TF (n = 130)					
Intercept	58.2685	16.6812	3.493	0.000656	
Species richness	0.5311	0.1181	4.499	1.51E-05	
					0.1365
PZ (n = 21)					
Intercept	86.5963	25.0805	3.453	0.00267	
Species richness	-0.4316	0.3561	-1.212	0.24035	
					0.07177
Model NTFP ~ Spp					
Aggregated (n = 151)					
Intercept	104.80933	12.59899	8.319	5.19E-14	
Species richness	-0.01695	0.09422	-0.18	8.57E-01	
					0.0002172
TF (n = 131)					
Intercept	96.25597	13.42427	7.17	5.32E-11	
Species richness	0.05704	0.095	0.6	5.49E-01	
					0.002808
PZ (n = 21)					
Intercept	175.9396	40.7178	4.321	0.000368	
Species richness	-1.3112	0.5781	-2.27E+00	0.035165	
					0.2131

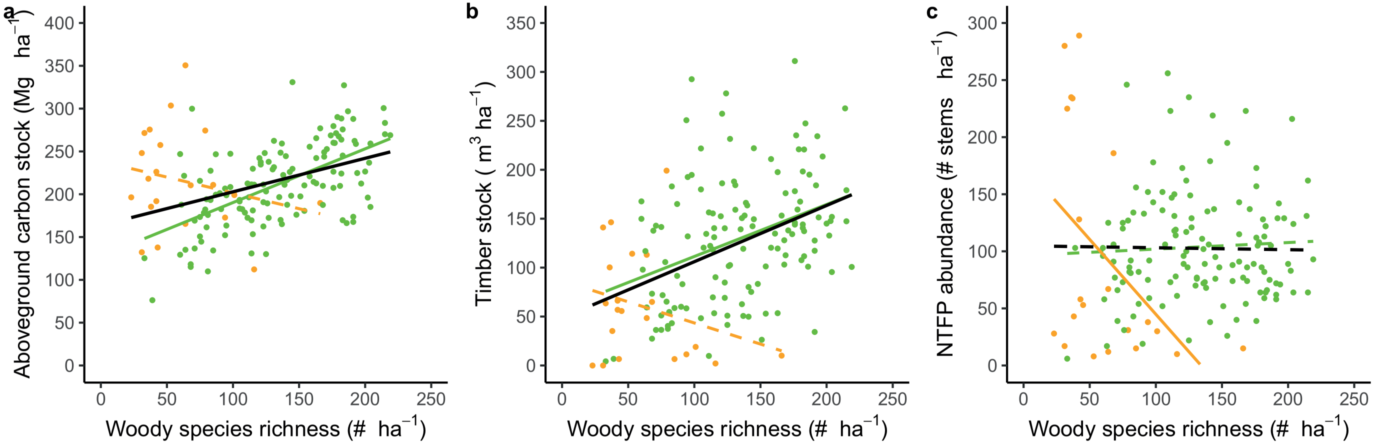

Figure S3.2.3. Visualisation of linear bivariate relationships between ecosystem services and species richness for different forest types and across all forest types for 151 1-ha tropical forest plots of the Guiana Shield. Showing relationships between carbon stock and species richness (panel a), timber stock and species richness (panel b), and NTFP abundance and species richness (panel c). Relationships across all forest types (aggregated): black lines; relationships for terra firme forests alone (TF, n = 130): green lines; relationships for white sand forests alone: orange lines (PZ, n = 21). Here, solid lines for $p < 0.05$ and dashed lines for $p \geq 0.05$. Forest plots coloured to forest types: terra firme forests: green; white sand forests: orange. Model details included in Table S3.2.7.

Table S3.2.8. Analysis of variance F-tests for aboveground carbon stock, timber stock, NTFP abundance and woody species richness across forest types in the Guiana Shield dataset (2 forest types, n = 151).

Model	**F-statistic**	**Df1**	**Df2**	**p-value**	**Multiple R-squared**
Carbon stock ~ Forest type	0.125	1	149	0.7242	0.0008381
Timber stock ~ Forest type	21.52	1	149	7.622e-06	0.1262
NTFP abundance ~ Forest type	0.3937	1	149	0.5313	0.002635
Species richness ~ Forest type	49.67	1	149	6.287e-11	0.25

Table S3.2.9. Summary of post-hoc Tukey contrasts of aboveground carbon stock, timber stock, NTFP abundance and woody species richness across forest types in the Guiana Shield dataset (2 forest types, n = 151). Simultaneous Tests for General Linear Hypotheses. Showing adjusted p values of single-step method.

Linear Hypothesis	**Estimate**	**SE**	**t-value**	**Adjusted p-value**
Carbon stock ~ Forest type				
H_0: PZ - TF = 0	4.126	11.671	0.354	0.724
Timber stock ~ Forest type				
H_0: PZ - TF = 0	-69.39	14.96	-4.638	7.62E-06
NTFP abundance ~ Forest type				
H_0: PZ - TF = 0	-8.567	13.654	-0.627	5.31E-01
Species richness ~ Forest type				
H_0: PZ - TF = 0	-72.55	10.29	-7.048	6.29E-11

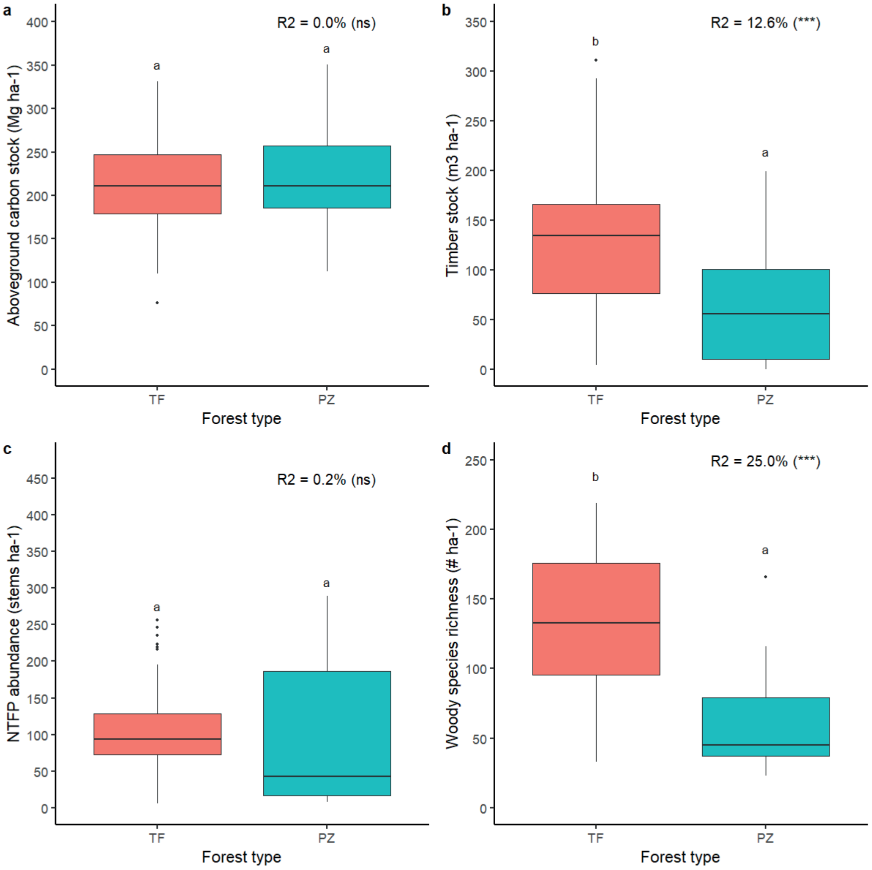

Figure S3.2.4. Box plots of mean aboveground carbon stock (Panel a), mean timber stock (Panel b), mean NTFP abundance (Panel c) and mean woody species richness (Panel d) per forest type across the Guiana Shield dataset (n = 151). R^2 is given, and the p-value rank of the F-test is given between parentheses. P-value ranks: $p < 0.001$ (***), $p < 0.01$ (**), $p < 0.05$ (*), $p \geq 0.05$ (ns). Significance differences between the means on the basis of Post-hoc Tukey Contrasts are indicated by unique letter combinations. Forest types were: TF = terra firme forests (n = 130) and PZ = white sand forests (n = 21). F-test values and Tukey contrasts are included in Tables S3.2.8-3.2.9.

Amazonia linear relationships across environmental covariables

Table S3.2.10. Detailed results for the bivariate linear models of the three ecosystem services of aboveground carbon stock, timber stock and NTFP abundance predicted by woody species richness across the Amazonia dataset (n = 283). Showing model coefficients with its standard error (SE), the t-test value, the p -value of the t-test (H_0: $b = 0$), and the R^2 of the total model.

Model	Coefficient	SE	t-value	p-value	R^2
Carbon stock					
Intercept	176.390492	8.679143	20.323	<2e-16	
Species richness	-0.007433	0.056021	-0.133	0.8950	
					6.264e-05

Table S3.2.11. Detailed results for the optimized linear models of aboveground carbon stock predicted by woody species richness and environmental covariables across the Amazonia dataset (n = 283). Originally included predictors were species richness, biogeographical region, forest type, latitude and longitude. Abbreviations are: GS = Guiana Shield, BS = Brazilian Shield, WAN = North-western Amazonia, WAS = South-western Amazonia, CA = Central Amazonia and EA = East Amazonia; TF = terra firme forests and PZ = white sand forests. Showing model coefficients (b) with their standard error (SE), t-test value, p -value of the t-test (H_0: $b = 0$) and relative contribution to total R^2; and total model R^2.

Model	Coefficient estimate	Coefficient SE	t-value	t-test p-value	Rel. contr. R^2	R^2
Carbon stock						
Intercept (GS & TF)	160.76682	7.70549	20.864	<2.00E-16		
Species richness	0.36773	0.05252	7.002	1.93E-11	0.03372553	
Biogeographical region					0.54889001	
BS	-98.00679	13.18136	-7.435	1.33E-12		
WAN	-119.64254	10.0467	-11.909	<2.00E-16		
WAS	-97.00299	6.18059	-15.695	<2.00E-16		
CA	-102.37756	10.52598	-9.726	<2.00E-16		
EA	-52.08941	10.30015	-5.057	7.78E-07		
Forest type					0.01710433	
PZ	29.33733	9.04465	3.244	0.00133		
						0.5997

Table S3.2.12. Detailed results for the multivariate linear models of aboveground carbon stock predicted by woody species richness and either biogeographical region or forest types across the Amazonia dataset (n = 283). Showing model coefficients with its standard error (SE), the t-test value, the p -value of the t-test (H_0: b = 0), and the R^2 of the total model. Abbreviations are: GS = Guiana Shield, BS = Brazilian Shield, WAN = North-western Amazonia, WAS = South-western Amazonia, CA = Central Amazonia and EA = East Amazonia; TF = terra firme forests and PZ = white sand forests.

Model	Coefficient estimate	Coefficient SE	t-value	t-test p-value	Rel. contr. R^2	R^2
Carbon stock						
Species richness	0.28893	0.04736	6.101	3.55E-09	0.02805688	
Biogeographical region					0.55634896	
GS (intercept)	174.65751	6.51541	26.807	<2.00E-16		
BS	-104.44702	13.25382	-7.881	7.57E-14		
WAN	-113.49069	10.03478	-11.31	<2.00E-16		
WAS	-100.29658	6.20088	-16.175	<2.00E-16		
CA	-96.79167	10.56174	-9.164	<2.00E-16		
EA	-54.54438	10.44798	-5.221	3.51E-07		
						0.5844
Carbon stock						
Species richness	0.06036	0.06063	0.996	0.32033	0.001754594	
Forest type					0.024563278	
TF (Intercept)	163.46102	9.78535	16.705	<2.00E-16		
PZ	36.24848	13.19202	2.748	0.00639		
						0.02632

Table S3.2.13. Detailed results for the bivariate linear models of aboveground carbon stock predicted by woody species richness, aggregated and separate per biogeographical region and per forest type, across Amazonia dataset (n = 283). Showing model coefficients with its standard error (SE), the t-test value, the p -value of the t-test (H_0: b = 0), and the R^2 of the total model.

Model - subset	Coefficient	SE	t-value	p-value	R^2
Model AGC ~ Spp					
Aggregated (n = 283)					
Intercept	176.390492	8.679143	20.323	<2e-16	
Species richness	-0.007433	0.056021	-0.133	8.95E-01	
					6.264e-05
GS (n = 165)					
Intercept	164.22352	9.11304	18.021	<2.00E-16	
Species richness	0.37436	0.06875	5.445	1.87E-07	
					0.1539
BS (n = 9)					
Intercept	51.6467	15.7236	3.285	0.0134	
Species richness	0.4853	0.1536	3.16	0.0159	
					0.5879
WAN (n = 21)					
Intercept	98.36182	9.52782	10.324	3.14E-09	
Species richness	0.11902	0.04188	2.842	0.0104	
					0.2983
WAS (n = 51)					
Intercept	111.4714	10.75578	10.364	6.06E-14	
Species richness	0.013	0.07668	0.169	0.866	
					0.0005858
CA (n = 22)					
Intercept	138.20344	34.51495	4.004	0.000697	
Species richness	0.04483	0.13768	0.326	0.748104	
					0.7481
EA (n = 15)					
Intercept	47.2778	44.5883	1.06	0.3083	
Species richness	0.7908	0.3022	2.616	0.0213	
					0.3449
TF (n = 257)					
Intercept	161.24536	9.87748	16.325	<2e-16	
Species richness	0.07515	0.06133	1.225	0.222	
					0.005853
PZ (n = 26)					
Intercept	227.1358	24.4714	9.282	2.06E-09	
Species richness	-0.3878	0.3499	-1.108	0.279	
					0.0487

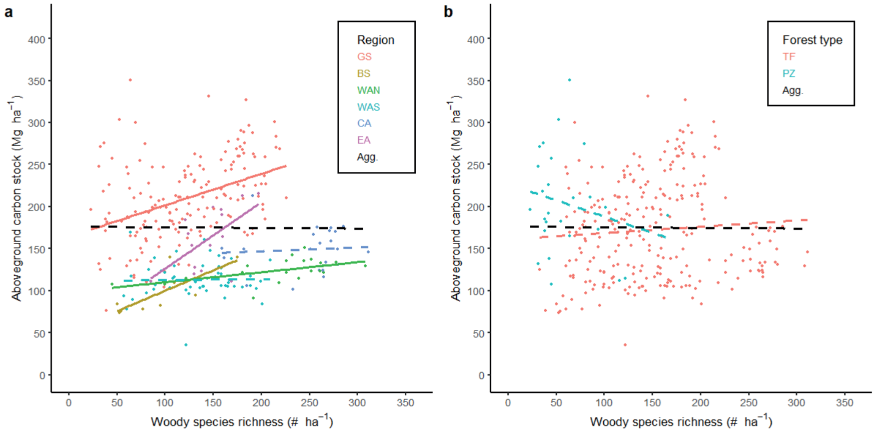

Figure S3.2.5. Visualisation of linear bivariate relationships between ecosystem services and species richness for different biogeographical regions (Panel a), forest types (Panel b) and aggregated ("Agg.", black line) across 283 1-ha Amazonian lowland tropical forest plots. Solid lines relationship $p < 0.05$ and dashed lines relationship $p \geq 0.05$. Abbreviations for regions: GS = Guiana Shield (n = 165), BS = Brazilian Shield (n = 9), WAN = North-western Amazonia (n = 21), WAS = South-western Amazonia (n = 51), CA = Central Amazonia (n = 22) and EA = East Amazonia (n = 15); for forest types: TF = terra firme forests (n = 257) and PZ = white sand forests (n = 26). Model details included in Table S3.2.13

Table S3.2.14. Analysis of variance F-tests for aboveground carbon stock and woody species richness across biogeographical regions and across forest types in the Amazonia dataset (6 regions, 5 forest types, n = 283).

Model	**F-statistic**	**Df1**	**Df2**	**p-value**	**Multiple R-squared**
Carbon stock ~ Region	62.06	5	277	< 2.2e-16	0.5284
Species richness ~ Region	38.16	5	277	< 2.2e-16	0.4078
Carbon stock ~ Forest type	6.577	1	281	0.01085	0.02287
Species richness ~ Forest type	55.77	1	281	1.032e-12	0.1656

Table S3.2.15. Summary of post-hoc Tukey contrasts of aboveground carbon stock and woody species richness across biogeographical regions and across forest types in the Amazonia dataset (6 regions, 5 forest types, n = 283). Showing adjusted p values of single-step method.

Linear Hypothesis	Estimate	SE	t-value	Adjusted p-value
Carbon stock ~ Region				
H0: BS - GS == 0	-112.415	14.025	-8.015	<0.001
H0: WAN - GS == 0	-85.53	9.493	-9.01	<0.001
H0: WAS - GS == 0	-9.67E+01	6.564	-14.735	<0.001
H0: CA - GS == 0	-60.661	9.3	-6.523	<0.001
H0: EA - GS == 0	-4.79E+01	11.05	-4.335	<0.001
H0: WAN - BS == 0	2.69E+01	16.324	1.647	0.54161
H0: WAS - BS == 0	1.57E+01	14.814	1.059	0.88549
H0: CA - BS == 0	51.754	16.212	3.192	0.01739
H0: EA - BS == 0	64.516	17.276	3.734	0.00269
H0: WAS - WAN == 0	-11.196	10.624	-1.054	0.88759
H0: CA - WAN == 0	24.869	12.5	1.99	0.32673
H0: EA - WAN == 0	37.631	13.851	2.717	0.06731
H0: CA - WAS == 0	36.065	10.451	3.451	0.00742
H0: EA - WAS == 0	48.827	12.035	4.057	<0.001
H0: EA - CA == 0	12.762	13.72	0.93	0.93085
Species richness ~ Region				
H0: BS - GS == 0	-27.578	16.734	-1.648	0.541
H0: WAN - GS == 0	96.771	11.326	8.544	<0.001
H0: WAS - GS == 0	12.357	7.832	1.578	0.588
H0: CA - GS == 0	125.048	11.096	11.27	<0.001
H0: EA - GS == 0	23	13.184	1.745	0.477
H0: WAN - BS == 0	124.349	19.477	6.384	<0.001
H0: WAS - BS == 0	39.935	17.675	2.259	0.196
H0: CA - BS == 0	152.626	19.344	7.89	<0.001
H0: EA - BS == 0	50.578	20.612	2.454	0.129
H0: WAS - WAN == 0	-84.415	12.675	-6.66	<0.001
H0: CA - WAN == 0	28.277	14.914	1.896	0.381
H0: EA - WAN == 0	-73.771	16.527	-4.464	<0.001
H0: CA - WAS == 0	112.692	12.47	9.037	<0.001
H0: EA - WAS == 0	10.643	14.359	0.741	0.973
H0: EA - CA == 0	-102.048	16.369	-6.234	<0.001
Carbon stock ~ Forest type				
H0: PZ - TF == 0	30.9	12.05	2.565	0.0108
Species richness ~ Forest type				
H0: PZ - TF == 0	-88.55	11.86	-7.468	1.03E-12

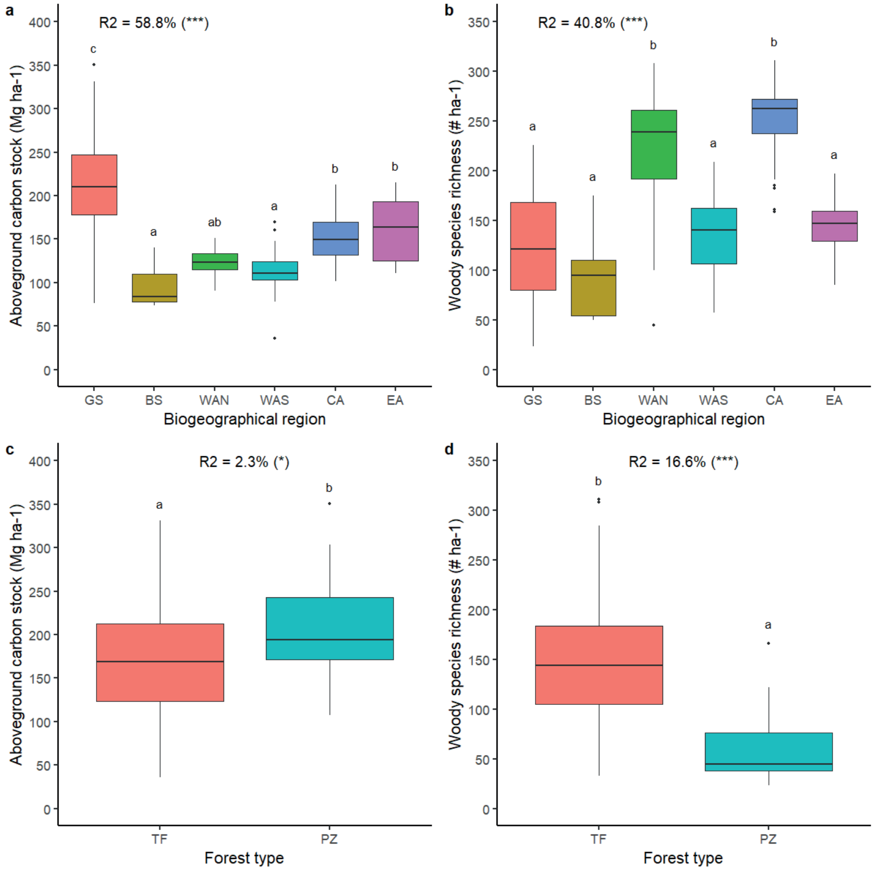

Figure S3.2.6. Box plots of aboveground carbon stock and woody species richness values per biogeographical region (Panels a and b) and per forest type (Panels c and d) across the Amazonia dataset (n = 283). R2 is given, and the p-value rank of the F-test is given between parentheses. P-value ranks: $p < 0.001$ (***), $p < 0.01$ (**), $p < 0.05$ (*), $p \geq 0.05$ (ns). Significance differences between the means on the basis of Post-hoc Tukey Contrasts are indicated by unique letter combinations. Abbreviations are: GS = Guiana Shield (n = 165), BS = Brazilian Shield (n = 9), WAN = North-western Amazonia (n = 21), WAS = South-western Amazonia (n = 51), CA = Central Amazonia (n = 22) and EA = East Amazonia (n = 15); for forest types: TF = terra firme forests (n = 257) and PZ = white sand forests (n = 26). F-test values and Tukey contrasts can be found in Table S3.2.14-S3.2.15.


Breakfast with tropical forest products. Photo by Gijs Steur.

4

Exploring relationships between abundance of non-timber forest product species and tropical forest plant diversity

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Abstract

Despite the importance of non-timber forest products (NTFPs) for local livelihoods in tropical countries and the increasing attention for biodiversity-ecosystem services relationships, it remained unclear how the ecosystem service of NTFP provisioning is related to plant diversity. Although it is generally assumed that plant diversity is positively related to ecosystem services, this had not been assessed for NTFP provisioning. We applied bivariate and multiple regression models to explore the relationships between the abundance of 58 commercially relevant NTFP species and woody plant diversity across 287 plots of tropical forests in Northern Suriname. We found that NTFP abundance showed both positive and negative relationships to plant diversity indicators. In contrast to expectations, NTFP abundance was negatively related to woody species richness. In addition, across the plots disproportionately few (2-6) NTFP species determined >50% of NTFP abundance. The occurrence and the identity of these 'NTFP oligarchs' was associated to specific floristic compositions. Overall, more than half, i.e. 55.9%, of the observed variation in NTFP abundance could be explained by a combination of taxonomic and structural plant diversity indicators. Our case study findings are relevant for conservation policies in general. In most countries NTFPs are not on the agenda of governments and current tropical conservation policies often focus on forests with high species richness and/or carbon stocks. Our findings indicate that current policies may not cover valuable forests in terms of high NTFP abundance. To support sustainable NTFP provisioning, additional conservation efforts would need to include those vegetation types with high NTFP abundance.

4.1 Introduction

The provisioning of wild non-timber forest products (NTFPs), such as food, medicines and cultural ornaments, constitutes important ecosystem services for communities in tropical areas, especially for poor rural communities (Ros-Tonen & Wiersum, 2005; Shackleton et al., 2018; Shackleton & Pandey, 2014; Timko et al., 2010; van Andel, Croft, et al., 2015). However, NTFP provisioning is threatened by the conversion and degradation of tropical forests worldwide (Barlow et al., 2018). Furthermore, in many countries NTFPs are not considered in policy making nor taken into account in land management (Shackleton & Pandey, 2014). As NTFP provisioning is difficult to quantify because it comprises different types and units of NTFPs and is ultimately defined by human use, it is often expressed as NTFP abundance, i.e. the total number of individuals of NTFP species (e.g. Marshall and Hawthorne, 2012; Newton et al., 2012; Baraloto et al., 2014). Yet, despite the scientific attention for tropical NTFPs (Ros-Tonen & Wiersum, 2005; Shackleton & Pandey, 2014; Sills et al., 2011) and for relationships between ecosystem services and biodiversity (Cardinale et al., 2012; Díaz et al., 2005; Mace et al., 2012), little is known on the extent to which NTFP abundance is related to tropical forest plant diversity.

A better understanding of the relationships between NTFP abundance and plant diversity is highly relevant for conservation of tropical NTFPs, as it can be used to identify potential synergies between NTFP supply and current biodiversity conservation efforts and may help to develop additional conservation measures. To date, tropical biological conservation has often been focused on species-rich ecosystems due to the intrinsic value of species and efficiency of conserving a high number of species per unit area (Asaad et al., 2017; Barlow et al., 2018; Corlett, 2016; Myers et al., 2000). It is also assumed that species-rich ecosystems provide a larger quantity and higher quality of ecosystem services (Cardinale et al., 2012; Díaz et al., 2005; Gamfeldt et al., 2013; Slade et al., 2019). However, the latter assumption has not been systematically tested for the relationship between species richness and NTFP abundance in tropical forests. In addition, we cannot predict how species richness will be related to NTFP abundance as the overall relationship between species richness and species abundance is currently not well understood (McGill et al., 2007).

To date, tropical forest plant diversity has mostly been related to carbon stocks and sequestration. It has been reported that taxonomic indicators such as species richness and Shannon diversity as well as structural indicators related to average tree diameter, basal area and stem density can be important predictors of variation in carbon stock (Poorter et al., 2015; Sullivan et al., 2017). Additionally, it has been found that species contributions to tropical carbon stock can be disproportionate. For example, across 530 plots from the Amazonian biome only 8.2% of all tree species contributed 50% of all stems that make up the local carbon stock (Fauset et al., 2015). However, it is unclear to what extent similar relationships can be expected between plant diversity and NTFP abundance, as we do not know to what extent NTFP species are a random subset of all species that constitute forests or a specific subset that has unique relationships with plant diversity.

Relationships between NTFPs and aspects of biodiversity have rarely been investigated (Shackleton et al., 2018). Recent studies on NTFPs have mainly focused on local quantification, economic and social valuation or on questions related to sustainable harvest and commercialization of NTFPs (Belcher et al., 2005; Belcher & Schreckenberg, 2007; Sheil & Wunder, 2002; Sills et al., 2011; Stanley et al., 2012). Furthermore, NTFP studies often included a limited extent of the variation in NTFP abundance and plant diversity by sampling few sites in one or few forests types or by focusing on a limited selection of NTFP species, i.e. certain species or genera or specific growth forms (Stanley et al., 2012). One of the few studies that directly related NTFP abundance to plant diversity was conducted by Baraloto et al. (2014). These authors correlated the forest use values of standing timber, carbon storage and NTFP abundance with plant taxonomic richness and Simpson diversity across 69 plots of never inundated 'terra firme' tropical forests in the Southwestern Amazon. They did not detect any significant correlations between NTFP abundance and plant diversity, but their analysis was limited to tree and palm diversity at the genus level and included only a few NTFP species and genera. Therefore, the question remains to what extent NTFP abundance can be related to plant diversity at the species level.

Despite the lack of systematic analyses of the relationships between NTFP abundance and plant species diversity, several indications point at the existence of such relationships. For instance, differences in NTFP abundance have been observed across different abiotic conditions, such as hydrology and soil types, and across disturbance gradients (e.g., Newton et al., 2012; Londres et al., 2017), yet such differences in NTFP abundance may also overlap with variation in plant species diversity. For example, concerning hydrology types, the abundance of NTFP species has been studied within and between terra firme forests and seasonally to permanently flooded forests. It has been found that terra firme forests in general are rich in plant species and can contain high NTFP abundances, while flooded forests in general are poor in plant species yet can also contain high NTFP abundances when they have a relatively low evenness in species abundances (Johnston, 1998; Peters, Balick, et al., 1989; van Andel, 2000). These indications suggest that NTFP abundance can be negatively related to the evenness of species abundance but that the evidence for a positive or negative relationship with species richness is inconclusive.

In addition, some studies provided indirect evidence that species composition may explain variation in NTFP abundance. It has been found that a limited set of tree and palm species can dominate the total number of stems, being labelled as 'oligarchic' when dominant at the local to regional geographical scales and ‘hyperdominant’ at larger geographical scales such as Amazonia (Morera-Beita et al., 2019; ter Steege et al., 2013; 2019a). These species cover large biogeographical ranges but are dominant in specific vegetation types. As some of these dominant species have also been identified as NTFP species, it may be expected that some NTFP species contribute disproportionately to NTFP abundance. For example, the palm species *Euterpe oleracea* Mart. is widely recognized as an NTFP species and is a dominant species in specific flooded forest types (Johnston, 1998; van Andel, 2000; ter Steege et al., 2013; van Andel and Ruysschaert, 2011). Although it has been suggested that *E. oleracea* could be highly relevant for NTFP extraction due to its dominating abilities (Johnston, 1998; van Andel, 2000; Ruysschaert 2018), its relative contribution to NTFP abundance has not been previously quantified, nor that of other NTFP species.

The aim of this paper is to systematically explore how NTFP abundance is related to taxonomical and structural woody plant species diversity, i.e. the diversity in tree and arborescent palm species. To this end, we use a broad selection of woody NTFP species and potentially relevant woody plant diversity indicators, including species richness, species evenness, relative species contribution to NTFP abundance, floristic composition, stem density and stem diameter. We analyse relationships for vegetation plots across a gradient of terra firme, seasonally flooded and marsh forest types. Specifically, we test the null hypothesis that NTFP abundance is positively related to plant species richness. We use the neotropical country of Suriname as a case study because the use and trade of commercial relevant NTFPs have been relatively well surveyed (e.g. van Andel et al., 2007; van Andel and Havinga, 2008; Ruysschaert, 2018) and the floristic composition of the northern part of Suriname has been well documented with the creation of a landscape- and ecology-based vegetation map (Teunissen, 1978).

4.2 Material and methods

Teunissen dataset

During 1974 to 1977, Pieter A. Teunissen carried out vegetation surveys to identify and map landscape- and ecology-based vegetation types of the coastal area of Suriname. The resulting vegetation map comprised 67 vegetation types according to structural and floristic characteristics (Teunissen, 1978). We digitized the unpublished underlying data on all trees and palms with a stem diameter at breast height (DBH) of min. 5 cm, hereafter ‘woody species’, as their abundances had been recorded. The digitized dataset comprises 287 tropical forest plots of 10 × 40 m (0.04 ha) distributed across the northern part of Suriname (Figure 4-1) and lie within a minimum rectangular spatial extent of ca. 44×10^3 km^2. The vegetation captured in the plots represented predominantly climax lowland wet tropical forest with a Köppen 'Af' climate. Here, 'climax' refers to the state of vegetation naturally occurring after historical or under contemporary disturbance by native indigenous people (sensu Levis et al., 2018). Soil hydrology of the vegetation surveys included terra firme (n = 138), seasonally flooded (70) and permanently inundated, 'marsh' (79) soils. After updating the taxonomic names of the woody species after the Amazon Tree Checklist (ter Steege et al., 2019b), the dataset contained 531 woody morphospecies, of which 79.8% were identified up to the species level, 94.7% up to the genus level, and 100.0% up to the family level.

Experiences based on re-visits of ten Teunissen plots in 2018 and other floristic fieldwork in Suriname during 2017-2019 showed that the climax vegetation captured by Teunissen in the 1970ties still provides a good characterization of the current climax vegetation in the coastal area of Suriname. Based on fieldwork by the first author and based on additional research on the ecological impacts of NTFP harvest in Suriname carried out in 2006 (Havinga, 2006), past or recent harvest of NTFPs is unlikely to have had an significant impact on the species composition. Although there has been some forest cover loss and forest conversion in the study area since the 1970ties, most of the vegetation around the localities of the Teunissen plots has remained intact. In support, the rate of forest cover loss in Suriname has been found to be relatively low, i.e. around 0.04% per year for the period between 2000-2015, to be geographically clustered around areas outside the coastal area, and has been mainly driven by activities related to gold mining, infrastructure development and urban development (i.e. not harvest of NTFPs; NIMOS, SBB and UNIQUE, 2017). More information on the Teunissen database, dataset and digitization is included in Annex S4.1.

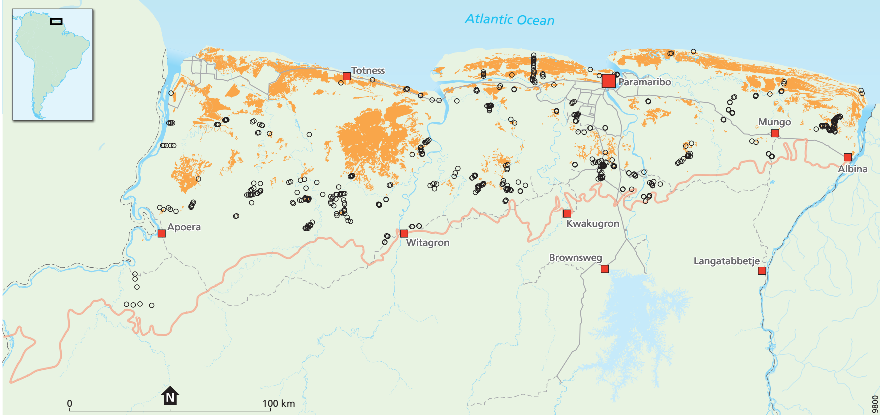

Figure 4-1. Map showing the locations of the 287 lowland tropical forest plots (black circles) of the Teunissen dataset in the coastal region of Northern Suriname. The coastal region of Suriname includes the young and old coastal plains and the savanna belt (i.e. the area between the Atlantic Ocean, the two Suriname border rivers and the thick, tan-coloured line). Major water bodies and rivers are shown in blue, major roads shown with unbroken and dashed lines, and several urban centres are shown as red squares. Non-forested natural areas, including herbal swamps and open savannas, are shaded in orange.

NTFP abundance

For each plot in the Teunissen database, we calculated the cumulative NTFP abundance (∑ number of stems of NTFP species). The selection of NTFP species included only wild plant species that produce NTFPs commercially traded on the markets of Suriname. Here 'wild' was defined as being self-replicating without human intervention (i.e. not domesticated, although possibly cultivated) and 'commercial' as being reportedly sold for money in 2017-2018. To obtain a list of all currently commercially relevant wild NTFP species, we combined the data of multiple Suriname NTFP surveys (i.e. van Andel et al., 2007; van Andel and Havinga, 2008; van Andel and Ruysschaert, 2011; Ruysschaert, 2018; van den Boog et al., 2018), and that of our own field work and market surveys carried out during 2017-2018 (see Annex S4.2 for more information). From the combined list, 58 wild and commercially relevant woody NTFP species were present across the plots (Annex S4.2, Table S4.2.1). Their cumulative abundance ranged from 0 to 120, with a mean of 18.49 (SD 22.78) (See also Annex S4.3, Table S4.3.1).

Plant diversity indicators

For each plot, we calculated six taxonomic and two structural diversity indicators at the species level. As taxonomic diversity indicators, we calculated the species richness, the Camargo index (E'), the Shannon-Wiener index (H'), the Gini-Simpson index (1-D), and the effective number of species based on the Shannon entropy (${}^{1}D$) and the Gini-Simpson index (${}^{2}D$). These indicators place different emphasis on components of diversity: where species richness emphasizes the number of species, the Camargo evenness index (E'; hereafter the 'Camargo evenness') emphasizes the evenness of the species abundances. The Shannon-Wiener index (H'; hereafter 'Shannon diversity') and the Gini-Simpson index (1-D; hereafter the 'Simpson diversity') are measures of both species richness and species evenness. Last, the effective number of species (${}^{q}D$; also called Hill diversity) emphasizes the theoretical maximal number of equally-abundant species. We included both original Shannon-Wiener (H') and Gini-Simpson (1-D) indices as well as their 'conversions' to effective number of species (${}^{1}D$ and ${}^{2}D$; hereafter the 'effective Shannon diversity' and the 'effective Simpson diversity'). Although the Shannon-Wiener and Gini-Simpson indices are more frequently used in the literature, their converted indices have statistically more convenient properties, including a more linear relationship to number of species (See Jost, 2006, and Tuomisto, 2012, for discussions). As structural diversity indicators, we calculated the stem density and the average of the maximum diameter at breast height per plot. The average of the maximum diameter at breast height (avr. max. DBH) is a measure of the size of the largest stems in a plot ((∑ maximum DBH per species) / number of species). More information on the methodology underlying the taxonomic and structural diversity indicators, including their formulae is included in Annex S4.3.

Because NTFP abundance and plant diversity indicators are inherently linked (interdependence), we also studied relationships between NTFP abundance and the plant diversity of the non-NTFP species to avoid double counting of NTFP species. To this end, we created three sets of plant diversity indicators, one calculated for all plant species, the 'all species group', one subset calculated from all plant species after removal of the NTFP species, the 'non-NTFP group', and one subset calculated from all NTFP plant species, 'the NTFP group'. More information about the sets of plant diversity indicators, including mean values, ranges and scatterplots is provided in Annex S4.3.

Statistical analyses

All statistical analyses were carried out in the R software (v. 3.6.1. ; R Core Team, 2019) and using several packages which are listed along with more detail on the methodology of the analyses in Annex S4.4.

Because NTFP abundance represented count data, did not follow a normal distribution and was not zero-inflated, we used Kendall's tau correlations and generalized linear regression models to investigate relationships between NTFP abundance and plant diversity indicators. Fitting general additive models did not considerably or consistently improve model fit in comparison to generalized linear models.

We used bivariate generalized linear regression models to investigate separate relationships between NTFP abundance and plant diversity indicators. In addition, we combined plant diversity indicators in multiple generalized linear regression models to investigate their independent relationships and to assess how much variation in NTFP abundance they could significantly collectively explain.

For our generalized linear regression models, we tested Poisson, pseudo-Poisson and negative binomial error distributions and found that a negative binomial distribution showed the best fit of residual errors, i.e. a dispersion of residual deviance/null deviance close to 1. Hence, for our regression analyses we applied generalized linear models using a negative binomial error distribution and a log-link function, hereafter 'NB GLMs'.

To find the optimal multiple NB GLM, we used the model optimization procedure described by Crawley (2015). In short, this procedure starts with a maximal model, i.e. a model including all non-collinear variables of interest. This maximal model is then iteratively simplified using a hypothesis driven selection procedure. One variable is removed at a time and using Log-Likelihood Ratio tests, 'LRTs', the hypothesis is tested that the simpler model does not explain a different amount of variance than the previous model. The procedure is repeated until no variable can be removed without the resulting simpler model explaining a different amount of variation than the previous model, or when all main variables that are left in the simpler model have a significant coefficient.

Collinearity between plant diversity indicators was checked according to the Variance Inflation Factor, 'VIF', where variables that had a VIF of 3 or higher were omitted (sensu Zuur, Ieno and Elphick, 2010). On the basis of the VIF values, Shannon diversity, effective Shannon diversity and effective Simpson diversity were not included in our multiple NB GLMs.

To examine the independent effects of the plant diversity indicators, we optimized a maximal NB GLM that was restricted to main variables (i.e. no interactions), hereafter the 'restricted model' and calculated the standardized beta coefficients for the main effects. To explore how much variation in NTFP abundance could be explained by variation in the plant diversity indicators, we optimized a maximal NB GLM in which all two-way interactions were allowed, hereafter the 'unrestricted model'. This maximal model fitted a total of 31 parameters, for which 9.3 samples per parameter were available (n = 287). This number of samples per parameter is just under the conservative value of 10, keeping the risk of overfitting such a model within reasonable limits (Crawley, 2015). Interactions with a significant coefficient were interpreted using interaction plots. All optimized models were validated before interpretation by visual checks of the residuals plotted against the linear predicted values and against the fitted values, a histogram of the residuals and a QQ-plot.

We calculated a 'pseudo-R^2' as a goodness-of-fit for each model (after Dobson, 2002, in Zuur et al., 2009) and compared these between nested NB GLMs. A pseudo-R^2 can be interpreted as the amount of variation in NTFP abundance explained by the model compared to the amount of variation in NTFP abundance explained by having no model (Zuur et al., 2009).

Last, we examined to what extent species composition can explain variation in NTFP abundance, including with floristic composition and with relative species contribution to overall NTFP abundance. To examine whether there were recognizable clusters in floristic composition, i.e. similar groups of plots according to species occurrence and abundance, hereafter 'floristic clusters', within the Teunissen dataset, we carried out a TWINSPAN clustering using the programme WinTWINS (Hill and Šmilauer, 2005; See Annex S4.7). To analyse potential differences in mean NTFP abundance and other variables between floristic clusters, we carried out omnibus LRTs comparing NB GLMs with and without floristic clusters included as dummy variables. We used Tukey Post-hoc tests to determine which mean values of floristic clusters differed from the others. To assess relative species contribution to overall NTFP abundance we created tables that ordered the NTFP species according to their cumulative contribution to NTFP abundance.

4.3 Results

Bivariate relationships between NTFP abundance and plant diversity indicators

Bivariate regression showed that NTFP species richness was positively related to NTFP abundance (coefficient +0.22; Table 4-1). However, the relationship explained little variation in NTFP abundance (i.e. 8.8% pseudo-R^2; see Annex S4.5, Output S4.5.1), indicating that other variables also determined NTFP abundance.

Table 4-1. Overview of bivariate generalized linear models between NTFP abundance and plant diversity indicators across all plots (n=287). Plant diversity indicators are calculated from all species (all species group), non-NTFP species (non-NTFP group) and NTFP species (NTFP group). For each relationship the model coefficient and the standard error of the coefficient (SE) is given. Significant coefficients, i.e. $p < 0.05$, are printed in bold. See Output S4.5.1 for p-values, pseudo-R^2 and other model details.

Predictor variable	All species group	Non-NTFP group	NTFP group
	Coefficient (SE)	Coefficient (SE)	Coefficient (SE)
Species richness (# spp)	**-0.04 (± 0.01)**	**-0.06 (± 0.01)**	**0.22 (± 0.03)**
Species Camargo evenness (E’)	**-4.18 (± 0.37)**	**2.75 (± 0.42)**	**-3.50 (± 0.22)**
Species Shannon diversity (H’)	**-0.62 (± 0.08)**	**-0.43 (± 0.10)**	-0.17 (± 0.12)
Species Simpson diversity (1-D)	**-2.49 (± 0.30)**	**-0.74 (± 0.38)**	**-1.63 (± 0.21)**
Species effective Shannon diversity (^{1}D)	**-0.07 (± 0.01)**	**-0.06 (± 0.01)**	**-0.10 (± 0.05)**
Species effective Simpson diversity (^{2}D)	**-0.09 (± 0.01)**	**-0.06 (± 0.01)**	**-0.27 (± 0.05)**
Stem density (# stems)	**0.01 (± 0.00)**	**-0.01 (± 0.00)**	Not available (perfect collinear)
Average maximum diameter (cm)	**0.04 (± 0.01)**	**0.03 (± 0.01)**	-0.01 (± 0.00)

The bivariate regression analyses of NTFP abundance predicted by the plant diversity indicators showed that all eight plant diversity indicators were significantly related to the NTFP abundance but in some cases, relationships with specific plant diversity indicators showed contrasting directions between the all species group and the non-NTFP group (Table 4-1, left and middle columns, respectively). NTFP abundance was negatively related to all species richness and with non-NTFP species richness (coefficients -0.04 and -0.06, respectively). All three plant diversity indicators associated to the evenness of all species abundance, i.e. all species Camargo evenness, Shannon diversity and Simpson diversity, showed negative relationships with NTFP abundance (coefficients -4.02, -0.62, -2.49, respectively). However, non-NTFP Camargo evenness showed a positive relationship with NTFP abundance (+2.91), while non-NTFP Shannon diversity and Simpson diversity were negatively related (-0.43 and -0.74, respectively). Relationships of the effective Shannon diversity and the effective Simpson diversity with NTFP abundance were in line with those of the original Shannon diversity and Simpson diversity. The two structural indicators of all stem density and all species average maximum diameter were positively related to NTFP abundance (+0.01 and +0.04, respectively). Yet, non-NTFP stem density was negatively related to NTFP abundance while non-NTFP average maximum diameter was positively related (-0.01 and +0.03, respectively). Tau correlations were in line with the bivariate regression models (See Annex S4.5, Output S4.5.1).

Predicting NTFP abundance with taxonomic and structural diversity indicators

Multiple regression analyses showed that a combination of the non-collinear five non-NTFP group plant diversity indicators with interactions could significantly explain about one-third, i.e. 37.2%, of the variation in NTFP abundance (pseudo-R^2; Table 4-2, unrestricted model). The optimized multiple regression model restricted to main variables explained 23.3% of the deviance in NTFP abundance (pseudo-R^2; Table 4-2, restricted model), indicating that interactions between the tested plant diversity indicators explained about one-seventh of the variation in NTFP abundance (i.e. 37.2% - 23.3% = 13.9% pseudo-R^2).

The main effects in the optimized multiple regression model restricted to main variables showed that both taxonomic and structural plant diversity independently significantly contributed to explaining variation in NTFP abundance and that independent relationships included positive and negative directions. Non-NTFP species richness and non-NTFP stem density showed negative main effects on NTFP abundance and non-NTFP Camargo evenness and non-NTFP Simpson diversity showed positive main effects while included in the same model (Table 4-2, right column). Although the differences between the standardized coefficients of the optimized restricted model were not large, the order of magnitude suggests that non-NTFP species richness, a taxonomic plant diversity indicator, explained most variation in NTFP abundance, being stronger than the other plant diversity indicators (both taxonomic and structural, i.e. $|0.019|$ versus $|0.011|$ and $|0.008|$; Table 4-2, right column).

Additionally, the significant interactions in the optimized unrestricted model showed that although non-NTFP average maximum diameter did not have independent main effects, it did significantly contribute to explaining deviance in NTFP abundance (Table 4-2, middle column). Interaction plots showed that all significant interactions took the form of a change in strength and ultimately the direction of the relationship between one plant diversity indicator with NTFP abundance across values of the other plant diversity indicator (see interaction plots in Annex S4.6, Figure S4.6.3). For example, the interaction plot of the interaction between non-NTFP Camargo evenness and non-NTFP stem density showed that at low non-NTFP stem densities, i.e. <5 0 stems, the relationship between non-NTFP Camargo evenness and NTFP abundance was positive but at high non-NTFP stem densities, i.e. >5 0 stems, the relationship was negative. As most of the vegetation samples had relatively low non-NTFP stem densities (i.e. ca. 78% had a stem density of <5 0 stems), the main effect of non-NTFP Camargo evenness on the NTFP abundance was positive (Table 4-2, right column).

Table 4-2. Summary of the optimized models of the NTFP abundance predicted by plant diversity variables calculated for the non-NTFP group (all species with the NTFP species removed), showing the optimized version of a maximal model of the five plant diversity indicators with interactions (unrestricted model, middle column) and the optimized version of a maximal model of the five plant diversity variables without interactions (restricted model, right column). For each optimized model the main effects and interactions are shown with their coefficient, standard error of the coefficient, Z-value and p-value of the z-test. Significant coefficients, i.e. $p < 0.05$, are printed in bold. For the restricted model the standardized coefficients of the main effects are shown. See Annex S4.6, for full model details.

	Unrestricted Model			**Restricted model**			
Predictor variable	Coefficient (SE)	Z-value	p-value	Coefficient (SE)	Z-value	p-value	standardized coefficient
Single variables							
Species richness (# spp)	**-0.05 (± 0.01)**	-3.390	**0.0007**	**-0.07 (± 0.01)**	-5.179	**0.0000**	**-0.019**
Camargo evenness (E′)	**12.47 (± 3.23)**	3.861	**0.0001**	**1.30 (± 0.47)**	2.755	**0.0059**	**0.008**
Simpson diversity (1-D)	0.74 (± 2.20)	0.338	0.7353	**1.08 (± 0.48)**	2.221	**0.0263**	0.008
Stem density (# stems)	-0.02 (± 0.02)	-1.164	0.2445	**-0.00 (± 0.00)**	-2.693	**0.0007**	**-0.011**
Average maximum diameter (cm)	**0.14 (± 0.05)**	2.843	**0.0045**				
Two-way interactions							
Camargo evenness × Simpson diversity	**-6.88 (± 2.70)**	-2.542	**0.0110**				
Camargo evenness × Stem density	**-0.03 (± 0.01)**	-2.323	**0.0202**				
Camargo evenness × Average max. diameter	**-0.24 (± 0.06)**	-3.719	**0.0002**				
Simpson diversity × Stem density	**0.08 (± 0.02)**	4.274	**0.0000**				
Simpson diversity × Average max. diameter	**0.08 (± 0.04)**	2.022	**0.0431**				
Stem density × Average max diameter	**0.00 (± 0.00)**	-3.655	**0.0003**				
Total model pseudo-R^2	37.3%			23.3%			

Relationships between NTFP abundance and species composition

On the basis of the TWINSPAN analysis of the 287 plots, we identified eleven distinct floristic clusters, each cluster having at least two indicator species and based on at least five samples (Annex S4.7, Figure S4.7.1. Most of these floristic clusters also corresponded to a dominant physiognomy and hydrology. For example, we found three clusters that were dominated by hydrophytic flooded vegetation (cluster #1, #9 and #11, respectively). Detailed TWINSPAN analysis is provided in Annex S4.7, including the relationships between the clusters and a full description of indicator species, number of plots and mean NTFP abundance per cluster.

Analysis of variance showed that the eleven floristic clusters were significantly different according to mean NTFP abundance (Omnibus Likelihood Ratio Test: $\chi^2_{(10)} = 232.02$, $p < 0.001$; Output S4.7.1). Post-hoc Tukey contrasts showed that the mean NTFP abundance differed significantly between the floristic clusters (Output S4.7.2), where the order of the floristic clusters by the TWINSPAN output followed an overall pattern of initially low mean NTFP abundances to increasingly higher mean NTFP abundances (Figure S4.7.2). For example, clusters #1 to #4 had the lowest mean NTFP abundance and clusters #9 to #11 had the highest mean NTFP abundance.

Adding the floristic clusters as dummy variables to the optimized unrestricted model resulted in a significant lower deviance (Omnibus Likelihood Ratio Test: $\chi^2_{(10)} = 106.30$, $p < 0.001$; Output S4.7.3), indicating that the floristic clusters explained variation in NTFP abundance additional to that explained by the previously included plant diversity indicators. The optimized unrestricted model with floristic clusters explained 55.9% of the deviance in NTFP abundance, 18.6% more than the same model without floristic clusters (i.e. 55.9% - 37.2% Pseudo-R^2; Output S4.7.4). Similar results were found when we added the floristic clusters as dummy variables to the optimized restricted model (See Annex S4.7, Outputs S4.7.5 & S4.7.6).

Analysis of the relative contribution of species to the total NTFP abundance across all 287 plots identified 20 species that together were responsible for 95% of the cumulative NTFP abundance (Table 3). Across all plots, the stems of 2 of the 58 occurring NTFP species (i.e. 3.4%) contributed more than 50% of the NTFP abundance: *Euterpe oleracea* and *Eperua falcata*. Of these two species, *E. oleracea* contributed most of the NTFP abundance (i.e. 49.5%), although it was only present in 102 of the 287 plots. Within the 185 plots without *E. oleracea*, 6 out of the 52 occurring NTFP species (i.e. 11.5%) contributed more than 50% of the NTFP abundance, i.e. *E. falcata*, *Attalea maripa*, *Protium heptaphyllum*, *Astrocaryum sciophilum*, *Copaifera guyanensis* and *Carapa guianensis* (Annex S4.8, Table S4.8.1; species also listed in Table 3).

Table 3. Top 20 NTFP species ordered by their relative contribution to NTFP abundance (number of stems) across all plots (n = 287). For each species, the total number of stems, its percentage of the total NTFP abundance and the cumulative percentage of NTFP abundance is shown (total number of NTFP stems = 5306). In addition, for each species, the total number of plots and its percentage of all plots is given.

Species	Family	NTFP abundance (# stems)	% Total NTFP abundance	Cumulative% NTFP abundance	Number of plots (n)	% Total number of plots
Euterpe oleracea	Arecaceae	2624	49.5	49.5	102	35.5
Eperua falcata	Fabaceae	499	9.4	58.9	47	16.4
Carapa guianensis	Meliaceae	304	5.7	64.6	54	18.8
Attalea maripa	Arecaceae	249	4.7	69.3	76	26.5
Symphonia globulifera	Clusiaceae	184	3.5	72.7	37	12.9
Copaifera guyanensis	Fabaceae	131	2.5	75.2	59	20.6
Astrocaryum sciophilum	Arecaceae	129	2.4	77.6	17	5.9
Protium heptaphyllum	Burseraceae	125	2.4	80.0	39	13.6
Parinari campestris	Chrysobalanaceae	124	2.3	82.3	68	23.7
Gustavia augusta	Lecythidaceae	120	2.3	84.6	30	10.5
Virola surinamensis	Myristicaceae	113	2.1	86.7	47	16.4
Goupia glabra	Goupiaceae	73	1.4	88.1	34	11.8
Oenocarpus bacaba	Arecaceae	59	1.1	89.2	35	12.2
Dimorphandra conjugata	Fabaceae	59	1.1	90.3	8	2.8
Jacaranda copaia	Bignoniaceae	55	1.0	91.4	35	12.2
Carapa surinamensis	Meliaceae	53	1.0	92.4	23	8.0
Zygia latifolia	Fabaceae	53	1.0	93.4	9	3.1
Mauritia flexuosa	Arecaceae	32	0.6	94.0	8	2.8
Hirtella paniculata	Chrysobalanaceae	28	0.5	94.5	12	4.2
Spondias mombin	Anacardiaceae	26	0.5	95.0	15	5.2

Follow-up analysis of the contribution of *E. oleracea* to NTFP abundance across all plots showed that mean abundance of *E. oleracea* differed significantly between the floristic clusters (Omnibus Likelihood Ratio Test: $\chi^2_{(10)} = 206.29$, $p < 0.001$; Output S4.8.1; Post-hoc Tukey contrasts shown in Output S4.8.2). The pattern in ranks of mean *E. oleracea* abundance between the floristic clusters resembled that of the ranks of mean NTFP abundance (Output S4.8.2; compare Figure S4.8.1 to S4.7.2). For example, clusters #9 to #11 had the highest mean *E. oleracea* abundance as well as the highest mean NTFP abundance.

4.4 Discussion

Our analysis revealed both positive and negative relationships between the abundance of commercially relevant woody NTFP species and plant species diversity indicators across a broad gradient of tropical forests. To our knowledge, this represents the first analysis of relationships between NTFP abundance and plant diversity at the species level. One previous study quantified similar relationships, but was restricted to the genus level and to terra firme forests (Baraloto et al., 2014). For a gradient of flooded and non-flooded tropical forests, we found that variation in NTFP abundance can be predicted by variation in taxonomic and structural plant species diversity, which is discussed in more detail below.

NTFP abundance negatively related to woody species richness

Based on previous research and current theory on the relationships between biodiversity and ecosystem services (Slade et al., 2019), it was expected that species-rich forests would harbour high NTFP abundances. In contrast to this expectation, we found a consistent negative relationship between NTFP abundance and woody plant species richness across bivariate and multiple regression models, and when compared with all woody species richness and with all woody species with the NTFP species removed. Only woody NTFP species richness was positively related to NTFP abundance. These findings suggest that forests that are rich in woody species, in general have a low NTFP abundance.

Disproportionately few NTFP species determine the largest share of NTFP abundance

Based on the fact that a set of tree and palm species can dominate local stands (i.e. have a high number of stems; ter Steege et al., 2013, 2019a; Morera-Beita et al., 2019) we expected that some NTFP species could have disproportionately large contributions to NTFP abundance. In congruence, we found that in our Suriname dataset 2 to 6 of occurring NTFP species (i.e. 3.4% to 11.5%) contributed more than 50% of the NTFP abundance. Although a few NTFP species were mentioned to potentially make a large contribution to NTFP supply (e.g., *Euterpe oleracea* in Johnston, 1998; van Andel, 2000), our analysis is first to quantify the relative contribution of species to total NTFP abundance. Analogue to our finding, 50% of carbon stock in plots across the Amazon was found to be determined by ~1% of all woody species (Fauset et al., 2015). This indicates that at least two tropical ecosystem services are largely determined by relatively few species.

Morera-Beita et al. (2019) labelled species with a disproportionately large contribution to stems at the landscape to regional scale as 'oligarchs'. Based on our findings, we propose the term 'NTFP-oligarchs' when referring to a small fraction of NTFP species with a disproportionately large contribution to NTFP supply. Although NTFP-oligarchs apparently can produce a large part of the NTFP abundance, we also found evidence that

NTFP oligarchs might reach high abundances only in specific floristic vegetation types. In particular, we found that the mean abundance of one NTFP-oligarch (i.e. *Euterpe oleracea*) varied significantly across the different floristic vegetation types. Such a characteristic of NTFP oligarchs is analogue to the finding that stem-dominant woody species across the Amazon are only stem-dominant in specific vegetation types (e.g. hyperdominants; ter Steege et al., 2013). Ultimately, these findings illustrate that floristic composition, in terms of floristic vegetation types and occurrence of NTFP oligarchs, is highly relevant in predicting NTFP abundance.

Taxonomic and structural plant diversity explain large part of variation in NTFP abundance

Optimization of multiple generalized linear regression models showed that a combination of plant diversity indicators associated to species richness, evenness of species abundances, floristic composition, stem density and average diameter, explained more than half (i.e. 55.9%) of the variation in NTFP abundance. This can be seen a considerate part of the variation in NTFP abundance that can be expected from the broad gradient of tropical forests included in our study. In addition, when we restricted the multiple regression to only main effects, we found that three plant diversity variables significantly and independently contributed to explaining variation in NTFP abundance. Non-NTFP species richness and non-NTFP stem density showed a negative relationship to NTFP abundance, while evenness of non-NTFP abundances showed a positive relationship to NTFP abundance. These findings show that taxonomic and structural plant diversity indicators can be important predictors of NTFP abundance.

The positive relationship found between NTFP abundance and evenness of non-NTFP species abundance was not in line with general expectations. Based on the observations that flooded forests can have high NTFP abundances with relatively uneven species abundances (Johnston, 1998; Peters, Balick, et al., 1989; van Andel, 2000), it would be expected that NTFP abundance is generally negatively related to the evenness of species abundance. However, in the observations, a comparison was made with the evenness of all plant species abundances. In line with this, NTFP abundance was found to be negatively related to evenness of all species abundance in bivariate regression. These findings show that different sets of plant diversity can also show contrasting relationships to NTFP abundance. In support, the relationships between NTFP abundance and stem densities showed similar contrasting directions, where NTFP abundance showed a negatively relationship to non-NTFP stem density and positive relationship to all species stem density.

Relationships between plant diversity and tropical forests ecosystem services have also been previously studied for carbon stocks (e.g., Poorter et al., 2015; Sullivan et al., 2017).

Although these studies have used partly different models and plot sizes than that of our analyses, and, therefore, findings are not always directly comparable (see Whittaker, 2010), their findings can be used to make general comparisons. In contrast, all woody species richness has been reported to be positively related to carbon stock across 0.04 ha plots (Sullivan et al., 2017), while our analysis found it to be negative related to NTFP abundance. In congruence, all species stem density has been reported to be positively related to carbon stock (although across 0.1 ha plots; Poorter et al., 2015), and in our analysis found to be positively related to NTFP abundance. The evenness of species abundance has, to our knowledge, not been related to tropical forest carbon stocks. These tentative comparisons suggest that forests with high carbon stock do not necessarily contain high NTFP abundance.

Limitations in addressing relationships between NTFP abundance and plant diversity

Besides being restricted to a specific study area and a specific plot size, our study was limited by the type of data included. Our study did not consider tropical savannas and secondary forests and herbs, lianas and epiphytes, while it may be expected that including these vegetation types and NTFP growth forms can lead to different relationships between NTFP abundance and plant diversity. In our view, this limitation needs to be addressed before we can gauge to what extent the identified relationships can be generalized beyond our analysis. Tropical savannas and secondary forests have been reported to be important source areas for NTFPs, including for Suriname (e.g. van Andel and Havinga, 2008; Andel et al., 2015), but can be expected to be structurally and floristically different from the wet tropical forests included in our study. Furthermore, it has been found that herbs, lianas and epiphytes can also contribute commercially relevant NTFPs, including in Suriname (e.g. van Andel, 2003; van Andel and Ruysschaert, 2011; Stanley, Voeks and Short, 2012). These growth forms can be related to different life strategies, potentially resulting in different patterns in NTFP abundance and plant diversity.

In our analyses, we did not account for any ecological effects that NTFP harvesting may have on the species composition. We expected that the harvest of the selected NTFPs in Suriname did not have a significant impact on the species composition because, in our experience, the harvest of the selected NTFPs involves either the removal of only a part of the individual or the removal of only a part of the seeds. In addition, during our fieldwork we found no indication that the selected NTFPs were overharvested. Nevertheless, we cannot exclude the possibility that harvest of these NTFPs may result in a modification of the species composition.

Implications for conservation and management of NTFPs

In this study we have set out to analyse how NTFP abundance is related to taxonomic and structural plant species diversity for a dataset of Suriname tropical forests and NTFPs. Although our analysis was limited to this country and included only lowland tropical forests and woody NTFP species, we found two patterns that are relevant for the conservation of ecosystem services and the use of NTFPs beyond our dataset. First, we found that the NTFP abundance in a tropical forest is not a simple function of NTFP species richness, where taxonomic and structural plant diversity predict a large part of the NTFP abundance (55.9% in this study), and disproportionately few NTFP species (2 to 6) contribute the largest share of the NTFP abundance (the 'NTFP oligarchs'). Although this shows that predicting NTFP abundance is more complex than just deriving it from the number of NTFP species, it also points at the possibility of predicting the NTFP abundance by patterns in other plant diversity indicators. Second, our findings imply that species-rich tropical forests are not necessarily associated to high NTFP supply. Instead, NTFP abundance varies with floristic vegetation types and the occurrence of NTFP oligarchs that do not necessarily coincide with species-rich or carbon stock-rich forests.

As contemporary conservation strategies for both biodiversity and ecosystem services, such as REDD+, have focused primarily on species-rich ecosystems (Asaad et al., 2017; Harvey et al., 2010), our findings urge for a broader conservation approach. Not only species-rich tropical forests need to be protected in order to conserve higher quantities and qualities of relevant ecosystem services, also tropical forests that are relatively species-poor but rich according to NTFP abundance need to be considered. Protection of the latter category of tropical forests could be included in multiple use protected areas and indigenous territories, as NTFPs are highly relevant for indigenous people and other local communities. A meta-analysis of protected areas has shown that local communities can be relatively successful in combining the harvesting of biological resources while at the same time achieving biological conservation (Oldekop et al., 2016).

Similar to other tropical countries, in Suriname the use and marketing of NTFPs represent an important contribution to local livelihoods and well-being, but is currently not or barely considered in economic planning or development policy, which risks NTFP overexploitation (Shackleton & Pandey, 2014; van Andel et al., 2003, 2007; van den Boog et al., 2018). Although not all NTFPs will be commercially utilized due to differences in socio-economic factors such as physical access, distance to markets and market demand (Schaafsma et al., 2014) as well as ecological variation, such as differences in production across space and time, NTFP abundance represents the source of NTFP supply and is therefore an important indicator of the theoretical potential of commercial NTFP provisioning. Our findings revealed relevant patterns in abundance of commercially relevant NTFPs, indicating that floristic vegetation types play a key role in the total NTFP supply. Such patterns can be used to inform and develop new policies and management strategies aiming at the conservation and sustainable use of commercially relevant NTFPs.

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SUPPLEMENTARY MATERIAL CHAPTER 4

Annex S4.1 Teunissen dataset

Material and Methods Teunissen data

During 1974 to 1977, Pieter A. Teunissen carried out research to identify and map the natural and semi-natural ecosystems of the Coastal Plain and Savanna Belt of Suriname in order to identify sites of biological importance and to facilitate the establishment of protected areas. Here, 'ecosystems' refer to vegetation units delimited by edaphic and hydrological conditions, 'natural ecosystems' refer to ecosystems that have naturally formed under no to relatively little human disturbance, including historical disturbance, and 'semi-natural ecosystems' refer to ecosystems that naturally form under continuous human disturbance, such as savannas. Around the period of research, the independence for Suriname had been announced for 1975 and plans were suggested to develop large areas in Northern Suriname in order to strengthen economic development. It was perceived that the suggested plans for development could threaten the state of unique natural and semi-natural ecosystems of Northern Suriname. However, there was insufficient knowledge on the diversity and distribution of these ecosystems.

For his fieldwork, Teunissen focused on 36 key areas in the study area (Figure S4.1.1), which were identified in two steps. First, a map of preliminary ecosystems was drawn up. These preliminary ecosystems were based on available topographical maps (CBL, 1974a, 1974b), geomorphological maps, including landforms (e.g. flat, low, undulating), landscapes (i.e. geological deposition phases, e.g. Coronie landscape), landscape elements (e.g. ridges, swamps), soil types (e.g. sand, clay) and hydrology classes (e.g. well-draining, poorly drained) (DBK, 1977b, 1977a), and aerial photographs (Aerocarto, 1973). Second, key areas were identified as areas with a high diversity of preliminary ecosystems and were set out to sample both north-south and west-east gradients equally. These key areas were then prioritized on the basis of to what extent they had not been previously extensively sampled for other research and to what extent the areas were accessible.

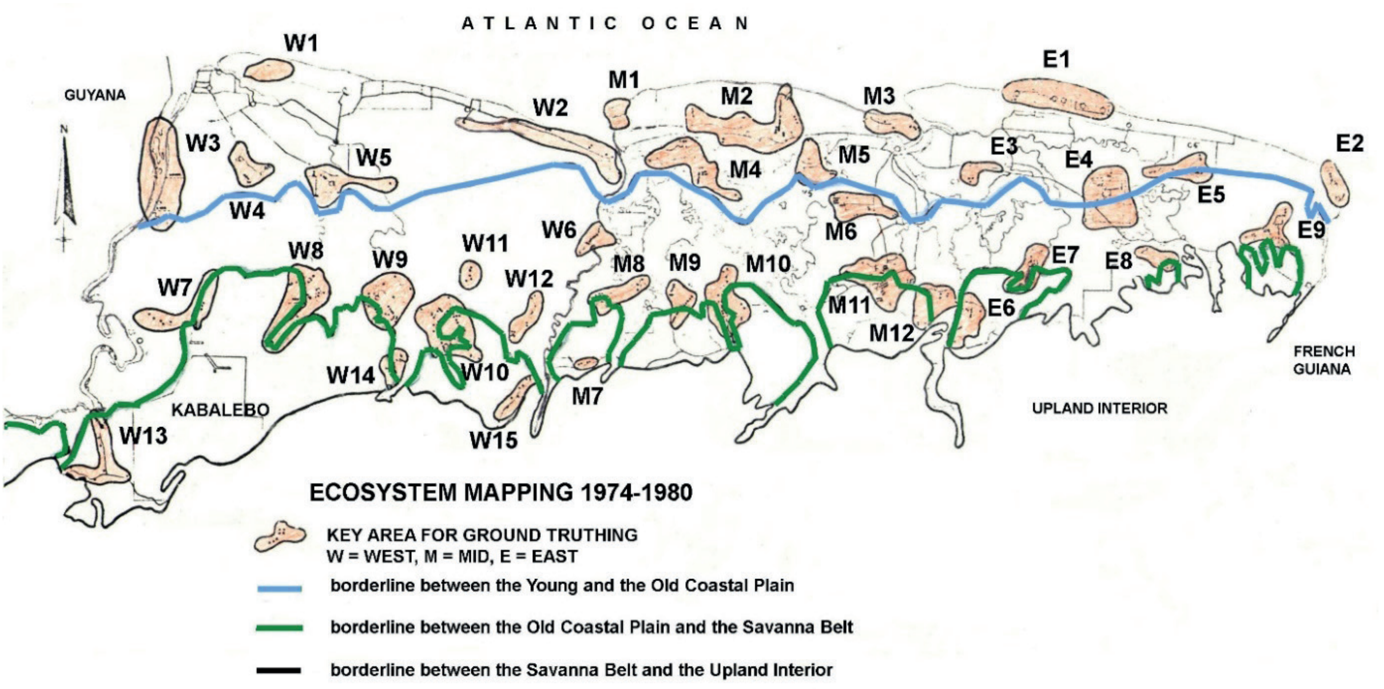

Figure S4.1.1 The 36 "key areas" of preliminary ecosystem sampling in Northern-Suriname.

During 1975 and 1976, each preliminary ecosystem in a key area was surveyed using a number of plots. For forest vegetation, plots of 0.04 ha (consisting of 4 subplots of 10 × 10 m) were used, for 'open' vegetation, such as savannas and herbaceous swamps, plots of 0.01 ha (i.e. 1 subplot of 10 × 10 m) were used. Within each preliminary ecosystem a number of plots were surveyed until the impression was reached that the local flora was sufficiently sampled. Within each subplot, trees, palms, shrubs, herbs and macrophytes were inventoried. Lianas and epiphytes were not systematically included. For each plot, the soil was sampled to cross-reference soil typology given in the available soil maps (DBK, 1977a, 1977b). For all tree species, the number of stems and their diameter at breast height (i.e. at c.a. 1.3 m) class was noted (See Table S4.1.1). For upperstory palm species, the number of stems was noted. For understory plant species, either or a Braun-Blanquet type abundance scale was used (mostly in open vegetation, such as herbaceous swamps and savannas, see Table S4.1.2) or a relative frequency scale was used (mostly in forests; See Table S4.1.3). Identification was carried out in the field by parabotanist Mr. Frits van Troon and Mr. Pieter A. Teunissen and ex-situ in the National Herbarium of Suriname (BBS), mainly by Ms. Marga C.M. Werkhoven, and the former Utrecht Herbarium (U), mainly by Mr. Jan C. Lindeman. Any collected material that was fertile was made into vouchers and was stored at the BBS and U (now National Herbarium Netherlands, NHN), see for an overview of voucher references Ek (1991).

During 1974-1977 Teunissen carried out a total 302 forest vegetations surveys and 156 open vegetation surveys. In addition, Teunissen included vegetation surveys carried out prior or during this period by other researchers (i.e. students from Utrecht and Wageningen Universities which were supervised by Teunissen). Combined, Teunissen created a database of 713 surveys, of which 334 represented samples of forest vegetation and 379 represented samples of open vegetation.

To summarize this database of 713 surveys, Teunissen created vegetation tables in which survey data was simplified. Survey data was split into upperstory data, i.e. plants that were able to reach a DBH of at least 5 cm, and understory data, i.e. plants that are not able to reach a DBH of 5 cm. In these vegetation tables, Teunissen manually grouped surveys of similar floristic composition together in an iterative manner. Within these vegetation tables, all surveys were set to represented a standard area. For forest vegetation this was 0.04 ha and for open vegetation this was 0.01 ha. To this end, some surveys needed to be cropped or extrapolated. For the surveys of forest vegetation 24 of the total 334 surveys (7.2%) were smaller than 0.04 and were extrapolated to 0.04 ha. These 24 surveys represented relative species poor forests consisting of one tree layer.

Teunissen used these vegetation tables to identify 140 floristic groups in the Coastal Plain and Savanna Belt that were compatible with all previously published floristic groups.

At the time, these 140 floristic groups could not be mapped separately on a scale of 1: 200,000 and therefore they were aggregated into 67 larger clusters of "vegetation types" (legend units) which were published in the 'Reconnaissance map of Surinam lowland ecosystems (Coastal plain and savanna belt)', scale 1: 200,000 (Teunissen, 1978). Data on the 140 floristic groups was incorporated in a report providing recommendations for areas to be included in protected areas (Teunissen et al., 1979) and in a report providing the relative frequency of plant species within the 140 floristic groups (Teunissen, 1980).

During 1974-1977, Mr. Teunissen was employed by the Netherlands Foundation for the Advancement of Tropical Research ("Wetenschappelijk Onderzoek van de Tropen, WOTRO", now 'NWO-WOTRO') and the fieldwork was co-financed by the Nature Conservation Department of the State Forest Service (" 's Lands Bosbeheer, LBB") . After this period, no follow-up funding could be secured, forcing Teunissen to publish the abovementioned map of 1978 and the reports of 1978-1980 *pro bono*. The works by Teunissen led to the establishment of four nature reserves covering an area of 1,310 km^2 by the Surinamese Government in 1987 (Natuurbeschermingsbesluit 1986, 1986).

Table S4.1.1. Diameter at breast height (DBH) class.

CLASS	DBH
0	< 5 cm
1	5-15 cm
2	15-25 cm
3	25-35 cm
[…]	[…]
12	115-125 cm

Table S4.1.2. Braun-Blanquet type abundance scale.

SCALE 1	INTERPRETATION	SCALE 2 (OPTIONAL)	INTERPRETATION
r	rare: 1-2 individuals, negligible cover	f	frequent in number
+ / x / p	present: 2-5 individuals, cover < 5%	a	abundant in number
1	numerous, cover < 5%	va	very abundant in number
2	Numerous, cover ≥ 5%	D	dominant in cover
3	cover 25-50%		
4	cover 50-75%		
5	cover 75-100%		

Table S4.1.3. Relative frequency scale.

CLASS	RELATIVE FREQUENCY
1	present in 1 out of 4 subplots
2	present in 2 out of 4 subplots
3	present in 3 out of 4 subplots
4	present in 4 out of 4 subplots

Digitization of Teunissen data

During 2018-2019 we digitized the upperstory dataset of the Teunissen database on the basis of the vegetation tables. We focused on the upperstory data as this was recorded in numerical abundances instead of abundance classes (i.e. Braun-Blanquet type abundance scale or a relative frequency scale).

First, vegetation tables were digitized into Excel. Within the vegetation tables, per plot each species was represented by a metric. For upperstory species this consisted of the total abundance of the species with the lowest and largest DBH class. Some of the surveys in the upperstory vegetation tables contained only presence/absence data and were not further considered for this research. During digitizing into Excel, species names were kept according the then used nomenclature, correcting for potential spelling mistakes. Any plants unidentified at the species level in the vegetation tables were cross-referenced to the available correspondence on the deposited vouchers (deposited at BBS or U) and checked by Pieter Teunissen for a contemporary identification (i.e. a species scientific name might have been unknown to him in the period of sampling, but known now). When a species remained unidentified, it was updated to a unique morphospecies.

Second, after digitization into Excel, the data were combined with the program *R* to one single dataset. Taxonomic names of all the species were first updated by using the Taxonomic Name Resolution Service (TNRS v4.0; Boyle et al., 2013). We cross-referenced the updated names of all species with the Checklist of the plant of the Guiana Shield (Funk et al., 2007) to avoid erronous synomy. For example, in the case of *Carapa procera*, all individuals of these species in the Neotropics are currently considered to belong to *Carapa surinamensis*, while the name *C. procera* is still valid for individuals in the African tropics. TNRS will in this case accept the name *C. procera*, while the correct name should be *C. surinamensis*. Last, we updated the names of the woody species accoring to the Amazon Tree Checklist as this is currently the most up to date list of neotropical woody species taxonomic names (ter Steege et al., 2019b). For this research an updated version of this list was used, version 20200401.

Dataset characteristics

The digitized Teunissen dataset comprised of 287 0.04 ha plots of tropical forests that were distributed across the northern part of Suriname, i.e. the Coastal Plain and Savanna Belt, which lies between 4°45 to 6° N (Figure 1). Of the 287 plots representing 0.04 ha, 24 (8.3%) had been extrapolated to 0.04 ha by Teunissen from a smaller survey area (i.e. 4 x 0.01 ha, 6 x 0.02 ha and 14 x 0.03 ha). According to the National Planning Atlas of Suriname (SPS et al., 1988), within the study area of the Coastal Plain and Savanna Belt, altitude varied between 0 to 100 m above average sea level ("Normaal Surinaamse Peil", NSP), the climate could be mostly classified as 'Af' within the Köppen climate classification (i.e. the mean temperature is always higher than 18 °C and the monthly average rainfall is always more than 60 mm), where only a narrow strip along the coast of the Coronie District had a 'Am' climate (i.e. the mean temperature is always higher than 18 °C but the monthly average rainfall can be less than 60 mm and total annual rainfall is less than 1750 mm). The average annual rainfall for this area between 1971-1980 ranged from ca. 1500 at the coast to about 2500 mm towards the interior and the mean monthly temperature for Suriname between ranged between 26.2-28.2 °C with an annual amplitude to 2-3 °C (SPS et al., 1988). Most plots represented predominantly climax lowland wet tropical forest, except for a few that contained patches of regenerating forest on old cotton plantations. These plantations have been abandoned since around 1914-1917 and its vegetation has been regenerating towards climax vegetation. Here, 'climax' refers to the state of vegetation naturally occurring after historical or under contemporary disturbance by native indigenous people (sensu Levis et al., 2018). Soil hydrology varied across terra firme (n = 138), seasonally flooded (n = 70) and permanently inundated, 'marsh' or 'swamp' (n = 79) soils. The dominant surface soil type varied between clay and silty clay in the Coastal Plant to white and brown sands in the Savanna Belt (SPS et al., 1988).

Experiences based on re-visits of ten Teunissen plots in 2018 and other floristic fieldwork in Suriname during 2017-2019 gave the impression that the climax vegetation that has been captured in the Teunissen surveys in the 1970ties still provides a good characterization of the climax vegetation that can be currently found in Suriname. Based on our experiences on how NTFPs are harvested, past or recent harvest of NTFPs is unlikely to have had an significant impact on the standing vegetation. In support, in 2006 the MSc student Havinga supervised by van Andel studied the ecological implications of the harvest of medicinal plant-based NTFPs in Suriname and concluded that there were no indications for "large scale unsustainable extraction" of medicinal NTFPs (Havinga, 2006). For his analysis, Havinga carried out interviews and walks-in-the-woods with multiple harvesters of plant-based NTFPs, including all growth forms of NTFP species. Although there has been some forest cover loss and forest conversion in the study area since the 1970ties, it is our impression that up to now most of the climax vegetation in Suriname has remained intact. In support, the rate of forest cover loss in Suriname has been found to be relatively low, i.e. around 0.04% per year for the period between 2000-2015, to be geographically clustered around the area outside the coastal area (i.e. around the Greenstone belt and the Brokopondo reservoir), and has been mainly driven by activities related to gold mining, infrastructure development and urban development (i.e. not harvest of NTFPs; NIMOS, SBB and UNIQUE, 2017).

To calculate the structural plant diversity indicator of the average of the maximum diameters, we converted the DBH class to the mean cm of the diameter range that that class represented, e.g. DBH class 2 (15-25 cm) was converted to 20 cm.

Annex S4.2 NTFP species selection

For our NTFP species selection we only included wild plant species that produce commercially traded NTFPs in Suriname. Here 'wild' was defined as being self-replicating without human intervention (i.e. not domesticated, although possibly cultivated) and 'commercial' as being reportedly sold for money in 2017-2018. To identify the commercially relevant NTFP species we first combined data of multiple NTFP surveys carried out in Suriname during 2004-2006 and 2016 (Ruysschaert, 2018; van Andel et al., 2007; van Andel & Havinga, 2008; van Andel & Ruysschaert, 2011; van den Boog et al., 2018), pooling 393 unique NTFP producing plant species, hereafter 'NTFP species'. Second, to verify that the mentioned NTFP species were still commercially traded in Suriname between 2017-2018, we carried out market surveys of our own. We focussed our market surveys primarily on the main NTFP trade hub in Suriname, the 'Vreedzaammarkt'. In the course of February to April 2017, February to April 2018 and August 2018 we made a total of 31 market visits during which we inventoried the floristic composition of the NTFPs sold. We always inventoried multiple stands and carried out multiple interviews. In total, we interviewed a subgroup of 25 unique market vendors of the estimated ca. regular 200 vendors selling wild plant-based NTFPs in the markets in Paramaribo, as observed during the period 2017-2018. In addition, we built up a trust-relationship with 4 market vendors for in-depth interviews. We always asked the vendors for their consent to be interviewed and their permission to use the data for research. We offered financial compensation to all interviewed vendors for their time.

From the list of NTFP species inventoried during the market surveys we selected only wild NTFP species on the basis of interview data, field observation and literature, and we updated the Taxonomy of the NTFP species names after the Amazonian Tree Checklist. This resulted in a preliminary selection of 358 wild and commercially relevant NTFP plant species. Of these 358 NTFP plant species, 58 tree and palm species were present in the Teunissen dataset (Table S4.2.1).

Table S4.2.1. The 58 commercially relevant tree and palm species present in the Teunissen dataset. Taxonomy sensu the Amazon Tree Checklist (ter Steege, et al., 2019b).

Species	Family	Growth form	Parts sold	Uses	Refs
Ambelania acida Aubl.	Apocynaceae	Tree	Leaves	General health	Ruysschaert (2018)
Astrocaryum aculeatum G.Mey.	Arecaceae	Palm	Oil from seeds	Fractures	van Andel & Ruysschaert (2011)
Astrocaryum sciophilum (Miq.) Pulle	Arecaceae	Palm	Seeds, Oil from seeds, Fat from seeds	Ritual	van Andel et al. 2007; van Andel & Havinga 2008; van Andel & Ruysschaert (2011)
Astrocaryum vulgare Mart.	Arecaceae	Palm	Aerial roots, Oil from seeds, fruit	Pregnancy, Fractures	van Andel et al. 2007; van Andel & Havinga 2008; van Andel & Ruysschaert (2011); Ruysschaert (2018)
Attalea maripa (Aubl.) Mart.	Arecaceae	Palm	Ashes, Oil from seeds, fruit, Young Leaves, Aerial roots, Spathe	Ritual, Pregnancy, Stimulant	van Andel et al. 2007; van Andel & Havinga 2008
Byrsonima crassifolia (L.) Kunth	Malpighiaceae	Tree	Leaves	Genital bath, Headache	Ruysschaert (2018)
Byrsonima spicata (Cav.) Rich. ex Kunth	Malpighiaceae	Tree	Twigs and Leaves	Genital bath	van Andel & Havinga 2008; van Andel & Ruysschaert (2011); Ruysschaert (2018)
*Carapa guianensis** Aubl.	Meliaceae	Tree	Oil from seeds, Bark	Skin cosmetic, Diabetes	van Andel et al. 2007; van Andel & Havinga 2008; van Andel & Ruysschaert (2011)
*Carapa surinamensis** Miq.	Meliaceae	Tree	Oil from seeds, Bark	Skin cosmetic, Diabetes	van Andel & Ruysschaert (2011)
Casearia arborea (Rich.) Urb.	Salicaceae	Tree	Ashes	Ritual	van Andel & Havinga 2008; van Andel & Ruysschaert (2011)
Cecropia obtusa Trécul	Urticaceae	Tree	Twigs and Leaves	Ritual	Havinga (2006); van Andel & Ruysschaert (2011)
Copaifera guyanensis Desf.	Fabaceae	Tree	Oil from seeds, Bark	Diabetes, Hypertension, Skin cosmetic, General health	van Andel et al. 2007
Cordia tetrandra Aubl.	Boraginaceae	Tree	Twigs and Leaves	Genital bath	van Andel et al. 2007; van Andel & Havinga 2008
Couratari guianensis Aubl.	Lecythidaceae	Tree	Fruits	Ritual	van Andel et al. 2007; van Andel & Havinga 2008; van Andel & Ruysschaert (2011)

Species	Family	Growth form	Parts sold	Uses	Refs
Couratari stellata A.C.Sm.	Lecythidaceae	Tree	Bark	Ornamental, Ritual	Havinga (2006); van Andel & Ruysschaert (2011)
Didymopanax morototoni (Aubl.) Decne. & Planch. (syn. *Schefflera morotoni*)	Araliaceae	Tree	Leaves	General health, Genital bath	Havinga (2006); van Andel et al. 2007; van Andel & Havinga 2008; van Andel & Ruysschaert (2011)
Dimorphandra conjugata (Splitg.) Sandwith	Fabaceae	Tree	Leaves	Ornamental, Insect repellent	Ruysschaert (2018)
Eperua falcata Aubl.	Fabaceae	Tree	Fruits	Ritual	van Andel & Ruysschaert (2011); Ruysschaert (2018)
Eugenia patrisii Vahl	Myrtaceae	Tree	Twigs and Leaves	General health	Havinga (2006); van Andel et al. 2007; van Andel & Havinga 2008
Euterpe oleracea Mart.	Arecaceae	Palm	Young leaves, Infloresence, Fruits, Aerial roots	Ritual, Food, Pregnancy	Havinga (2006); van Andel et al. 2007; van Andel & Havinga 2008; van Andel & Ruysschaert (2011); Ruysschaert (2018)
Goupia glabra Aubl.	Goupiaceae	Tree	wood to burn	Fauna attractant	Havinga (2006); van Andel & Ruysschaert (2011)
Guatteria schomburgkiana Mart.	Annonaceae	Tree	Leaves	Genital bath	van Andel & Havinga 2008
Gustavia augusta L.	Lecythidaceae	Tree	Bark	General health	Havinga (2006); van Andel & Ruysschaert (2011)
Hirtella paniculata Sw.	Chrysobalanaceae	Tree	Twigs and Leaves	Genital bath	van Andel et al. 2007; van Andel & Havinga 2008; van Andel & Ruysschaert (2011); Ruysschaert (2018)
Hymenaea courbaril L.	Fabaceae	Tree	Bark, Oleoresin, fruit	Hypertension, Diarrhea	Havinga (2006); van Andel et al. 2007; van Andel & Havinga 2008; van Andel & Ruysschaert (2011)
Inga alba (Sw.)Willd.	Fabaceae	Tree	Bark	Wounds, Sores, Ritual	van Andel et al. 2007; van Andel & Havinga 2008; van Andel & Ruysschaert (2011)
Inga edulis Mart.	Fabaceae	Tree	Fruits	Food	van Andel & Ruysschaert (2011)

Species	Family	Growth form	Parts sold	Uses	Refs
Inga heterophylla Willd.	Fabaceae	Tree	Twigs and Leaves	Ritual	Havinga (2006); van Andel et al. 2007; van Andel & Havinga 2008; van Andel & Ruysschaert (2011)
Jacaranda copaia (Aubl.) D. Don	Bignoniaceae	Tree	Leaves	Skin health; ocular health	Havinga (2006); van Andel & Ruysschaert (2011
Lueheopsis rosea (Ducke) Burret	Malvaceae	Tree	Twigs and Leaves	Ritual	Havinga (2006); van Andel et al. 2007; van Andel & Ruysschaert (2011)
Maprounea guianensis Aubl.	Euphorbiaceae	Tree	Twigs and Leaves	Genital bath, Dental health	Havinga (2006); van Andel et al. 2007; van Andel & Havinga 2008; van Andel & Ruysschaert (2011); Ruysschaert (2018)
Mauritia flexuosa L.f.	Arecaceae	Palm	Aerial roots	Pregnancy	van Andel et al. 2007; van Andel & Havinga 2008; van Andel & Ruysschaert (2011)
Miconia lepidota Schrank & Mart. ex DC.	Melastomataceae	Tree	Twigs and Leaves	Genital bath	Havinga (2006); van Andel et al. 2007; van Andel & Havinga 2008; van Andel & Ruysschaert (2011)
Miconia prasina (Sw.) DC.	Melastomataceae	Tree	Twigs and Leaves	Genital bath	Havinga (2006); van Andel et al. 2007; van Andel & Havinga 2008; van Andel & Ruysschaert (2011)
Ocotea guianensis Aubl.	Lauraceae	Tree	Twigs and Leaves	Hair improvement	Havinga (2006); van Andel et al. 2007; van Andel & Havinga 2008
Oenocarpus bacaba Mart.	Arecaceae	Palm	Aerial roots, Fruits, Young leaves	Pregnancy, Ritual	van Andel et al. 2007; van Andel & Havinga 2008; van Andel & Ruysschaert (2011); Ruysschaert (2018)
Parinari campestris Aubl.	Chrysobalanaceae	Tree	Twigs and Leaves	Ritual	Havinga (2006); van Andel et al. 2007; van Andel & Havinga 2008; van Andel & Ruysschaert (2011)
Parkia pendula (Willd.) Walp.	Fabaceae	Tree	Bark, Leaves	Ritual, Genital bath	van Andel et al. 2007; van Andel & Havinga 2008; van Andel & Ruysschaert (2011); Ruysschaert (2018)
Parkia ulei (Harms) Kuhlm.	Fabaceae	Tree	Bark	Ritual, Genital bath	van Andel et al. 2007; van Andel & Havinga 2008

Species	Family	Growth form	Parts sold	Uses	Refs
Protium altissimum (Aubl.) Marchand (syn. *Tetragastris altissima*)	Burseraceae	Tree	Oleoresin	Ritual	Havinga (2006); van Andel & Ruysschaert (2011)
Protium heptaphyllum (Aubl.) Marchand	Burseraceae	Tree	Leaves, Oleoresin	Genital bath, Ritual	Havinga (2006); van Andel et al. 2007; van Andel & Havinga 2008; van Andel & Ruysschaert (2011)
Protium stevensonii (Standl.) Daly (syn. *Tetragastris panamensis*)	Burseraceae	Tree	Oleoresin	Ritual	van Andel et al. 2007; van Andel & Havinga 2008; van Andel & Ruysschaert (2011)
Quararibea guianensis Aubl.	Malvaceae	Tree	Stem	Ritual	Havinga (2006); van Andel et al. 2007; van Andel & Havinga 2008; van Andel & Ruysschaert (2011)
Simaba orinocensis Kunth	Simaroubaceae	Tree	Twigs and Leaves	Ritual	Havinga (2006)
Spondias mombin L.	Anacardiaceae	Tree	Leaves, Bark	Genital bath, Wounds, Kidney problems	Havinga (2006); van Andel et al. 2007; van Andel & Havinga 2008; van Andel & Ruysschaert (2011)
Symphonia globulifera L.f.	Clusiaceae	Tree	Oleoresin	Ritual	Havinga (2006); van Andel et al. 2007; van Andel & Havinga 2008; van Andel & Ruysschaert (2011)
Tabernaemontana undulata Vahl	Apocynaceae	Tree	Leaves	Skin sores	Havinga (2006); van Andel et al. 2007; van Andel & Havinga 2008; van Andel & Ruysschaert (2011)
Tachigali melinonii (Harms) Zarucchi & Herend. (syn. *Sclerolobium melinonii*)	Fabaceae	Tree	Leaves	Ritual	Havinga (2006); van Andel & Ruysschaert (2011)
Terminalia amazonia (J.F.Gmel.) Exell	Combretaceae	Tree	Twigs and Leaves	Genital bath	Havinga (2006); van Andel et al. 2007; van Andel & Havinga 2008; van Andel & Ruysschaert (2011); Ruysschaert (2018)
Trema micrantha (L.) Blume	Cannabaceae	Tree	Twigs and Leaves	General health	Havinga (2006); van Andel & Ruysschaert (2011)
Virola surinamensis (Rol. ex Rottb.) Warb.	Myristicaceae	Tree	Fruits	Female sterility	van Andel et al. 2007; van Andel & Havinga 2008; van Andel & Ruysschaert (2011)

Species	**Family**	**Growth form**	**Parts sold**	**Uses**	**Refs**
Vismia cayennensis (Jacq.) Pers.	Hypericaceae	Tree	Twigs and Leaves	Genital bath	van Andel et al. 2007; van Andel & Havinga 2008; van Andel & Ruysschaert (2011)
Vismia guianensis (Aubl.) Pers.	Hypericaceae	Tree	Twigs and Leaves	Genital bath	van Andel et al. 2007; van Andel & Havinga 2008; van Andel & Ruysschaert (2011)
Zanthoxylum pentandrum (Aubl.) R.A.Howard	Rutaceae	Tree	Roots	Ritual	van Andel et al. 2007; van Andel & Havinga 2008; van Andel & Ruysschaert (2011)
Zygia latifolia (L.) Fawc. & Rendle	Fabaceae	Tree	Leaves	Ritual	Havinga (2006)

* including 3 *Carapa* morphospecies (most likely belonging to *C. surinamensis* or *C. guianensis*)

Annex S4.3 Scatterplots between NTFP abundance and plant diversity indicators

For each plot, we calculated six taxonomic and two structural diversity indicators at the species level. As taxonomic diversity indicators, we calculated the species richness, the Camargo index (E'), the Shannon-Wiener index (H'), the Gini-Simpson index (1-D), and the effective number of species based on the Shannon-Wiener index (^{1}D) and based on the Gini-Simpson index (^{2}D).

The Camargo index (E'; hereafter the Camargo evenness) is a measure of the relative evenness of species abundances, ranging from 0, indicating uneven abundances, to 1, indicating even abundances, and is considered to be relatively independent from species richness (Tuomisto, 2012). It is calculated approximately as $E' = 1 - (\sum |p_i - p_j|) / S$, where S is the species richness, p_i is the observed relative abundance of the ith species, p_j is the observed relative abundance of the jth species (for the full formula see under 'Mean pairwise similarity' in Table 2 of Tuomisto, 2012).

The Shannon-Wiener index (H'; hereafter the Shannon diversity) and the Gini-Simpson index (1-D; hereafter the Simpson diversity) are measures of both species richness and species evenness, ranging from 0, indicating species poor and uneven abundances, to 1 (for 1-D) and 4 (for H'), indicating species rich and even abundances. Simpson and Shannon diversity differ in the weight assigned to abundant species, where the Simpson diversity is more sensitive to abundant species (Tuomisto, 2012). The Shannon-Wiener index is calculated approximately as $H' = - \sum (p_i \ln p_i)$ and the Gini-Simpson index is calculated as $1 - D$, where $D = \sum p_i^2$ (for the full formulae see under 'Shannon-entropy' and 'Gini-Simpson index' in Table 1 of Jost, 2006).

The effective number of species (^{q}D; hereafter called effective species diversity; also called Hill diversity) is the theoretical maximal number of equally abundant species that a given community can be expected to hold (Jost, 2006; Tuomisto, 2012). The effective number of species (^{q}D) ranges from 1 to the total number of species (S), where values close to 1 indicate that a community is little diverse (i.e. it has only one species or one species is extremely dominant) and values close to S indicate that a community is very diverse (i.e. it is maximally diverse in terms of equally abundant species).

The effective species diversity (^{q}D) can be calculated on the basis of different *q* indexes, including species richness, the Shannon-Wiener index and the Gini-Simpson index, which represent increasing emphasis on abundant species (Tuomisto, 2012). With species richness as index all species have equal weight and here the *q* index is '0', while with the Shannon-Wiener index and with the Gini-Simpson index abundant species have an increasing weight and here the q indexes are '1' and '2', respectively. These *q* indexes are also called Hill numbers. For our dataset, we calculated ^{q}D on the basis of the Shannon-Wiener index (i.e. exp(H'); ^{1}D; hereafter called the effective Shannon diversity) and on the basis of the Gini-Simpson index (1/(1-(1-D)); ^{2}D; hereafter the effective Simpson diversity) (for the full formulae see under 'Shannon-entropy' and 'Gini-Simpson index' in Table 1 of Jost, 2006).

Converted Shannon-Wiener or Gini-Simpson diversity indexes to effective Shannon diversity and effective Simpson diversity has two advantages above the unconverted, original versions of diversity: it follows the 'doubling' property, where with double the amount of diversity its value doubles as well, and it has a more linear relationship to species richness, where a particular difference in diversity values always corresponds to roughly the same difference in amount of species (See Jost, 2006, for a discussion). Although the original versions of Shannon-Wiener diversity and Gini-Simpson diversity have less convenient statistical properties, we included them in our analyses because we found that they are frequently used in the literature and our aim was to generate relationships that were comparable to other reported relationships.

As structural diversity indicators, we calculated the stem density and the average of the maximum diameter at breast height. The average of the maximum diameter at breast height (avr. max. DBH) is a measure of the size of the largest stems in a plot ((∑ maximum ø per species) / number of species).

Table S4.3.1. Range, mean and standard deviation (SD) values of the eight diversity indicators across all plots for all plant species, non-NTFP species and NTFP species.

Plant diversity indicator	**All species**		**Non-NTFP species**		**NTFP species**	
	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range
Species richness (# spp)	15.96 (± 6.96)	1 - 37	12.75 (± 6.12)	1 - 31	3.21 (± 1.94)	0 - 11
Species Carmago evenness (E')	0.53 (± 0.15)	0.19 - 1	0.63 (± 0.15)	0.25 - 1	0.66 (± 0.18)	0.25 - 1
Species Shannon diversity (H')	2.14 (± 0.72)	0 - 3.42	2.08 (± 0.66)	0 - 3.25	0.76 (± 0.55)	0 - 1.79
Species Simpson diversity (1-D)	0.78 (±- 0.19)	0 - 0.96	0.8 (± 0.17)	0 - 0.96	0.47 (± 0.30)	0 - 1
Effective Shannon diversity (^{1}D)	10.63 (± 6.33)	1 - 30.50	9.57 (± 5.27)	1 - 25.71	2.47 (± 1.33)	1 - 6.01
Effective Simpson diversity (^{2}D)	7.82 (± 5.19)	1 - 23.77	7.62 (± 4.45)	1 - 22.50	2.25 (± 1.12)	1 - 5.44
Stem density (# stems)	59.66 (+- 34.80)	10 - 248	41.17 (± 34.81)	3 - 216	18.49 (± 22.78)	0 - 120
Average maximum diameter (cm)	22.08 (+- 6.93)	10 - 80	21.16 (± 8.02)	10 - 80	27.12 (± 13.13)	2.5 - 100

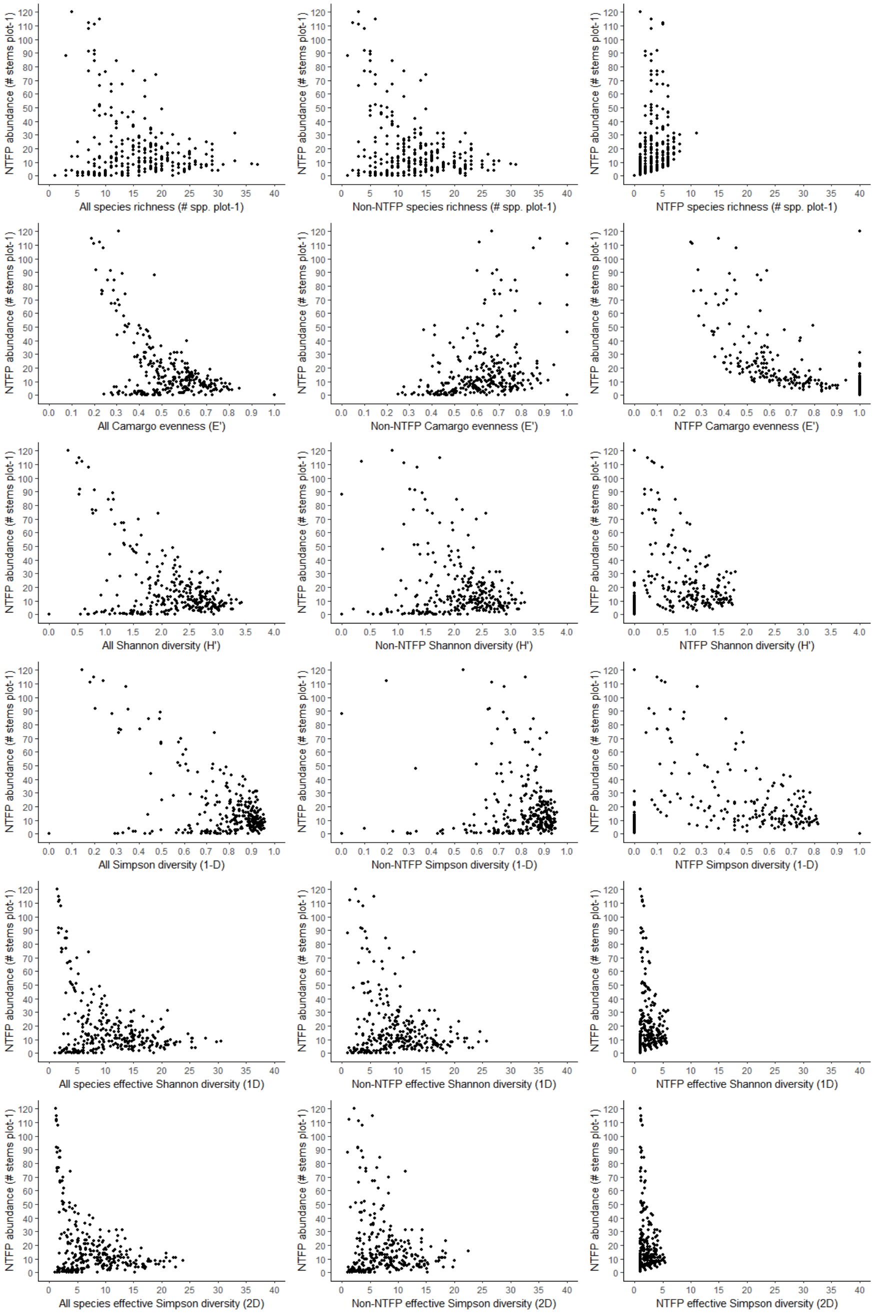

Figure S4.3.1. Scatterplots of the NTFP abundance versus taxonomic plant diversity indicators across all plots (n=287), calculated from the all-group (left column), non-NTFP group (middle column) and NTFP group (right column).

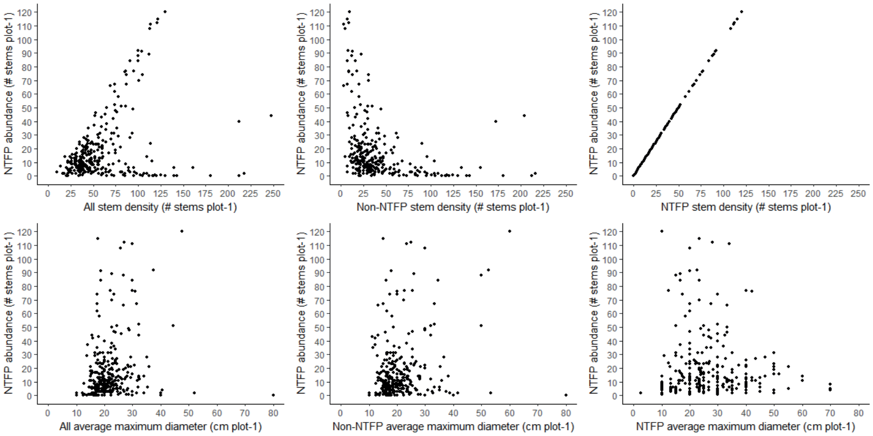

Figure S4.3.2. Scatterplots of the NTFP abundance versus structural plant diversity indicators across all plots (n=287), calculated from the all-group (left column), non-NTFP group (middle column) and NTFP group (right column).

Annex S4.4 Methodology

Correlations

Kendall's tau (τ) correlation tests were chosen as the NTFP abundance and plant diversity indicators values did not follow a normal distribution and can contain a large number of tied data (i.e. numbers of the exact same values). Because of the latter, Kendall's tau is preferable to the Spearman's rho. Kendall's tau is based on the number of concordant and discordant pairs: both variables are ranked, and if at a given position the ranks of both variables agree in their relative ranking, then it counts as a concordant pair. The number of concordant pairs is divided by the total number of possible concordant pairs to give the value of tau, which ranges from -1, meaning a strong negative correlation, to 1, meaning a strong positive correlation, and where 0 means that there is no correlation. Note that as Kendall's tau correlation test is based on the ranks of the value, the absolute difference between values does not matter. This is a big contrast with how linear models work, such as Pearson correlation tests or the generalized linear models that we used in this paper.

Generalized linear regression models

The distribution of NTFP abundance was left-skewed but not zero-inflated as it contained 18 zero values out of 269 non-zero values.

GLMs are preferable above the procedure of transformation non-normal variables to linearize them and then using them in a linear model because when outcomes of the latter procedure need to be interpreted, the mean and error values need to be back-transformed, but the relationship between the mean and the errors changes due to the back transformation. In contrast, in GLMs the log-link between Y and X is specified but it does not produce error values that need to be back—transformed in order to be interpretable. Moreover, as we have count-data, values are never negative, while transforming a non-linear distribution still can contain negative values (Zuur, Leno and Smith, 2007; Chpt 5 and 6).

We used a VIF of 3 as this is perceived to be relatively conservative in comparison to the other propagated value of 10 (Zuur et al., 2010).

The unrestricted maximal model contained 5 single variable and 10 two-way interactions. With a sample size of 287 this meant that for this model we had a sample size of 19 per parameter, which is well above the conservative 10, keeping the risk of overfitting such a model low (Crawley, 2015; p.206).

Model optimization

The hypothesis driven backward selection procedure is described in table 9.2 in Crawley et al. (2007). In short, with each step a non-significant parameter is dropped, and this new model is compared to the old model with a Log-Likelihood Ratio Test, 'LTR', under the null hypothesis that there is no significant difference in the amount of deviance that the models explain. For each step the priority is given to the least significant parameter (i.e. the highest p-value) and at the highest level of interactions, subsequently working towards lower level interactions and stopping at the single variables (main effects).

After the best practice for model optimization (sensu Crawley, 2007; p. 329):

- Our dataset was orthogonal, as all of the treatment combinations are equally represented and there are very few missing values (i.e. 3 NAs in n = 287 for the Camargo evenness), thus the order of variables entered in the models do not matter and we can use both Type I and Type III which type ANOVAs;
- After VIF tests remaining variables were not correlated (i.e. VIF < 3); and
- All maximal models and minimal adequate models are provided in the Supplementary methods.

We choose not to show all optimization steps as this would take up much space. The restricted model was optimized after two steps, the unrestricted model was optimized after 22 steps.

Pseudo-R^2

We calculated a 'pseudo-R^2' as a goodness-of-fit for each model (after Dobson, 2002, in Zuur et al., 2009) and compared these between the restricted and unrestricted models to examine the potential added value of allowing interactions. Here, pseudo-R^2 = (null deviance – residual deviance model) / null deviance, which is synonymous to the McFadden's Pseudo-R^2. Note that the null deviance is the deviance that is explained by the null model, which is a model that does not have any coefficients and only an intercept. A pseudo-R^2 can be interpreted as the amount of variation in NTFP abundance explained by the model compared to the amount of variation in NTFP abundance explained by having no model (Zuur et al., 2009) and can only be compared between models when they are nested.

LRTs

We use LRTs for both NB GLM optimization (after Faraway, 2016, p.94; Field, Miles and Field, 2012, section 8.6.1) and as omnibus test in analysis of variance within NB GLMs. An LRT compares two Log-Likelihoods which are estimated in the NB GLMs with the maximum-likelihood method. As each Log-Likelihood estimation is based on the number of variables that is needs to estimate, it can be different for each model. The ratio between two Log-Likelihoods is therefore dependant on the number of variables and thus the difference in number of variables between two number or the degrees of freedom. This ratio is called the 'Log-Likelihood Ratio statistic', χ^2_{df}, and follows a Chi-square distribution for each number of freedom that is compared. An LRT requires that the models are nested—i.e. the more complex model can be transformed into the simpler model by imposing constraints on the former's parameters. For example, model 1 has Y predicted by the continuous variable X and categorial variable Z, and model 2 has Y predicted by continuous variable X. Model 2 is nested within model 1, no matter how much categories are in Z. Further assumptions of a LTR are that the data need to be independent and the sample size need to be larger than 5 (Field et al., 2012).

In NB GLM optimization, an LTR tests the null hypothesis that there is no significant difference in the amount of deviance that two models explain. In an omnibus LTR test, the hypothesis is tested that one or more mean values are different from each other.

ANOVA

We used Tukey Post-hoc tests to examine which clusters were different from each other (modified after t-tests in Field, 2012). The difference between two means are divided by the error of this difference to get a Z-value. As Z-values are assumed to follow a normal distribution, the Z-value is then checked against the normal distribution to detect if the difference between the two means is significant (i.e. $p < 0.05$). The Tukey Post-hoc test adjusts the p-value for multiple testing, controlling the family-wise error rate (i.e. the increased chance to get a false positive, Type I error, when multiple tests are carried out in sequence). In addition, the Tukey Post-hoc test carries out its comparisons on basis of the variance of all data (variance is used to get the error), in contrast to using the variance calculated on only the particular contrast, making the outcome of the test more robust against differences in sample sizes for a particular comparison (i.e. it is more conservative than other tests when samples sizes are not equal; Field, Miles and Field, 2012, section 10.5.2). By doing so, Tukey's post hoc tests assumes that the variances for each category are similar to each other (homogeneity of variance). In our data, we have not reason to assume otherwise, i.e., we assume that the variances for each category are similar. Last, Tukey's post hoc test assumes that the data are independent of each other.

R packages used

All taxonomic plant diversity indicators were calculated using the vegan R package (Oksanen et al., 2019) except for the Camargo evenness, for which a dedicated function was written by the main author.

All statistical analyses and model fitting were carried out using the '**stats**' and '**pastecs**' packages (Grosjean & Ibanez, 2018; R Core Team, 2019) unless stated otherwise below:

- Generalized linear models using a negative binomial error distribution and a log-link were fitted using the '**MASS**' package (Venables & Ripley, 2002).
- General additive models were fitted using the '**mgcv**' package (Wood, 2011).
- The Variance Inflation Factor, 'VIF', was calculated using the '**car**' package (Fox & Weisberg, 2019).
- Standardized beta coefficients were calculated using the '**lm.beta**' package (Behrendt, 2014).
- Tukey Post-hoc tests were applied using the '**multcomp**' package (Hothorn et al., 2008).

Graphical output was generated using the '**stringr**', '**ggplot2**', '**ggpubr**' packages (Kassambara, 2019; H. Wickham, 2016; Hadley Wickham, 2019).

Annex S4.5 Bivariate analyses

Annex S4.5 has been omitted to save paper. It can be accessed at the published version of this chapter (see the beginning of this chapter for a DOI and QR code).

Annex S4.7 TWINSPAN analysis

We carried out a TWINSPAN clustering in the WinTWINs programme for Windows, version 2.3 (M. O. Hill & Šmilauer, 2005).

Method and methodology

The TWINSPAN algorithm ('two-way indicator species analysis') combines a divisive ordination of the samples with clustering on the basis of indicator species. It firstly carries out a divisive ordination of the samples using a correspondence analysis. Secondly, it improves the floristic identity of the divisions by reordering species preference. Thirdly it uses indicator ordination of the most preferential species to construct a simplified ordination which is ultimately output. For each division, WinTWINS provides the eigenvalues (λ) of the primary ordination, the number of samples within that division, and the number of indicator species. For more information see the user guide provided by the WinTWINs programme.

Eigenvalues of the correspondence analysis (λ) can be interpreted as the correlation coefficient between species scores and sample scores, i.e. how well the species optima correspond to the ordered order of samples, hence the term 'correspondence analysis'. A high eigenvalue (approaching 1) thus indicates that the order of the samples closely follows the succession of species optima, i.e. suggesting that the axis is a good representation of a coenocline - a gradient of communities (see also http://ordination.okstate.edu/CA.htm).

To find the most optimal floristic clusters that were well defined by their species, we stopped delineation of each division at where further dividing would create sub-clusters that contained only two or less indicator species (i.e. ≤ 2). For example, if the cluster 'A' was divided into two sub-clusters, one 'AA' with >2 indicator species and one 'AB' with =2 indicator species, we retained the cluster 'A'. To avoid delineating floristic clusters that are actually part of another cluster but due to a too low sample size were recognized as separate clusters, we did not consider any clusters which were based on five or less samples, with the exception of the first branch, which separated two mangrove floristic clusters from the other clusters.

Data input

Used dataset had 287 samples and 531 species. The values ranged from 1 to 156.

Table S4.7.1 Used Cut levels in TWINSPAN analysis

	Cut level	Weight	Indicator?
Level 1	0	1	Y
Level 2	2	1	Y
Level 3	5	1	Y
Level 4	10	1	Y
Level 5	20	1	Y

No samples were deleted.
No species were deleted on the basis of their frequency in data or on other basis.
All species were kept as diagnostic species.
No samples were given a non-default weight.
No species were given a non-default weight.
Maximum number of division levels: 9. Note that TWINSPAN is limited to 9 divisions.
Minimum group size for division: 5.
Maximum number of indicators per division: 7.
Number of species in final tabulation: 531.

Data output

The TWINSPAN classification was simplified to facilitate interpretation (figure S4.7.1).

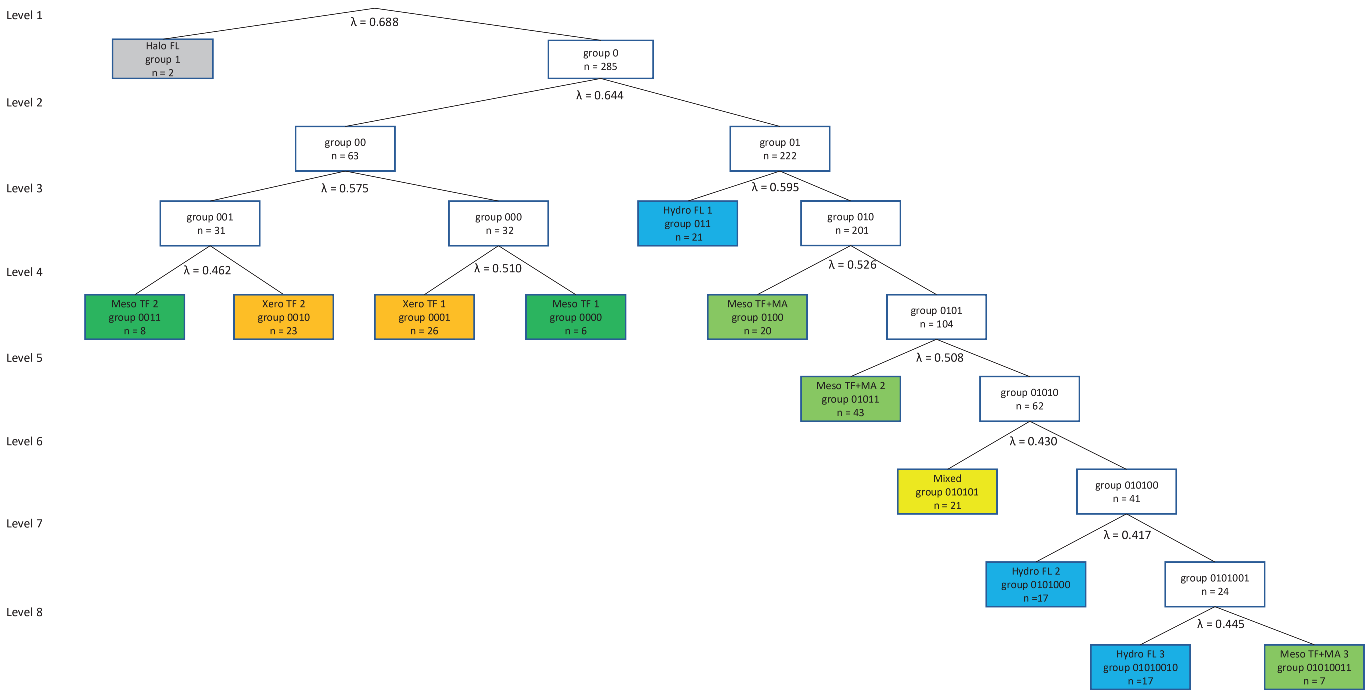

Figure S4.7.1 Simplified output of a TWINSPAN clustering of the digitized Teunissen dataset. At each division level, the eigenvalue is given (λ). Each cluster has a unique TWINSPAN group code and contains a number of samples (n; plots). The ultimate clusters have been given a working name based on the dominant physiognomy and hydrology patterns present in samples and have been coloured accordingly. Hydrology is labelled as: FL = Flooded, MA = Marsh and TF = Terra Firme; physiognomy is labelled as: Hydro = Hydrophytic, Meso = Mesophytic, Xero = Xerophytic, Halo = Halophytic. Colours represent: blue for hydrophytic flooded, light green for mesophytic terra firme and marsh, dark green for mesophytic terra firme, orange for xerophytic terra firme and yellow for mixed physiognomy and hydrology (no dominant patterns).

Indicator species per floristic cluster

Cluster 0: "Halo FL" was dominated by halophytic vegetation on flooded soils, and was indicated by the species *Avicennia germinans* (L.) L. This cluster represents Mangrove forest.

Cluster 1: "Hydro FL 1" was dominated by hydrophytic vegetation on flooded soil and indicated by the presence of *Annona glabra* L., *Ficus trigona* L.f., *Ficus pertusa* L.f., *Tabebuia insignis* (Miq.) Sandwith and *Pterocarpus officinalis* Jacq.

Cluster 2: "Meso TF 1" was dominated by mesophytic vegetation on terra firme, and indicated by the presence of *Licania incana* Aubl., *Clusia fockeana* Miq. and *Cybianthus fulvopulverulentus* (Mez) G.Agostini

Cluster 3: "Xero TF 1" was dominated by xerophytic vegetation on terra firme, and indicated by the absence of *Protium heptaphyllum* (Aubl.) Marchand, *Pera bicolor* (Klotzsch) Müll.Arg. and *Parinari campestris* Aubl.

Cluster 4: "Meso TF 2" was dominated by mesophytic vegetation on terra firme, and indicated by the presence of *Unonopsis glaucopetala* R.E.Fr. and *Tapirira guianensis* Aubl.

Cluster 5: "Xero TF 2" was dominated by xerophytic vegetation on terra firme, and indicated by the absence of *Eperua falcata* Aubl. and *Lecythis corrugata* Poit.

Cluster 6: "Meso TF + MA 1" was dominated by mesophytic vegetation on terra firme and marsh soils, and indicated by the presence of *Euterpe oleracea* Mart., *Diospyros guianensis* (Aubl.) Gürke, *Carapa guianensis* Aubl. and *Pterocarpus officinalis* Jacq.

Cluster 7: "Meso TF + MA 2" was dominated by mesophytic vegetation on terra firme and marsh soils, and indicated by the presence of *Attalea maripa* (Aubl.) Mart., *Carapa guianensis* Aubl. and *Trichilia quadrijuga* (Miq.) Kunth

Cluster 8: "Mixed" was not dominated by any physiognomy or hydrology type, and was indicated by the presence of *Diospyros guianensis* (Aubl.) Gürke, *Amanoa guianensis* Aubl. , *Myrcia neomontana* E.Lucas & C.E.Wilson, *Garcinia madruno* (Kunth) Hammel and *Caryocar microcarpum* Ducke.

Cluster 9: "Hydro FL 2" was dominated by hydrophytic vegetation on flooded soils, and was indicated by the absence of *Hymenopus heteromorphus* (Benth.) Sothers & Prance, *Tabebuia insignis* (Miq.) Sandwith, *Macoubea guianensis* Aubl., *Macrosamanea discolor* (Willd.) Britton & Killip, *Symphonia globulifera* L.f., and *Tapirira guianensis* Aubl.

Cluster 10: "Meso TF + MA 3" was dominated by mesophytic vegetation on terra firme and marsh soils, and indicated by the absence of *Pterocarpus officinalis* Jacq., *Euterpe oleracea* Mart. and *Symphonia globulifera* L.f.

Cluster 11: "Hydro FL 3" was dominated by hydrophytic vegetation on flooded soil and indicated by the presence of *Eschweilera subglandulosa* (Steud. ex O.Berg) Miers, *Duroia eriopila* L.f., *Diospyros guianensis* (Aubl.) Gürke and *Attalea maripa* (Aubl.) Mart.

Table S4.7.2 Summary of floristic clusters. Showing the working name, the TWINSPAN output group number, the number of plots, the counts per hydrology type and the mean NTFP abundance, NTFP species richness and non-NTFP species richness with their standard deviation.

Floristic cluster working name	TWINSPAN group	plots	Hydrology types	NTFP abundance	NTFP species richness	Non-NTFP species richness
				mean (± std.dev)	mean (± std.dev)	mean (± std.dev)
0: Halo FL	*1	2	FL = 2, MA = 0, TF = 0	0 (± 0)	0 (± 0)	1 (± 0)
1: Hydro FL 1	*011	21	FL = 21, MA = 0, TF = 0	7 (± 14.5)	1.3 (± 1.2)	5.5 (± 2.3)
2: Meso TF 1	*0000	6	FL = 0, MA = 1, TF = 5	12.8 (± 5.5)	4.2 (± 1.8)	15.8 (± 4)
3: Xero TF 1	*0001	26	FL = 0, MA = 1, TF = 25	4.2 (± 4.9)	1.1 (± 1)	11.7 (± 4.6)
4: Meso TF 2	*0011	8	FL = 0, MA = 0, TF = 8	7.8 (± 2.3)	3.1 (± 1.5)	20.6 (± 4.9)
5: Xero TF 2	*0010	23	FL =2, MA = 0, TF = 21	17 (± 7.4)	1.9 (± 1)	12.8 (± 4)
6: Meso TF+MA 1	*0100	97	FL =1, MA = 33, TF = 63	10.6 (± 8.8)	4.1 (± 1.8)	17.1 (± 5.5)
7: Meso TF+MA 2	*01011	42	FL =2, MA = 30, TF = 10	25 (± 23)	3.9 (± 1.8)	9.8 (± 4)
8: Mixed	*010101	21	FL =11, MA = 8, TF = 2	14.4 (± 15.4)	2.4 (± 1.5)	11.2 (± 3.4)
9: Hydro FL 2	*0101000	17	FL =15, MA = 1, TF = 1	43.9 (± 31.6)	4.1 (± 1.7)	11.9 (± 6.5)
10: Meso TF+MA 3	*01010011	7	FL =0, MA = 4, TF = 3	29 (± 18.3)	4.3 (± 2.1)	12.3 (± 4.9)
11: Hydro FL 3	*01010010	17	FL =16, MA = 1, TF = 0	70.1 (± 30.9)	3.6 (± 1.5)	6.9 (± 4)

Output S4.7.1 R output of Omnibus LRT test of variation in NTFP abundance across floristic clusters

```
Analysis of Deviance Table (Type II tests)

Response: ntfp.dens.up
           LR Chisq   Df         Pr(>Chisq)
flor.clus  232.02     10         < 2.2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Output S4.7.2 R output of Post-hoc Tukey Contrasts of NTFP abundance across floristic clusters

Output S4.7.2 has been partly omitted to save paper. It can be accessed at the published version of this chapter (see the beginning of this chapter for a DOI and QR code).

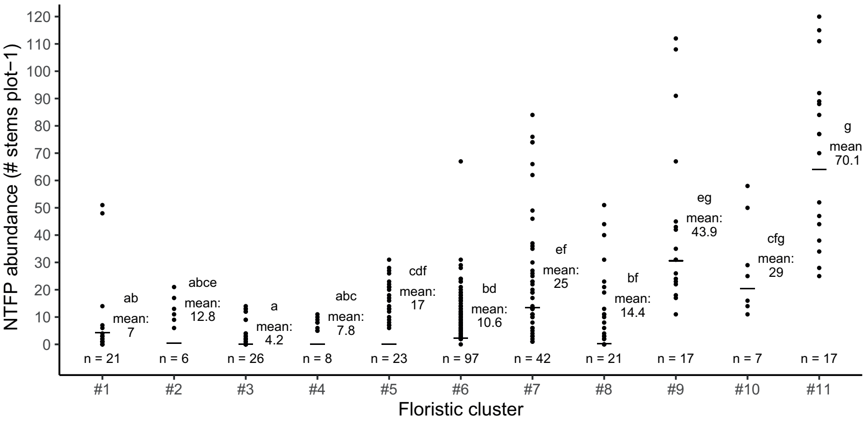

Figure S4.7.2. NTFP abundance (number of NTFP stems per plot) for 11 floristic clusters in order of identified by the TWINSPAN analysis. For each floristic cluster the number of samples (n) and the mean (horizontal line) is given. Significant differences between the means are indicated by unique letters (a to g), i.e. non-significant differences have the same letter. Total number of samples shown: 285.

Output S4.7.3. R output of LTR test of Unrestricted Model with and without floristic clusters as dummy

```
Likelihood ratio tests of Negative Binomial Models

Model: see Output S4.6.1

Model                           theta      Resid. Df   2 x log-lik    Test      d f
LR stat.                        Pr(Chi)
1 Model without floristic clusters 1.414372 275        -2110.549
2 Model with floristic clusters 2.145335   264         -2004.247      1 vs 2    1 1
106.3013   0
```

Output S4.7.4. R output of pseudo-R^2 of Unrestricted Model with and without floristic clusters as dummy

```
Pseudo-R2 Unrestricted full model without floristic clusters = ((506.9458 – 318.0974) / 506.9458)*100
= 37.2522

Pseudo-R2 Unrestricted full model with floristic clusters = ((711.8082 – 314.0385) / 711.8082)*100 =
55.8816

55.8816 - 37.2522 = 18.6294
```

Output S4.7.5. R output of LTR test of Restricted Model with and without floristic clusters as dummy

```
Likelihood ratio tests of Negative Binomial Models

Model: (NTFP abundance ~ non-NTFP species richness + non-NTFP Camargo evenness + non-NTFP
stem density)

Model                              theta       Resid. df     2 x log-lik      Test      d f
LR stat.                           Pr(Chi)
1 Model without floristic clusters 1.162291    282           -2174.087
2 Model with floristic clusters    1.893406    271           -2042.161        1 vs 2    1 1
131.9267     0
```

Output S4.7.6 R. output of pseudo-R^2 of Restricted Model with and without floristic clusters as dummy

Pseudo-R2 Restricted Model without floristic clusters = ((430.0206 – 329.9804) / 430.0206)*100 = 23.264

Pseudo-R2 Restricted Model with floristic clusters = ((643.9355 – 322.3347) / 643.9355)*100 = 49.943

49.943 - 23.264 = 26.67898

Annex S4.8 Supplementary material Relative species contributions

Table S4.8.1. Top10 NTFP species ranked by their relative contribution to NTFP abundance within the plots without Euterpe oleracea (total number of NTFP stems = 1685, total number of plots = 185). Dashed line indicated the rank at which the cumulative 50% of NTFP abundance is reached.

Species	**Family**	**NTFP abundance (# stems)**	**% Total NTFP abundance**	**Cumulative% NTFP abundance**	**Number of plots (n)**	**% Total number of plots**
Eperua falcata	Fabaceae	411	24.4	24.4	38	20.5
Attalea maripa	Arecaceae	119	7.1	31.4	34	18.4
Protium heptaphyllum	Burseraceae	110	6.5	38.0	35	18.9
Astrocaryum sciophilum	Arecaceae	110	6.5	44.5	15	8.1
Copaifera guyanensis	Fabaceae	84	5.0	49.5	32	17.3
Carapa guianensis	Meliaceae	83	4.9	54.4	20	10.8
Parinari campestris	Chrysobalanaceae	69	4.1	58.5	38	20.5
Symphonia globulifera	Clusiaceae	68	4.0	62.5	5	2.7
Goupia glabra	Goupiaceae	67	4.0	66.5	29	15.7
Gustavia augusta	Lecythidaceae	59	3.5	70.0	9	4.9

Output S4.8.1. R output of Omnibus LRT test of variation in Euterpe oleracea abundance across floristic clusters

```
Analysis of Deviance Table (Type II tests)

Response: Eut_ole_abun
          LR Chisq   Df          Pr(>Chisq)
flor.clus   206.29   10           < 2.2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Output S4.8.2. R output of post-hoc Tukey Contrasts of Euterpe oleracea abundance across floristic clusters

Output S4.8.2 has been partly omitted to save paper. It can be accessed at the published version of this chapter (see the beginning of this chapter for a DOI and QR code).

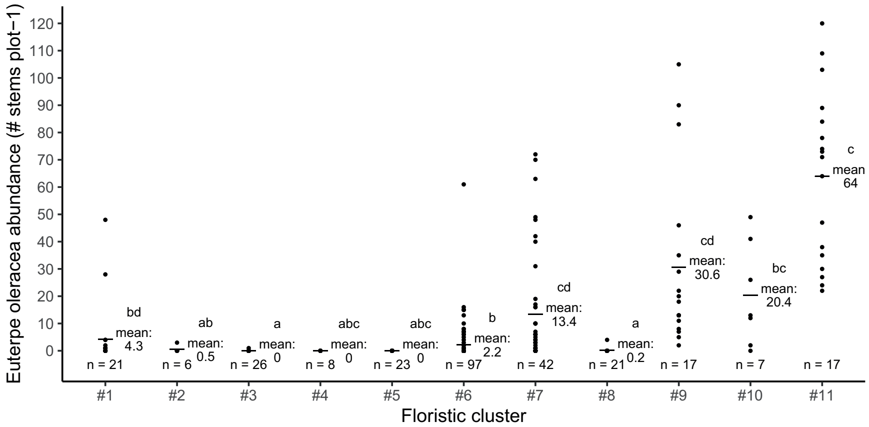

Figure S4.8.1. *Euterpe oleracea* abundance (number of stems per plot) for eleven floristic clusters recognized on the basis of a TWINSPAN analysis. For each floristic cluster the number of samples (n) and the mean (horizontal line) is given. Significant differences between the means are indicated by unique letters (a to g), i.e. non-significant differences have the same letter. Floristic cluster 0 is considered an outgroup and is not shown. Total number of samples shown: 285. See also Output S8.2.

Medicinal plants sold on the Vreedzaam market, Paramaribo, Suriname. Photo by Evelien Bos.

5

From forest stock to market: assessing the economic value of plant-based non-timber forest products and their conservation relevance in Suriname

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Abstract

In line with the 'conservation-through-use-paradigm', it has been suggested that the provisioning of non-timber forest products (NTFPs) by tropical forests can generate economic benefits that can act as incentives to keep tropical forests standing. However, it remains unclear to what extent the economic value generated by selling plant-based NTFPs can contribute to tropical forest conservation. Most studies of the economic value of NTFP provisioning estimated the potential value of the entire available NTFP supply according to current market prices, instead of a realized economic value that accounts for the volumes actually sold. In addition, most approaches do not include assessments of the economic benefits received by local stakeholders nor elaborate on the extent to which the use of NTFP provisioning may lead to overexploitation. To assess the economic value of NTFP provisioning, we developed a theoretical framework that mapped the flow of 13 plant-based NTFPs in Suriname from old-growth forest stock to the largest market of the country, thus linking harvestable NTFP supply in tropical forest to realized economic value coupled to actual NTFP sales. We found that the realized economic value of plant-based NTFP provisioning of old-growth tropical forests in Suriname was much lower (on average 0.17 USD ha^{-1} yr^{-1}) than the potential value of the harvestable supply (3,056 USD ha^{-1} yr^{-1}). The latter value was in line with previously reported potential economic values for similar use systems (ranging from 20 to 6,000 USD ha^{-1} yr^{-1}). Although harvesters of plant-based NTFPs sourced from old-growth tropical forests received on average only 37% of the realized value, our assessment of the endured costs and earned annual gross revenues suggests that most harvesters receive a reasonable income in comparison to the national minimum wage. We did not find evidence of overexploitation of the 13 plant-based NTFPs. Our findings therefore suggest a potential win-win situation for tropical forest conservation and local livelihoods. The low percentage of harvestable NTFP supply that was sold at the Vreedzaam market (on average 0.18%) illustrates that potential economic value can be a considerable overestimation of the value that is, or can be, realized. Ultimately, our findings show that the economic value of NTFP provisioning by tropical forests can only be assessed when information is available on both harvestable NTFP supply and the market for NTFPs.

5.1 Introduction

Tropical forests are treasure troves of biodiversity and ecosystem services, housing a disproportionate large number of species, storing more than a quarter of all terrestrial carbon, and providing important timber and non-timber forest products (NTFPs) (Barlow et al., 2018; Mitchard, 2018). However, tropical forests are increasingly being degraded or lost, which has been partly attributed to their perceived low socio-economic value (Barlow et al., 2018). In response to this, it has been suggested that quantifying the socio-economic values of tropical forest ecosystem services and capturing these values in financing mechanisms can help to keep tropical forests standing (Carvalho Ribeiro et al., 2018; Strand et al., 2018; Verweij et al., 2009).

NTFPs derived from wild plant, animal and mushroom species constitute important ecosystem services for communities living in and around tropical forests, generating economic value in multiple ways (Ros-Tonen & Wiersum, 2005; Shackleton et al., 2018; Shackleton & Pandey, 2014; Timko et al., 2010). The use of NTFPs such as food, medicines and crafts, avoids costs of substitute goods (Alcántara Rodríguez et al., 2020; van Andel, Croft, et al., 2015). In this way, NTFPs can also act as a 'safety-net' in economic lean years for forest dwelling communities (Shackleton & Pandey, 2014). In addition, the sale of NTFPs, including those used according to cultural traditions, provides a source of a cash income for many people involved in the market chain (Ros-Tonen & Wiersum, 2005; Shackleton & Pandey, 2014; van Andel et al., 2007). This source of cash income can be especially important for rural communities. For instance, for several forest-dwelling communities in Colombia and Suriname the sale of NTFPs is one of the few sources of cash income, while their need for cash has been increasing over the last few decades (Ramirez-Gomez et al., 2015, 2016, 2017). In particular, it has been suggested that the cash income received by local stakeholders may function as an incentive to keep tropical forests standing, in line with the 'conservation-through-use paradigm' (Kusters et al., 2006; E. Marshall et al., 2006; A. C. Newton, 2008).

Since the 1980s, there has been increasing scientific attention for the economic value of NTFP provisioning by tropical forests in light of the conservation-through-use paradigm (Godoy et al., 1993; A. C. Newton, 2008). Studies focusing on this subject are characterized by ethnobotanical, ecological or economical approaches, or a combination thereof. Ethnobotanical studies focus on the identity, use and value of NTFPs from the perspective of the users, for example, how and why NTFP are used in a particular way, and in what social and economic settings (e.g. Monteiro et al., 2010; van 't Klooster et al., 2018; van Andel, Ruysschaert, et al., 2015). Ecological studies focus on the species that provision NTFPs from the perspective of the tropical forests, for example, how species are distributed across different forests, the volume of NTFPs produced over time, and to what extent harvest impacts plant and animal populations (e.g. P. Newton et al., 2011, 2012; Stanley et al., 2012; Steur et al., 2021). Last, economic studies focus on the value of NTFPs from the perspective of the economy, for example, how much NTFPs are used, what economic value is associated to its use, and how benefits are distributed across value chains (e.g. Hilfiker et al., 2006; Jensen, 2009; Williams et al., 2007). However, it is becoming increasingly clear that assessing the role of NTFP use in tropical forest conservation requires knowledge and information derived from elements of all three approaches (e.g. de Beer & McDermott, 1996; Godoy et al., 1993; Gram, 2001; van Andel et al., 2003). Although some recent studies have combined multiple approaches (Mahonya et al., 2019; Schaafsma et al., 2014; van Andel et al., 2007), these studies do not link use to the NTFP supply in the forest, obscuring to what extent the economic value of NTFP provisioning by tropical forests can contribute to the conservation of tropical forests.

In this paper, we focus on the economic value derived from the sale of plant-based NTFPS sourced from old-growth tropical forest. Scientific studies aiming to quantify the economic value of NTFP provisioning have often quantified this in terms of a theoretical 'potential' value per hectare. In such studies, commonly an expected harvestable volume of NTFPs is calculated for a given area of tropical forest, which is then valued on the basis of actual market prices. For example, such approaches have been applied to forest plot surveys (e.g. Gavin, 2004; Peters et al., 1989) or, more recently, in combination with spatially-explicit models of plant distributions (e.g. Jaramillo-Giraldo et al., 2017; Lopes et al., 2019; Strand et al., 2018). However, this approach has been criticised as likely overestimating the actual economic value of NTFP provisioning by tropical forests (e.g. see the reviews by Belcher & Schreckenberg, 2007; Godoy et al., 1993; Gram, 2001; Shackleton & Pandey, 2014; Sheil & Wunder, 2002), by pointing at two erroneous assumptions: 1) all available supply will be used, and 2) market prices are stable.

First, most studies implicitly assume that the entire NTFP supply will be harvested. However, it is likely that only a small share will end up being harvested due to of various institutional, social, physical and economic limitations. For instance, a harvester may have limited access to the standing stock due to institutional constraints: customary rules, policies or legislation may prohibit harvesting in certain areas, or the harvest of particular species (Gram, 2001; Timko et al., 2010). In addition, increasing marginal costs, such as the time and money invested in harvest and transport, will ultimately limit harvesters in the area covered and amount of NTFPs harvested (Schaafsma et al., 2014 and references therein). Thus, only a subset of the available NTFP stock can be considered harvestable. Although some studies have accounted for marginal costs, for example by only valuing tropical forest plots nearby human habitation (Gavin, 2004; Peters, Balick, et al., 1989) or including distance related operators in spatially explicit models (Jaramillo-Giraldo et al., 2017; Lopes et al., 2019; Strand et al., 2018), they still implicitly assume that virtually the entire NTFP supply is ultimately harvested. Although this shortcoming is commonly acknowledged (Godoy et al., 1993; Sheil & Wunder, 2002), few studies have quantified the share of NTFP supply that is actually harvested. An exception is the study by Ribeiro et al. (2014), who estimated both available supply and actual harvested volumes of Brazil nuts among several forest communities in a Brazilian indigenous territory and found that the communities harvested between 7.2 - 41.3% of the supply in harvest areas, representing between 2.5 - 12.7% of the total available stocks in their territory.

Second, studies that assess the economic value of NTFP provisioning implicitly assume that market prices of NTFPs are stable, independent of the marketed volume of NTFPs. This may not be the case for relatively small and isolated domestic markets of NTFPs, where distortions are likely to strongly affect market prices (Belcher & Schreckenberg, 2007; Shackleton & Pandey, 2014; Sheil & Wunder, 2002). For example, when NTFP supply increases while the demand remains constant, this may lead to market saturation and an eventual drop of the price. In support, Hilfiker et al. (2006) found that the market price of several plant-based NTFPs in Vietnam fluctuated between 20 – 50% throughout the year, which was partly due to seasonal differences in supply and demand. Therefore, economic valuations of NTFPs need to consider market prices of NTFPs in relation to the supply and demand.

However, quantifying the realized economic value of NTFPs sold at the market is not enough to evaluate its relevance for tropical forest conservation. Additional information is needed on the share of economic benefits received by different actors and regarding the impact of NTFP exploitation on plant species populations (Belcher & Schreckenberg, 2007; da Silva et al., 2017; Kusters et al., 2006; A. C. Newton, 2008; Sheil & Wunder, 2002), for two reasons. First, it has become clear that actors involved in the commercial trade of NTFPs do not receive equal shares of the generated economic benefits (Belcher & Schreckenberg, 2007; Jensen, 2009; A. C. Newton, 2008; te Velde et al., 2006). Harvesters at the start of the NTFP value chain often gain lower benefits from their product than market vendors at the end. For example, Jensen (2009) analysed the value chain of processed NTFPs (agarwood) sourced from tropical forests in Laos and sold on the international market, and found that harvesters, representing the first of a total of four actors, received only 13% of the value added across the value chain. Although the decisions of local stakeholders cannot be predicted on the basis of received economic benefits, a low economic value per hectare may unlikely function as an incentive to conserve tropical forests (A. C. Newton, 2008). Second, it has become clear that selling plant-based NTFPs can lead to overexploitation, questioning to what extent commercial trade contributes to tropical forests conservation (Kusters et al., 2006; E. Marshall et al., 2006). For example, a review of 101 studies on the ecological impact of NTFP extraction across the tropics and subtropics by Stanley et al. (2012), found that 36.6% of the studies reported either unclear or negative impacts on the natural population of the providing species (18.8 and 17.8%, respectively). In extreme cases of NTFP overexploitation, this may result in the collapse of its market (Ruiz-Pérez & Arnold, 1996). For example, Ruysschaert (2018) found anecdotal evidence of a plant-based NTFP that was overharvested in Suriname, resulting in collapse of its national market due to excessive marginal costs of harvesting (i.e. the case of the terrestrial palm species *Geonoma baculifera* Kunth).

Therefore, accurate and credible assessments of the economic value of commercial plant-based NTFPs derived from tropical forests and assessments of its relevance for tropical forest conservation require information on at least three aspects. First, information is needed on the share of the NTFP supply that is actually used, and the monetary value this use actually generates: the 'realized' economic value (Godoy et al., 1993; Sheil & Wunder, 2002). Second, information is needed on where and how economic value is generated, and to what extent this value is received by local stakeholders of tropical forests (Kusters et al., 2006; A. C. Newton, 2008). Third and last, information is needed on the extent to which harvesting of the NTFP stock is ecologically sustainable (Kusters et al., 2006; A. C. Newton, 2008). To our knowledge, no study exists that has determined the economic value of commercial traded plant-based NTFP provisioning by old-growth tropical forests in this way. Although studies have quantified the economic value of NTFPs on the basis of household use (e.g. Gavin, 2004; Godoy et al., 2000; Gram, 2001; Gram et al., 2001; Schaafsma et al., 2014) or by the volumes sold on markets (e.g. Padoch, 1992; Shanley et al., 2002; van Andel et al., 2007), studies have not linked economic value to the harvestable NTFP supply. Padoch & de Jong (1989) looked at the difference between the potential and realized economic values of tropical agroforestry products that were sold on a local market, but these products were sourced from heavily managed, agroforestry systems.

Accurate and credible information on the economic value of the NTFP flow from tropical forests, and the extent to which this can provide incentives to conserve tropical forests is highly needed to develop effective forest management and conservation policies (A. C. Newton, 2008; Shackleton & Pandey, 2014; Sheil & Wunder, 2002). However, there is strong variation in reported economic values of NTFP provisioning by tropical forests. This variation has been partly caused by differences in focus of the studies. For example, previous studies have focused on either managed, secondary or old-growth tropical forests, on either single or multiple NTFPs, and on plant-, animal- and/or mushroom-based NTFPs. Yet, even across studies with a similar focus, reported economic values vary greatly. For example, studies that estimated the value of multiple commercial plant-based NTFPs from old-growth tropical forests, reported economic values ranging from 20 to 6,330 USD ha^{-1} yr^{-1} (Grimes et al., 1994; Peters, Gentry, et al., 1989; Pinedo-Vasquez et al., 1992). Monetary values can be used to inform policy makers, but if their order of magnitude and social context are clear, using them can potentially lead to ineffective policies (Sheil &

Wunder, 2002; Strand et al., 2018).

Therefore, in this paper, we explore how economic value of plant-based NTFPs in old-growth tropical forests is determined by selling these products, and assess how this contributes income for local stakeholders. To this aim, we develop a theoretical framework that maps the flow of NTFPs from forest stock to the market, linking the gross economic value that is realized up to and including the market to the harvestable NTFP supply in old-growth tropical forests. The framework describes NTFP provisioning by mapping the flow from forest to the final market, identifying relevant flow components on the basis of relevant ecological and socio-economic factors reported in the literature. We use this theoretical framework to quantify the per hectare economic value of plant-based NTFP supply in old-growth tropical forest according to actual market sales for the case of the neotropical country of Suriname. We focus on NTFPs that are sourced from tree and arborescent palm species and are traded on the Vreedzaam market, the largest plant-based NTFP market of the country. This is because plant-based NTFP use in Suriname, including their harvest and trade, has been relatively well studied previously (e.g. Ruysschaert, 2018; van Andel et al., 2007; van Andel & Havinga, 2008; van den Boog et al., 2018). Furthermore, a large dataset of old-growth tropical forest plots is available for Suriname, which can be used to quantify the NTFP supply from the tree and arborescent palm species (e.g. ATDN, 2022; Steur et al., 2021). To quantify the flow components of the framework, we employ both quantitative and qualitative methods, including forest plot surveys, walks-in-the woods with harvesters, market surveys, and interviews with harvesters, middle-men and market vendors.

5.2 Material and Methods

Theoretical framework

To quantify the economic value of NTFP provisioning by tropical forests, we developed a theoretical framework that maps NTFP provisioning from the forest to the final market (Figure 5-1). The framework identifies important flow components, such as the NTFP stock (NTFP abundance), the harvestable NTFP supply, and the sales volumes (blue boxes), which are influenced by specific ecological and socio-economic factors as reported in the literature (white boxes with dashed lines), which is further explained below.

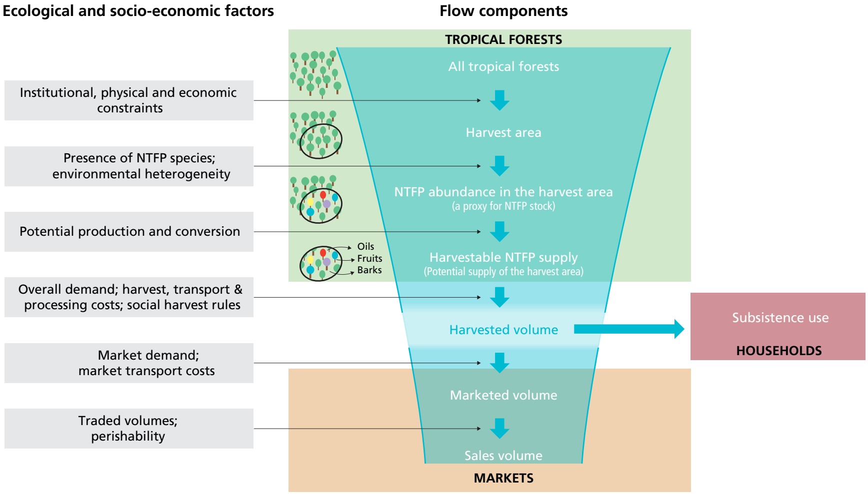

Figure 5-1. Theoretical framework describing the flow of non-timber forest products (NTFPs) from tropical forest to the market, identifying important flow components (blue funnel) influenced by ecological and socio-economic factors (grey boxes). The flow components that have not been quantified for this study are indicated by a light-blue (harvested volume).

Due to institutional, physical and economic constraints faced by harvesters, only a certain area of tropical forest will be harvestable (Godoy et al., 1993; Gram, 2001; Schaafsma et al., 2014; Timko et al., 2010), the 'harvest area'. In the tropical forests of the harvest area, only certain plant species will be used to produce NTFPs, the 'NTFP species', whose identity can vary across cultures. For example, the palm *Euterpe oleracea* Mart. can be used to extract palm heart, but while this product is used in Guyana, it is not in neighbouring Suriname (van Andel et al., 2003). The number of NTFP species individuals in tropical forests, the 'NTFP abundance', will vary according to the environmental heterogeneity, the amount of variation in biotic elements, such as the vegetation, pollinators and predators, and in abiotic factors, such as topography, soil and climate. For example, an NTFP species may be highly abundant on flooded soils, while on terra firme soils the same NTFP species can be rare (P. Newton et al., 2012; Steur et al., 2021). After the definition of an ecosystem service potential supply by Hein et al. (2016), NTFP species individuals can be expected to produce a theoretical amount of ecologically sustainable harvestable NTFP stock per year, the 'potential NTFP supply'. In the literature, NTFP stock (the number of harvestable NTFPs, regardless of a temporal dimension) is seldomly calculated. Either NTFP abundance is used as a proxy for NTFP stock (e.g. Baraloto et al., 2014; C. A. Marshall & Hawthorne, 2012; P. Newton et al., 2012) or the potential NTFP supply is calculated instead (Grimes et al., 1994; Jaramillo-Giraldo et al., 2017; Lopes et al., 2019; Peters, Gentry, et al., 1989). In the framework, the potential NTFP supply of the harvest area is referred to as the 'harvestable NTFP supply'. Because of environmental heterogeneity, harvestable NTFP supply differs between forest types and across seasons. For example, variation in production by NTFP species has been associated to differences in hydrological and climatic conditions (Dantas et al., 2016; P. Newton et al., 2011; Phillips, 1993). In addition, some material will require processing before use, involving a reduction in volume. For example, the NTFP crabwood oil is made by drying, rotting and baking the seeds of *Carapa* spp., which reduces biomass (van den Boog et al., 2018). The conversion efficiency of processing may vary according to the potential technical installations involved and the specific knowledge, skills and preferences of the actor conducting the processing. On the basis of the interaction between overall demand, the costs of harvest, transport and processing for NTFPs, and social rules concerning harvest practices, a certain amount of NTFP supply will ultimately be harvested (Schaafsma et al., 2014), the 'harvested volume'. Overall demand is the combined demand from households for subsistence needs and market demand. The harvested volume may be equal or less than the harvestable NTFP supply, indicating a sustainable harvest, or may be higher, indicating overexploitation (Hein et al., 2016). Depending on market access, market demand, market price and transport costs, a share of the harvested NTFP volume will be marketed (Ghate et al., 2009; Godoy et al., 1993; van Andel & Havinga, 2008), the 'marketed volume'. Last, depending on day-to-day demand and the perishability of the products, a proportion of the marketed volume will be sold to customers (Sheil & Wunder, 2002), the 'sales volume'.

Data collection and approach

During February-March 2017, February-March 2018 and June-July 2018, we collected both quantitative and qualitative information on NTFP abundance, potential NTFP supply, harvest practices and the volumes sold on the market for a selection of plant-based NTFPs sourced from old-growth tropical forests in Suriname. For each NTFP, we applied the theoretical framework as described in Figure 5-1, excluding the harvested volume and household use. To this end, we performed market surveys on the Vreedzaam market, the largest plant-based NTFP market of the country to record data on units, volumes and prices of traded NTFPs, and to identify source areas of NTFPs by interviewing middlemen and harvesters offering NTFPs for wholesale (Annex S5.1, Figures S5.1.3.1 and S5.1.3.2). The Vreedzaam market represents about 53% of the estimated total market stalls selling medicinal plant-based NTFPs in Suriname (van Andel et al., 2007), and handles at least 60% of the total volume of plant-based NTFP that is sold each week in Suriname. In addition, we carried out walks-in-the-woods and interviews with harvesters to asses ecological sustainability aspects of harvest, questioning harvesters on harvest practices and their perceived impact on natural populations, and observing harvest practices and natural populations in tropical forests. For all market measurements, interviews, and walks-in-the-woods, we obtained prior informed consent from our informants, making sure they understood we wanted to use the recorded data for scientific study and publication. We paid informants and field assistants a financial compensation for their time. Our interviews were conducted using a semi-structured and open-ended approach: using a set list of topics to ask about, but allowing the interviewee to lead the interview. The language spoken was either Dutch or Sranantongo, the *lingua franca* of Suriname. Most interviews took between half an hour and an hour, depending on signs of interview fatigue. Interviews of an hour and longer were usually taken with main informants. During the interviews we used pen and paper to minute the interview, while the minutes were digitized in Microsoft Word on the same day. If recorded information was not clear, we went back to the interviewee to ask for elaboration. The walks-in-the-woods were georeferenced with a Garmin GPS and occasionally photographed (Figure S5.1.3.3).

Harvest area

Information on the source areas of the traded NTFPs was obtained by interviewing harvesters and middlemen who offered NTFPs for wholesale at the Vreedzaam market. NTFPs were offered during early mornings, usually between 04:30 and 07:00 a.m. (Figure S5.1.3.2). We carried out 29 early morning market surveys and interviewed 45 different harvesters and middle men. This supplied 384 records identifying 45 unique source areas. As the accumulation curve of number of reported source areas vs. the number of market surveys was almost saturated (Figure S5.1.3.4), the 45 identified areas likely represented the most common source areas of traded NTFPs at the Vreedzaam market. For each source area, we estimated the harvest area by extrapolating a common NTFP harvester action radius. Interviews and walks-in-the-woods with harvesters (n = 19 and 7, respectively), and several published forest use maps of forest dwelling communities in Suriname (Ramirez-Gomez et al., 2016, 2017; van den Boog et al., 2018) indicated that most plant-based NTFPs were harvested within a 10 km radius around villages within 5 km from roads up to 10 km from a village, and within 5 km from rivers up to 20 km from a village.

Selection of commercial traded NTFPs

On the basis of the recorded data, there was sufficient data to quantify the NTFP provisioning of 13 commercially relevant NTFPs (i.e. including data on abundance, production and market use) (Table 5-1). These 13 NTFPs included oil-based NTFPs (3 oils and 1 oleoresin), fruit-based NTFPs (1 fruit and 1 seed), and bark-based NTFPs (6 barks), and included the most expensive NTFPs of their type according to an earlier market survey in 2006 by van Andel et al. (2007). The 13 NTFPs were sourced from 11 tree and arborescent palm species (Table 5-1), whose identity was cross-refenced with the help of voucher material collected at the market and deposited at the National Herbarium of Suriname (BBS) and Naturalis Biodiversity Center (L). An overview of herbarium vouchers is provided in Table S5.1.1.1.

Table 5-1. Selected plant-based NTFPs sourced from wild tree and arborescent palms species in old-growth tropical forests and sold at the Vreedzaam market in Suriname in 2017-2018. Spelling of common vernacular names after van Andel et al. (2007), main uses after van Andel & Ruysschaert (2011). Oil-based NTFPs highlighted in green, fruit-based NTFPs in purple and bark-based NTFPs in orange.

Part used	Scientific species	Family	Common vernacular name	Main uses
Oil from seed	*Astrocaryum sciophilum* (Miq.) Pulle	Arecaceae	tjo tjo oli	Treatment of bone fractures
Oil from seed	*Attalea maripa* (Aubl.) Mart.	Arecaceae	maripa oli / fatu	Food, skin care
Oil from seed	*Carapa guianensis* Aubl. & *Carapa surinamensis* Miq.	Meliaceae	krapa oli	Skin care, treatment of various diseases
Oleoresin	*Copaifera guyanensis* Desf.	Fabaceae	opro oli	Skin care, treatment of various diseases
Fresh fruit	*Oenocarpus bacaba* Mart.	Arecaceae	kumbu siri	Food, treatment of anaemia
Dried seed	*Dipteryx odorata* (Aubl.) Willd.	Fabaceae	tonka siri	Cosmetic hair product
Bark	*Parkia pendula* (Willd.) Benth. ex Walp.	Fabaceae	kwatakama buba	Treatment of various diseases, rituals
Bark	*Carapa guianensis* Aubl. & *Carapa surinamensis* Miq.	Meliaceae	krapa buba	Treatment of various diseases
Bark	*Copaifera guyanensis* Desf.	Fabaceae	opro buba	Treatment of various diseases, tea
Bark	*Dipteryx odorata* (Aubl.) Willd.	Fabaceae	tonka buba	Rituals
Bark	*Pseudopiptadenia suaveolens* (Miq.) J.W. Grimes	Fabaceae	pikinmisiki buba	Rituals, baby care
Bark	*Spondias mombin* L.	Anacardiaceae	mope buba	Genital hygiene
Bark	*Hymenaea courbaril* L.	Fabaceae	loksi buba	Treatment of various diseases, tea, rituals

All 11 tree and palm species represented wild species that occurred mainly in old-growth tropical forests, except for the palm *Attalea maripa*, which was also widely cultivated around villages and agricultural fields. Nevertheless, to our knowledge, *A. maripa* has not been domesticated, and we observed that a substantial part of the harvested material of *A. maripa* was taken from wild individuals. Although 'tjo tjo oli' was reported by market vendors to be produced from both the wild *Astrocaryum sciophilum* and the domesticated *Astrocaryum vulgare* Mart. palm species, we observed that most, if not all, tjo tjo oil presented on the market was made from *A. sciophilum*. We did not record any tjo tjo oil processing in coastal Suriname, and informants stated that only in the interior, where *A. sciophilum* is abundant and *A. vulgare* scarce, people still have the traditional huts and can dedicate the time necessary to produce this oil.

The included tree and palm species produce 24 traded NTFPs (Table S5.1.1.2). Although the fruit and juice of the wild palm species *Euterpe oleracea* Mart. is commonly commercialized in Suriname, it was excluded from our analyses as it was not sold at the Vreedzaam market. At the time of this study this fruit was labelled as an agricultural product by the government of Suriname and could therefore not be sold without a specific permit, which none of the Vreedzaam market vendors possessed.

NTFP abundances

To account for spatial variation in NTFP abundance across old-growth tropical forests, we recognized eight different old-growth forest types across Suriname (Table 5-2). Forest types included: 1) mangrove forests, 2) swamp forests, 3) marsh forests, 4) terra firme forests of the Coastal plains, 5) terra firme forests of the Savanna belt, 6) terra firme forests of the interior, 7) white sand forests of the interior and 8) mountain forests. Mangrove forests are halophytic forests along the coast; swamp and marsh forests are both hydrophytic forests, either permanently inundated or seasonally flooded, occurring across Suriname; terra firme forests are mesophytic forests situated on well-drained and relatively fertile soils, and differing in their species composition according to geological substrate (Coastal plains, Savanna belt or the Interior); white sand forests are xerophytic forests on well-drained but relatively nutrient poor sandy white soils in the Savanna belt; and mountain forests are xerophytic forests on well-drained soils at an altitude above 500 meters, occurring in the Interior. The eight forest types were based on the old-growth forest types recognized and mapped for Suriname by the company Sarvision according to structural and hydrological properties measured by JAXA ALOS PALSAR satellite radar in 2009 (Quiñones & Hoekman, 2011). These forest types were split or aggregated to better accommodate expected differences in NTFP abundances according to well-known floristic differences. Terra firme forests were split into forests of the Coastal plains, Savanna belt and the Interior (Banki, 2010; J. C. Lindeman & Moolenaar, 1959; ter Steege & Zondervan, 2000; Teunissen, 1978; van Andel et al., 2009). The creek forest types and marsh forest types were aggregated into creek forests and marsh forests, respectively. Because the deforestation in Suriname between 2009 and 2017 has been limited (NIMOS, SBB and UNIQUE, 2017), we assumed that the surface areas mapped by Sarvision in 2009 were representative for the surface areas during 2017-2018.

Table 5-2. Forest types recognized in this study, including the estimated surface area across Suriname based on the Sarvision vegetation map (Quiñones & Hoekman, 2011) and the corresponding number of forest plots set out by their size.

Tropical forest types	Surface area in Suriname		Tropical forest plots					
			0.04 ha	0.1 ha	0.125 ha	0.55 ha	1 ha	Total
Mangrove forests	415 km^2	0.26%	3	0	0	0	0	3
Swamp forests	2,483 km^2	1.55%	61	0	0	0	0	61
Marsh forests	20,979 km^2	13.11%	82	0	2	0	4	88
Terra firme forests of the Coastal plains	6,374 km^2	3.98%	52	0	0	0	0	52
Terra firme forests of the Savanna belt	7,920 km^2	4.95%	0	0	10	0	20	30
Terra firme forests of the Interior	116,895 km^2	73.04%	38	0	0	0	6	44
White sand forests of the Savanna belt	1,670 km^2	1.04%	40	2	1	0	10	53
Mountain forests of the Interior	3,296 km^2	2.06%	0	0	0	1	14	15
Total	160,032 km^2	100%						346

Mean NTFP abundance per species per forest type (# stems ha^{-1}) was calculated with its standard deviation using 346 stratified tropical forest plots in Suriname (Table 5-2). This dataset was compiled from 340 previously published plots and 6 new plots surveyed in 2017 (Figure S5.1.2.1 and Table S5.1.2.1). In all plots, all tree and arborescent palm NTFP species with a minimum Diameter at Breast Height ('DBH'; 1.3 m) of 10 cm were measured and identified. Some of the plots had its data originally recorded as DBH $\geq$ 5 cm, but this data was converted to represent measurements of DBH $\geq$ 10 cm prior to analysis. Species taxonomy was updated after the 'Dynamic Amazon Tree Checklist' (ter Steege et al., 2019b; updated version 20200422). Although several forest plots in the coastal area have been logged since measurement (NIMOS, SBB and UNIQUE, 2017), we assumed that the vegetation captured in these plots still represented current old-growth forests. Plot size varied between 0.04 and 1 ha. As smaller plots have a higher risk of excluding rare species and/or large individuals, we compared the number of species per area and the relative diameters of the NTFP species per plot prior to analysis, but found no differences.

Potential NTFP supply

Potential NTFP supply (# NTFP units ha^{-1} yr^{-1}) was quantified according to the units sold on the Vreedzaam market, for example oils in litres and barks in square meters. For each NTFP, its potential supply was calculated by multiplying the mean NTFP abundance per species with a species-specific NTFP production value. Production values were based on interview data from harvesters and other actors who processed NTFPs, and were cross-referenced and appended with available literature data. For oil and fruit-based NTFPs, losses in volume due to processing were considered. Although interviews and literature indicated that some NTFP species showed a large variation in their phenology across

DBH and forest type, and interviewees indicated that the efficiency of processing varied according to the skill and preferences of the actor, we choose to use a single average for all forest types per species because our data did not adequately cover the suggested variation. For bark-based NTFPs, we used a production value which was dependant of the DBH of the individual. Here, harvestable bark per year was calculated as $2\pi*0.5DBH*H*R$, where H is the height up to which harvest can take place, and R is the regeneration factor equivalent to the number of times per year the bark may be harvested. Interview data indicated a common rule among harvesters in Suriname that dictated that 25% of the tree stem could be debarked up to 2 m *at a time* to allow for tree survival (van Andel & Havinga, 2008; this study).

Harvestable NTFP supply was calculated by first calculating a mean potential NTFP supply per old-growth forest type (# NTFP units ha^{-1} yr^{-1}), second multiplying these means with the surface areas of the forest types present in the harvest area.

NTFP volumes sold at the Vreedzaam market

Annual volumes of NTFPs sold at the Vreedzaam market (# NTFP units yr^{-1}) were calculated by multiplying the estimated average volumes sold per week per type of market vendor with the number of stands selling plant-based NTFPs across the active 50 market weeks per year. Estimates of average sold volumes per week were based on in-depth interviews with eight market vendors, and were cross-referenced with observations of other market stalls. On the basis of the weekly sold volumes of NTFPs, we recognized two types of market vendor for each NTFP: fast selling and slow selling vendors. The number of vendors at the Vreedzaam market selling plant-based NTFPs varied between around 80 and 200 across the field work periods, but averaged around 100 per week across the year. Of these average 100, 80 vendors sold small volumes of NTFPs each week, whereas 20 sold large volumes. During market surveys, the weight of fruit was measured using a scale, the volume of bark with a ruler, and the volume of oil with a graduated cylinder.

Realized and potential economic value

For each NTFP, we used the economic value of the market sales volume (volume multiplied by market price) to value the harvestable NTFP supply, the 'realized economic value'. For comparison, we also quantified the economic value based on the potential NTFP supply multiplied with the actual market prices, the 'potential economic value'. We expressed economic value as gross revenue and not net revenue, as the costs reported by actors could not be attributed to specific NTFPs. Instead, we quantified the revenues and costs per actor, and related these two to each other. For harvesters, we assessed costs of harvest, transport and processing, and for market vendors we assessed costs of operating a market stand.

To assess how economic benefits were distributed across different stakeholders, we recorded both the price paid for NTFPs by market vendors, the 'forest exit price' (similar to the farm exit or farm gate price, see also Gavin, 2004; Godoy et al., 1993), and compared this to the market price. On the basis of this we calculated the percentage of the economic benefits received by harvesters. Observed value chains of the commercial trade in plant-based NTFPs in Suriname typically comprised two actors, where only in rare cases 'middle-men' offered NTFPs for wholesale. Interviews indicated that in these cases often a family member or friend of the harvester functioned as middle-man, charging no additional fee for their services. Therefore, in this paper we assumed that all analysed value chains comprised two actors.

For each measured NTFP, we recorded the market price per NTFP, and, where possible, also the forest exit price. Recording the forest exit price was not always possible as NTFP volume was offered in bundles during wholesale, and only when all items from a bundle were still available at the time of the survey, the forest exit price for a single NTFP from the bundle could be reconstructed. All prices were recorded in SRD, the Suriname Dollar, and converted to USD (1 SRD = 0.13 USD at the time of fieldwork). Recorded units and prices were regularly cross-referenced.

Statistical Analyses

As a measure of uncertainty in our estimates, we calculated the mean with its standard deviation (SD) and propagated the SDs where possible. When multiple means with SD were multiplied, the combined SD was calculated as $\mathrm{SD}_{\mathrm{new}} = \surd(\ (\mathrm{SD}_1/\mathrm{mean}_1)^2 + (\mathrm{SD}_2/\mathrm{mean}_2)^2 + \ldots\ ) * \mathrm{mean}_{\mathrm{new}}$. For each NTFP species, we carried out analysis of variance of mean NTFP abundance across forest type by using an F-test, and we analysed the amount of variation in mean NTFP abundance explained by forest types by using a standard linear model. Associations between harvestable NTFP supply, volumes traded, the percentage of harvestable NTFP supply sold at the market, forest exit price, market price, were tested using Kendall's tau correlation tests. All calculations and statistical analyses were carried out in R (v. 3.6.2.; R Core Team, 2019).

5.3 Results

Harvestable NTFP supply

The identified 45 source areas of the plant-based NTFPs corresponded to a combined harvest area of about 9809 km^2, including 7668 km^2 of old-growth forests belonging to all eight categories of forest type (Figure 5-2). Combined, these old-growth tropical forests in the harvest area covered just below 5% of the total old-growth forest area of Suriname (Table S5.1.3.1). In the harvest area, terra firme and marsh forest types covered 94.3%, while mountain, mangrove, white sand and swamp forests added up to 5.7%.

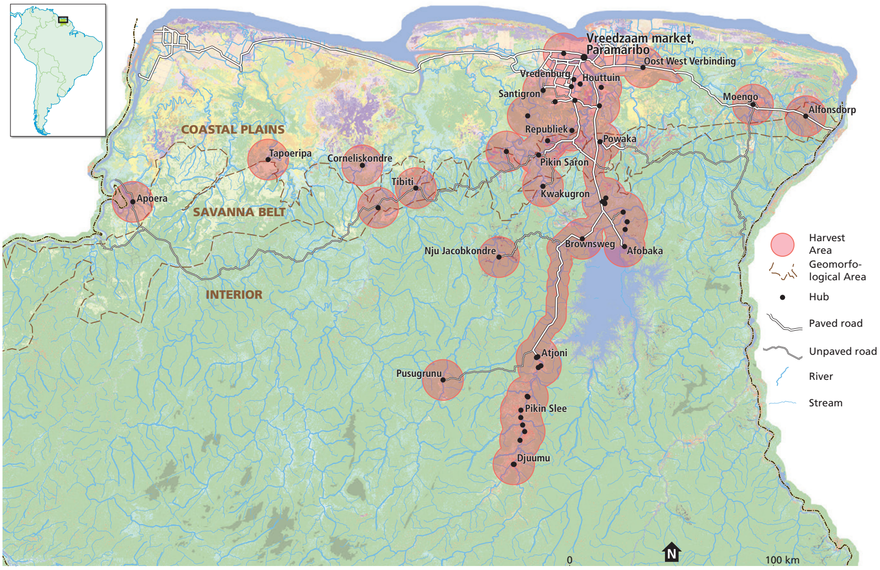

Figure 5-2. Section of the Sarvision vegetation map of Suriname (Quiñones & Hoekman, 2011), with the harvest areas indicated by the area in red, important NTFP hubs by black dots (locations where harvesters collected harvested NTFPs; not all names shown), paved and unpaved roads by white lines and main rivers and creeks by blue lines. The three main geomorphological areas: the Coastal plains, Savanna belt and Interior, are indicated by dashed brown lines. Background colours represent coverage types according to the original Sarvision map. For example, mesophytic forests are indicated by medium and dark green, marsh and swamp forests by light blue, herbal swamps and mangrove forests by light and dark purple, and cities and agricultural field by peach. For the complete legend see Quiñones & Hoekman (2011).

Across the eight old-growth forest types, 7 of the 11 NTFP species showed significant variation in their mean abundance (# stems ha^{-1}; F-tests $p \leq 0.0001$), where 4 did not (F-tests $p \geq 0.0836$; Table S5.1.3.3). Although the calculated mean abundances had relatively large standard deviations (Table S5.1.3.2), the patterns in species presence and mean abundance across the forest types were in line with the known ecology of the 11 NTFP species as mentioned in the Flora of Suriname (1932-1986), Timber trees of Suriname (Bhikhi et al., 2016; J. C. Lindeman & Mennega, 1963) and van Andel & Ruysschaert (2011).

Estimated average NTFP production for similar NTFPs showed considerable variation (Table S5.1.3.4). For example, NTFP species that were used to produce oil-based NTFPs were estimated to produce an equivalent of NTFP oil between 15 to 1,500 ml of oil each year, and depending on the regenerative capacity of the species, barks could be harvested between 1 to 3 times every year.

Inherent to the variation in the abundance and NTFP production across species and the variation in the surface area across old-growth tropical forests, both estimated number of stems and calculated harvestable NTFP supply varied considerably per species (Figure 5-3). For example, the palm *Astrocaryum sciophilum* was relatively abundant across the harvest area, with 11.3 ± 14.0 x 10^3 calculated stems, whereas the tree *Dipteryx odorata* was relatively rare, with 50 ± 115 x 10^3 stems. In addition, although both palm species *A. sciophilum* and *Attalea maripa* were relatively abundant across the harvest area, having similar numbers of calculated stems, the calculated equivalent amount of oil that could be produced from these stems was low for *A. sciophilum* (1.7 ± 2.1 x 10^4 L oil yr^{-1}), and high for *A. maripa* (880.2 ± 999.1 x 10^4 L oil yr^{-1}).

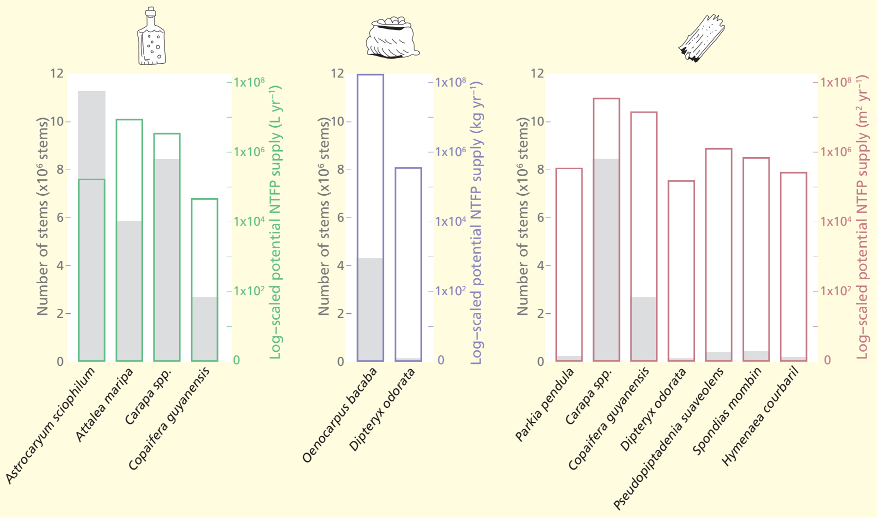

Figure 5-3. Estimated number of stems of NTFP species (grey area, left axes) and potential NTFP supply in the harvest area concerning: oils (in green; left panel), fruits (in purple, middle panel), and barks (in red, right panel). The left y-axes correspond to the number of stems on a linear scale, the right y-axis the volume of NTFPs on a log-scale: for oils in L yr^{-1}, fruits in kg yr^{-1}, and barks in m^2 yr^{-1}. See Tables S1.3.5 and S1.3.6 for the original data. Icons representing oils (left panel), fruits (middle panel) and bark (right panel) taken from Shanley et al. (2011).

Sales volume of NTFPs and their value

At the Vreedzaam market, NTFPs were presented in different units. Market survey and interview data indicated that the oil-based NTFPs and the fruits of *Oenocarpus bacaba* were sold by the volume, the seeds of *Dipteryx odorata* by the number, and all barks by the surface area. By contrast, weight of these NTFP was unimportant. In addition, some NTFPs were presented in different quantities, with different market prices per quantity. For example, oil of *Carapa* spp. was presented on the market in bottles varying in their volume of 50 ml to 1 L, where the price per quantity was lower for the 1 L bottles (22.8 USD L^{-1}) than for the 100 ml bottles (39 USD L^{-1}).

Although the market price per quantity differed per quantity sold, all NTFPs had a 'standard' market unit: a quantity and market price at which NTFPs units were mostly sold (Table 5-3). Oil-based NTFPs were commonly sold in plastic bottles of max. 130 ml (Figure S5.1.3.4-left), the fruits of *O. bacaba* were sold per standard 0.5 L tin can (Figure S.1.3.4-right), the seeds of *D. odorata* by number (Figure S5.1.3.5-left), and barks in standard sizes at a certain price, usually 1.35 USD (10 SRD) (Figure S5.1.3.5-right). The mean quantity of the standard market units was relatively stable across market vendors. Standard deviations of the mean quantity of barks were somewhat larger, which may have been due to differences in the thickness of the bark.

Table 5-3. Standard market units of 13 NTFPs traded on the Vreedzaam market (2017-2018), including measured mean quantity and mean market price per quantity. SD = standard deviation, n = number of measurements.

NTFP type	NTFP species	Standard market unit	Quantity (mean ± SD)		n	Market price per quantity (mean ± SD)		n
Oil	*Astrocaryum sciophilum*	130 ml bottle	125.4 ± 5.0	ml	23	53.6 ± 2.1	USD L^{-1}	21
Oil	*Attalea maripa*	130 ml bottle	117.2 ± 6.6	ml	20	27.0 ± 4.2	USD L^{-1}	20
Oil	*Carapa guianensis* + *C. surinamensis*	130 ml bottle	123.1 ± 6.5	ml	85	16.6 ± 0.9	USD L^{-1}	83
Oleoresin	*Copaifera guyanensis*	130 ml bottle	123.8 ± 5.1	ml	20	41.5 ± 20.8	USD L^{-1}	13
Fruit	*Oenocarpus bacaba*	0.5 L tin can	60.58	g	1	11.1	USD kg^{-1}	1
Seed	*Dipteryx odorata*	single seed	2.36[a]	g	148	71.3	USD kg^{-1}	1

NTFP type	**NTFP species**	**Standard market unit**	**Quantity (mean ± SD)**		**n**	**Market price per quantity (mean ± SD)**		**n**
Bark	*Parkia pendula*	1.35 USD bark piece	426.8 ± 126.4	cm^2	51	3.4 ± 1.1	USD m^{-2}	51
Bark	*Carapa guianensis* + *C. surinamensis*	1.35 USD bark piece	381.4 ± 87.1	cm^2	5	3.7 ± 0.8	USD m^{-2}	5
Bark	*Copaifera guyanensis*	1.35 USD bark piece	351.2 ± 115.3	cm^2	43	4.4 ± 0.8	USD m^{-2}	4
Bark	*Dipteryx odorata*	1.35 USD bark piece	141.6	cm^2	1	14.3	USD m^{-2}	1
Bark	*Pseudopiptadenia suaveolens*	1.35 USD bark piece	373.9 ± 122.6	cm^2	51	4.3 ± 2.8	USD m^{-2}	51
Bark	*Spondias mombin*	1.35 USD bark piece	215.0	cm^2	1	6.3	USD m^{-2}	1
Bark	*Hymenaea courbaril*	1.35 USD bark piece	356.7 ± 132.3	cm^2	26	4.1 ± 0.9	USD m^{-2}	26

[a] Weight per dried seed data taken from separate market survey (van Andel et al., 2007); standard deviation was not available.

For most of the 13 NTFPs, little variation was observed in the mean market price per quantity (Table 5-3). Only for the oleoresin of *Copaifera guyanensis* and the bark of *Pseudopiptadenia suaveolens* the variation was larger, probably due to differences in forest exit price. Interviewed market vendors indicated that prices and availability of most of the 13 NTFPs on the market had been stable over the last few years. Only the fruit of the palm *O. bacaba* was seasonally available, between February and May, but the price per quantity was said to be stable during that period. Last, the bark of *D. odorata* was measured only once, but the recorded price per quantity was considerably higher than the mean prices per quantify for other bark-based NTFPs. Although the measurement of the bark of *D. odorata* could have been an outlier, we believe that the recorded price reflects the ecological scarcity of the providing species. Market vendors indicated that *D. odorata* bark was "hard to get" because the species was rare in the forests, and the regeneration of its bark was relatively slow.

Estimated annual volumes sold at the Vreedzaam market and their realized monetary value varied per NTFP (Table 5-4). On average, oil-based NTFPs represented the highest average realized economic value (20,491 USD yr^{-1}; n = 4), followed by the fruit of *O. bacaba* (16,750 USD yr^{-1}; n = 1), the seed of *D. odorata* (1,996 USD yr^{-1}; n = 1) and bark-based NTFPs (1,352 USD yr^{-1}; n = 7).

Table 5-4. Estimated average annual sales volume on the Vreedzaam market per NTFP between 2017 and 2018, and their realized market value calculated as the sales volume multiplied with the mean price per quantity. Quantities have been rounded to the nearest whole number. SD = standard deviation.

NTFP type	NTFP species	Sales volume		Realized market value (mean ± SD)		
Oil	*Astrocaryum sciophilum*	112	L yr^{-1}	6,003	± 235	USD yr^{-1}
Oil	*Attalea maripa*	600	L yr^{-1}	16,200	± 2,520	USD yr^{-1}
Oil	*Carapa guianensis* + *C. surinamensis*	1,600	L yr^{-1}	26,560	± 1,440	USD yr^{-1}
Oleoresin	*Copaifera guyanensis*	800	L yr^{-1}	33,200	± 16,640	USD yr^{-1}
Fruit	*Oenocarpus bacaba*	1,509	kg yr^{-1}	16,750		USD yr^{-1}
Seed	*Dipteryx odorata*	28	kg yr^{-1}	1,996		USD yr^{-1}
Bark	*Parkia pendula*	726	$\text{m}^2\ \text{yr}^{-1}$	2,468	± 799	USD yr^{-1}
Bark	*Carapa guianensis* + *C. surinamensis*	221	$\text{m}^2\ \text{yr}^{-1}$	818	± 177	USD yr^{-1}
Bark	*Copaifera guyanensis*	379	$\text{m}^2\ \text{yr}^{-1}$	1,668	± 303	USD yr^{-1}
Bark	*Dipteryx odorata*	17	$\text{m}^2\ \text{yr}^{-1}$	243		USD yr^{-1}
Bark	*Pseudopiptadenia suaveolens*	636	$\text{m}^2\ \text{yr}^{-1}$	2,735	± 1,781	USD yr^{-1}
Bark	*Spondias mombin*	26	$\text{m}^2\ \text{yr}^{-1}$	164		USD yr^{-1}
Bark	*Hymenaea courbaril*	606	$\text{m}^2\ \text{yr}^{-1}$	2,485	± 545	USD yr^{-1}

Potential versus realized economic values of NTFP supply

The potential economic value of harvestable NTFP supply, i.e. the harvestable NTFP supply multiplied with the market price per quantity, was considerable, providing an average economic value of 3,056 USD $\text{ha}^{-1}\ \text{yr}^{-1}$ for all 13 NTFPs (Table 5-5). However, the estimated annual sales volumes of NTFPs at the Vreedzaam market were considerably smaller. Across all 13 NTFPs, on average 0.18% of harvestable NTFP supply was sold at the market, varying between 0.0006 and 1.7% (Table S5.1.3.7). Accounting for this, the realized economic value of the harvestable NTFP supply amounted to about 0.17 USD $\text{ha}^{-1}\ \text{yr}^{-1}$, which represented only 0.0003% of the average per hectare potential economic value (3,056 USD $\text{ha}^{-1}\ \text{yr}^{-1}$) (Table 5-5).

Table 5-5. Potential and realized economic value of harvestable NTFP supply for 13 NTFPs. Potential economic value is the harvestable NTFP supply multiplied by their market values at the Vreedzaam market, realized economic value is the potential economic value compensated for the amount of actually sold volumes at the Vreedzaam market. The sums of potential and realized economic value of harvestable NTFP supply across the 13 NTFPs has been compensated for differences in old-growth forest type surface areas, see Tables S5.1.3.8 and S5.1.3.9 for the calculations. The total old-growth forest surface area in the harvest area was estimated at 766,882 ha.

NTFP type	**NTFP species**	**Potential economic value of harvestable NTFP supply**		**Realized economic value of harvestable NTFP supply**	
Oil	*Astrocaryum sciophilum*	9.177	M USD yr^{-1}	6,028	USD yr^{-1}
Oil	*Attalea maripa*	238.057	M USD yr^{-1}	16,229	USD yr^{-1}
Oil	*Carapa guianensis* + *C. surinamensis*	95.340	M USD yr^{-1}	43,754	USD yr^{-1}
Oleoresin	*Copaifera guyanensis*	1.966	M USD yr^{-1}	33,220	USD yr^{-1}
Fruit	*Oenocarpus bacaba*	1,768.798	M USD yr^{-1}	16,807	USD yr^{-1}
Seed	*Dipteryx odorata*	24.866	M USD yr^{-1}	1,998	USD yr^{-1}
Bark	*Parkia pendula*	1.211	M USD yr^{-1}	2,502	USD yr^{-1}
Bark	*Carapa guianensis* + *C. surinamensis*	128.743	M USD yr^{-1}	814	USD yr^{-1}
Bark	*Copaifera guyanensis*	62.467	M USD yr^{-1}	1,664	USD yr^{-1}
Bark	*Dipteryx odorata*	2.189	M USD yr^{-1}	242	USD yr^{-1}
Bark	*Pseudopiptadenia suaveolens*	5.501	M USD yr^{-1}	2,730	USD yr^{-1}
Bark	*Spondias mombin*	4.396	M USD yr^{-1}	162	USD yr^{-1}
Bark	*Hymenaea courbaril*	1.082	M USD yr^{-1}	2,477	USD yr^{-1}
	SUM harvest area	2,343,794,584	USD yr^{-1}	128,627	USD yr^{-1}
	SUM per ha	3,056	USD ha^{-1} yr^{-1}	0.17	USD ha^{-1} yr^{-1}

The realized economic value of NTFP provisioning varied per old-growth forest type (Table S5.1.3.9). Marsh forests had the highest realized value (0.38 USD ha^{-1} yr^{-1}), followed by terra firme forests of the Coastal plains (0.18 USD ha^{-1} yr^{-1}), terra firme forests of the Interior (0.11 USD ha^{-1} yr^{-1}), mountain forests of the Interior (0.07 USD ha^{-1} yr^{-1}), terra firme forests of the Savanna belt and swamp forests (both 0.05 USD ha^{-1} yr^{-1}), white sand forests of the Savanna belt (0.01 USD ha^{-1} yr^{-1}) and mangrove forests (0 USD ha^{-1} yr^{-1}).

The percentage harvestable NTFP supply sold at the Vreedzaam market ('percentage supply sold'), was not significantly correlated to NTFP abundance, the forest exit price, or market price (all three $p \geq 0.3574$; Table S5.1.3.10). Although for oil-based NTFPs a visual trend could be observed, where for oil-based NTFPs the percentage supply sold increased with forest exit price (Figure S5.1.3.6, panel c), we did not analyse these trends further due to low sample sizes.

Harvesters received lower prices for the NTFPs than market vendors (Table S5.1.3.11). Across 9 NTFPs, forest exit price represented on average 37.7% of the market value, varying between 20.9 – 81.4% for specific NTFPs. Accounting for the average percentage of market value received, the realized economic value of harvestable NTFP supply represented only about 0.06 USD ha^{-1} yr^{-1} to the harvesters (37.7% of 0.17 USD ha^{-1} yr^{-1}).

Sustainability aspects of harvest and marketing

On the basis of the gross revenues that harvesters and market vendors made from selling plant-based NTFPs at the Vreedzaam market, we estimated that harvesters earned an annual gross revenue of between 780 – 3,120 USD yr^{-1}, and market vendors between 2,730 – 3,900 USD yr^{-1} (Annex S5.1.4). The averages of these ranges either centred around or were higher than the estimated 'annual minimum wage gross revenue', the annual gross revenue that could be earned with the minimum wage in Suriname in 2017 and 2018 based on a similar number of working days as harvesters and market vendors: 1,596 USD yr^{-1}. For harvesters, the estimated maximum costs of harvest and processing were small compared to the estimated gross revenues, collectively ranging between 0.03 to 0.12%. By contrast, the estimated costs of transport were considerable, ranging from only 5% for harvesters living near the capital, to about 72% for harvesters living in remote areas in the interior. These costs of transport did not increase linearly with the distance to the Vreedzaam market, as the harvesters deep in the interior needed to travel along rivers and/or along unpaved (laterite) roads, which was considerably more expensive than traveling along the present tarmac roads near the capital. For market vendors, estimated annual costs of operating a market stall and perished products proved to be likewise relatively small compared to the estimated range in earned annual gross revenues, ranging between 0.0008 to 0.34%.

All interviewed harvesters (n = 19) stated that there were common social rules concerning harvest practices for the 13 plant-based NTFPs, which they also adhered to. According to the harvesters, these rules were in place mainly to allow the equitable and sustainable use of the providing plant species and not to displease the supernatural entities that would live in the forests. They stated that when harvesters did not respect social rules concerning harvest practices, in most cases they would be punished, either by their peers or by supernatural entities. As an example of a social rule, harvesters stated that the bark of a tree could only be harvested up to a maximum height of 2 m and only for about a quarter of the surface area below this height at a time per harvester. This would allow the tree to survive and regenerate its bark and give other harvesters also the chance to harvest bark. In some cases, permission for bark harvesting was first asked to a supernatural entity. In support of the assumed ecological sustainability of this rule, during and outside the field work we observed several trees from which the bark had been removed up to 2 m around the whole trunk while the trees appeared to be healthy with regenerating bark (see for example Figure S5.1.3.3). All interviewed harvesters stated that, according to their perception, over the last decades the exploitation of the 13 plant-based NTFPs had not led to either widespread or consistent reduced natural populations of the providing plant species. In support of this perception, in the field we did not observe any deceased tree or arborescent-palm species that had apparently died from overharvesting. In addition, during our excursions in old-growth tropical forests, observed relative abundances were in line with the calculated mean abundances of the different forest types based on old-growth forest plots (surveyed between 1970 and 2017). The only exception was the arborescent palm species *Oenocarpus bacaba*, which we observed to be far less abundant in terra firme forests of the Coastal Plains than its mean abundance calculated from the forest plots (less than 1 individual per ha vs. 5.2 ± 10.8 per ha; Table S5.1.3.2).

5.4. Discussion

Low realized economic values per hectare of plant-based NTFPs from tropical forests

Our analysis resulted in a relatively low estimate of the per hectare realized economic value of plant-based NTFPs from old-growth tropical forests in Suriname. We found that only small volumes of the harvestable NTFP supply were actually sold at the Vreedzaam market, on average only 0.18%. When accounting for the sales volumes, the harvestable NTFP supply corresponded to an average gross revenue value of 0.17 USD ha^{-1} yr^{-1}. This was a considerably lower value than previous estimates of the economic value of plant-based NTFPs from old-growth tropical forest reported in the literature, which ranged between 20 and 6,330 USD ha^{-1} yr^{-1} (Grimes et al., 1994; Peters, Gentry, et al., 1989; Pinedo-Vasquez et al., 1992). However, these estimates from the literature concerned potential economic values, implicitly assuming that almost all harvestable NTFP supply can be valued at current market prices. By contrast, our estimate of realized value accounted for the fact that not all harvestable NTFP supply will be harvested and traded due to institutional constraints and costs of harvest, processing and transport (Gram, 2001; Schaafsma et al., 2014; Timko et al., 2010), and considered the influence of supply and demand mechanisms of the market on the traded volume, as highlighted by the study of Hilfiker et al. (2006). Our estimated per hectare potential economic value of the potential NTFP supply in the harvest area was about 3,000 USD ha^{-1} yr^{-1}, which fell within the range of estimates of potential economic value from the literature (Grimes et al., 1994; Peters, Gentry, et al., 1989; Pinedo-Vasquez et al., 1992).

Our estimates of the harvestable NTFP supply and the sales volumes were only as good as the precision, sample size and coverage of the data that we used. It is important to note that our estimates included only a subset of the potential commercial plant-based NTFPs reported for Suriname. For instance, a previous study of the sale of plant species in Suriname by van Andel & Havinga (2008) identified 28 commercial species harvested exclusively from old-growth tropical forests, while our analysis of the flow of NTFPs to the

Vreedzaam market included only 11 of such species, and only 13 of the 24 NTFPs that were provided by them. Although for some variables we were able to account for uncertainties by analysing standard deviations of the mean, for example for NTFP abundance and NTFP market price, this was not possible for those variables measured with limited sample sizes, for example NTFP production values and the common NTFP harvester action radius. Overall, we think that the largest uncertainty in our estimates of the potential and realized economic value is related to the average NTFP production values that we used, for three reasons. First, because it was not feasible during the fieldwork to measure production values, we used interview data to estimate the production values. However, interview data are less reliable than direct measurements, as actors seldomly keep records and their judgement of quantitative units may be subjective (Gram, 2001). Although we cross-refenced estimates provided by interviews with literature data, for most NTFPs this was not available or insufficient. Second, because of the fragmented state of knowledge on NTFP production, we chose to use a single average production value for oil- and fruit-based NTFPs per species for all forest types. However, as the production of NTFPs may differ across forest types and across DBH (e.g. Dantas et al., 2016; P. Newton et al., 2011; Phillips, 1993), this may have resulted in over- or underestimation of the actual NTFP supply. Third and last, several NTFPs were sourced from the same species, and although we did not find any evidence from interviews with harvesters or the literature that the harvest of one of these 13 NTFP would negatively impact the harvest of another, we cannot exclude that the NTFP supplies are overestimated for species with multiple products. In spite of these limitations, we believe that our estimates of harvestable NTFP supply, sales volumes and corresponding economic values are representative of their actual values, at least in their order of magnitude.

Important revenues for local stakeholders from selling plant-based NTFPs

Our analyses suggested that harvesters of received substantial annual gross revenues from selling wild plant-based NTFPs. Value chains up to and including the Vreedzaam market were generally two actors long, where the harvesters received on average 37% of the total gross revenue. Although the estimated per hectare value for harvesters was on average only 0.06 USD ha^{-1} yr^{-1} (37% of 0.17 USD ha^{-1} yr^{-1}), we also estimated that most harvesters received gross revenues from the trade of plant-based NTFPs sources from old-growth tropical forests ranging between 780 and 3,120 USD yr^{-1}. This can be considered an important source of income, as the gross revenues received by the majority of harvesters is above the minimum wage in Suriname (1,590 USD yr^{-1}). During the fieldwork we encountered hundreds of harvesters who were providing plant-based NTFPs for wholesale at the Vreedzaam market. Besides harvesters, we recorded a number of active market vendors at the Vreedzaam market, ranging between 80 on quiet days to almost 200 on busy days. Because there are also other, smaller markets for NTFPs in Suriname and some products are traded on international markets (e.g. in the Netherlands, see van Andel et al., 2007), overall, the sale of plant-based NTFPs should provide an important source of cash-income to many Suriname households.

Little evidence of overexploitation of plant-based NTFPs

Interviews and walks-in-the-woods with harvesters did not provide evidence of widespread overexploitation of the studied plant-based NTFPs. All interviewed harvesters claimed to adhere to social rules that should avoid overexploitation, and during walks-in-the-woods with harvesters we did not observe signs that harvesters used harvest practices that were detrimental to plant species populations. In addition, most of the calculated mean abundances of the considered NTFP species were in line with our field observations. The only exception was the arborescent palm species *Oenocarpus bacaba*, which we observed to be far less abundant in terra firme forests of the Coastal plains than its calculated mean abundance suggested (< 1 vs. on average 5.2 individuals per ha), indicating potential local overharvesting. Harvesters explained that the fruit of this palm species should be harvested by climbing the stem, as cutting down the stem results in plant mortality. However, harvesters also stated that they “sometimes” cut down the stem in order to save time. It might therefore be that for terra firme forests of the Coastal plains, either more harvesters of this species are active than in other forests, or that the claimed harvest practices are being less adhered to in these forests than elsewhere. Our general findings on the ecological sustainability of the 13 plant-based NTFPs are in line with previous similar assessments for Suriname. For Suriname, anecdotal evidence of overharvesting of wild NTFPs has only been found for two species: the epiphyte *Begonia glabra* Aubl. and the terrestrial palm *Geonoma baculifera* Kunth. (Rijpkema, 2016; Ruysschaert, 2018; van Andel & Havinga, 2008; van den Boog et al., 2018). However, as assessments of long-term impacts of harvest practices on plant species populations are currently lacking for Suriname, we cannot exclude that commercial use of plant-based NTFPs may result in overexploitation, currently or in the future.

Market sale of plant-based NTFPs relevant for tropical forest conservation in Suriname

Based on our assessment of the economic benefits received by harvesters and the ecological sustainability of harvest practices, the market sale of these common 13 NTFPs is at least relevant for tropical forest conservation in Suriname. Under the ‘conservation-through-use-paradigm’, commercial trade of NTFPs is likely to contribute to conservation when 1) the economic value received by local stakeholders is adequality high, and 2) it does not lead to a reduction of natural populations (Kusters et al., 2006; A. C. Newton, 2008). Although the average revenues per hectare were low, most harvesters received reasonable economic benefits from selling the studied NTFP species. In addition, we found no evidence of widespread overexploitation of the considered plant-based NTFPs, where only one NTFP showed signs of potential local overharvesting. However, as our study did not analyse the decision-making process of harvesters, it is uncertain to what extent the generated economic benefits actually function as an incentive to keep tropical forests standing. For example, even when the perceived profits are high, harvesters might choose to overexploit the plant-based NTFPs when they have a short planning horizon, for instance because of limited land tenure security (Stanley et al., 2012). The actual contribution of selling plant-based NTFPs to tropical forest conservation therefore merits further study. It is important to note that not all NTFPs are eligible to contribute to the conservation of old-growth tropical forests. For example, in Suriname many plant-based NTFPs are sourced from secondary vegetation and tropical savannas (e.g. van Andel & Havinga, 2008), and it is expected that many animal-based NTFPs from old-growth tropical forests are unsustainably exploited, mainly because of their generally high unit prices (e.g. van Andel et al., 2003; van den Boog et al., 2018; Verheij, 2019). Although the interviewed harvesters in our study were not involved in the regular trade of animal-based NTFPs, we cannot exclude that animal-based NTFPs are used to supplement the income of local actors of old-growth tropical forests.

Harvestable NTFP supply and realized market value vary across forest types and species

Our analyses illustrated that harvestable NTFP supply and its realized economic value can vary considerably across NTFPs and across space. Harvestable NTFP supply varies according to differences in the average production values per NTFP species and variation in NTFP abundance across forest types. Differences in sales volumes according to different standard market units also added to the variation in realized economic value of NTFPs. However, most importantly, NTFPs differed in the extent to which their harvestable supply was actually marketed, where the percentage of harvestable NTFP supply sold at the Vreedzaam market ('percentage supply sold') varied between 0.0006 and 1.7%. This percentage was not significantly correlated to NTFP abundance nor to forest exit price or market price. Although we observed a visual trend for oil-based NTFPs, where more of the potential supply was sold when the forest exit price was higher, our sample sizes were too low to analyse these patterns further. Ultimately, our findings confirm that, in order to assess the economic value of NTFP provisioning of tropical forest areas, information is needed on both harvestable NTFP supply and the market for NTFPs. Although this has been suggested before (e.g. Belcher & Schreckenberg, 2007; Godoy et al., 1993; Sheil & Wunder, 2002), our study is the first to systematically map and quantify the flow of NTFPs from forest to the market and analyse variation in the components of this flow.

Consistent large gap between potential and realized economic values of NTFP supply

With the help of our framework, we were able to compare the potential economic value of harvestable NTFP supply with the economic value realized by actual market sales. Across the 13 NTFPs, we found a consistent large gap between the potential economic value and the realized economic value, where the realized economic value represented between

0.0006 and 1.7%, on average 0.18%, of the potential economic value (the percentage supply sold being identical). This shows that potential economic value of NTFP supply tends to strongly overestimate the economic value derived from actual market sales. Although scholars had suggested that potential economic values were likely to be overestimations of the realized economic value, for reasons discussed earlier (e.g. Belcher & Schreckenberg, 2007; Godoy et al., 1993; Sheil & Wunder, 2002), this difference had not been quantified before for old-growth tropical forests, only for agroforestry systems (Padoch & de Jong, 1989). However, it is important to note that our assessment was based on the demand of a single national market, excluding NTFP use by local communities for subsistence, the demand of other domestic markets as well as most of the demand of the international market. We observed that at least some volume that is traded internationally is bought at the Vreedzaam market. Including multiple NTFP markets may decrease the gap between potential and realized economic values somewhat, although the harvest area covered by their supply is also expected to be larger.

Concluding remarks

In this paper, we developed a theoretical framework that allowed us to assess the economic value of plant-based NTFPs derived from tropical forests by mapping the flow of NTFPs from forest to market. We applied this framework to quantify the economic value of 13 commonly traded plant-based NTFPs in Suriname according to their actual market sales, and assess the distribution of economic benefits across local actors. Although the economic benefits received by harvesters were important, the extent to which the selling of NTFPs can act as an incentive for tropical forest conservation (in line with the 'conservation-through-use-paradigm') remains unclear. The framework can help to generate more realistic and accurate estimations of the economic value of harvestable NTFP supply from tropical forests. However, additional empirical research will be needed to assess the impact of NTFP use on natural plant populations and the extent to which the realized economic value is acting as an incentive to preserve tropical forests.

For Suriname, we found that the economic benefits of plant-based NTFPs are highly important to the economy, local livelihoods and tropical forest conservation. First, we observed a large number of actors involved in the marketing of plant-based NTFPs, representing an important source of income to a large number of households in Suriname. The total added value that is generated by the entire commercial trade of plant-based NTFPs can be considerable. For example, the entire domestic and international trade of medicinal plants (many of which are NTFPs) was estimated at around 1.5 million USD in 2006, approaching the then value of the entire commercial legal timber export (2.3-4.2 million USD; van Andel et al., 2007). Second, bringing plant-based NTFPs to the market provides an increasingly important source of cash-income for Suriname people living in the interior, where other sources of a cash-income are scarce (Ramirez-Gomez et al., 2016, 2017). Third and last, although the actors who sell plant-based NTFPs and use them for subsistence often do not have secured tenure rights over these tropical forests (Ramirez-Gomez et al., 2016, 2017), the received economic benefits from this use can be considerable, which could contribute to forest conservation. Therefore, there seems to be potential for a win-win situation for local livelihoods, i.e. securing a means of generating a cash-income while also contributing to old-growth tropical forests conservation. In line with Oldekop et al. (2016), old-growth tropical forest that supply important NTFPs could be designated as extractive reserves or as multiple-use-zones, as such designations are more likely to lead to positive conservation and socio-economic outcomes.

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SUPPLEMENTARY MATERIAL CHAPTER 5

Annex S5.1 Supplementary Material

S5.1.1 Supplementary information on NTFPs and their botanical species

Table S5.1.1.1. Collected botanical vouchers during this study (2017-2018).

Table S5.1.1.1 has been omitted to save paper. It can be accessed at the published version of this chapter (see the beginning of this chapter for a DOI and QR code).

Table S5.1.1.2. All known NTFPs sold on herbal markets in Suriname sourced from the 11 trees and palms included in this study. Spelling of vernacular names after van Andel et al. (2007), main uses after van Andel & Ruysschaert (2011).

Scientific species	Family	NTFP type	Vernacular name (Sranantongo)	Main uses	Included in this study
Astrocaryum sciophilum (Miq.) Pulle	Arecaceae	Oil from seed	tjo tjo oli	Treatment of bone fractures	Yes
Attalea maripa (Aubl.) Mart.	Arecaceae	Oil from seed	maripa oli / maripa fatu	Baking, skin care	Yes
		Arial roots	maripa lutu	Pregnancy	No
		Ash from spathe	maripa boto asisi	Rituals	No
		Young leaf	maripa mosoku / tongo	Rituals	No
		Spathe	maripa boto	Rituals	No
Oenocarpus bacaba Mart.	Arecaceae	Fresh fruit	kumbu siri	Drink, anaemia	Yes
		Arial roots	kumbu lutu	Pregnancy	No
		Young leaf	kumbu tongo	Rituals	No
Spondias mombin L.	Anacardiaceae	Bark	mope buba	Genital hygiene	Yes
		Fruit	mope futa	Food	Yes
		Leaf	mope uwii	Rituals	No
Copaifera guyanensis Desf.	Fabaceae	Oleoresin	opro oli	Skin care, treatment of various diseases	Yes
		Bark	opro buba	Tea, treatment of various diseases.	Yes
Dipteryx odorata (Aubl.) Willd.	Fabaceae	Dried seed	tonka siri	Cosmetic hair product	Yes
		Bark	tonka buba	Rituals	Yes
Hymenaea courbaril L.	Fabaceae	Bark	loksi buba	Treatment of various diseases, tea, rituals	Yes
		Resin	loksi kandea	Rituals	No
		Fruit	loksi futa	Food	No
Parkia pendula (Willd.) Benth. ex Walp.	Fabaceae	Bark	kwatakama buba	Treatment of various diseases, rituals	Yes
		Leaf	kwatakama uwii	Rituals	No
Pseudopiptadenia suaveolens (Miq.) J.W. Grimes	Fabaceae	Bark	pikinmisiki buba	Rituals, baby care	Yes
Carapa guianensis Aubl. + *Carapa surinamensis* Miq.	Meliaceae	Oil from seed	krapa oli	Skin care, Treatment of various diseases.	Yes
		Bark	krapa buba	Treatment of various diseases	Yes

S5.1.2 Plot metadata

Plot dataset

For the calculation of mean abundance per forest type, we compiled a dataset of 346 tropical forest plots in Suriname (Figure S1.2.1; Table S1.2.1). Of these plots, 340 were previously published plots, including datasets of research consortia (datasets 'ATDN', 'CI TEAM', 'FCAM') and individual researchers (datasets 'Teunissen' and 'Ruysschaert') (references provided in Table S1.2.1), and 6 were newly censused by the lead author during 2017 (dataset 'Steur'). These latter 6 plots were located around the Marron (Matawai) village of Pusugrunu along the Upper Saramacca River. For all plots except for those from the Teunissen dataset, all tree and arborescent palm NTFP species with a DBH of ≥ 10 cm were measured and identified. The Teunissen dataset originally included data that was stored as DBH ≥ 5 cm. This was converted to represent measurements of DBH ≥ 10 cm by taking 40% of the stems with DBH ≥ 5 cm on the basis of the analyses on stem number and DBH class by Lindeman and Moolenaar (1959). According to the analysis by Lindeman and Moolenaar (1959), the relationship between stem number and DBH class was logarithmic for each of the forest types included in the Teunissen dataset. In these forest types, the DBH class ≥ 5 and < 10 cm contained about 60% of all measured stems (See Fig. 7 in Lindeman & Moolenaar, 1959). Species taxonomy was updated after the 'Dynamic Amazon Tree Checklist' (ter Steege et al., 2019b; updated version 20200422).

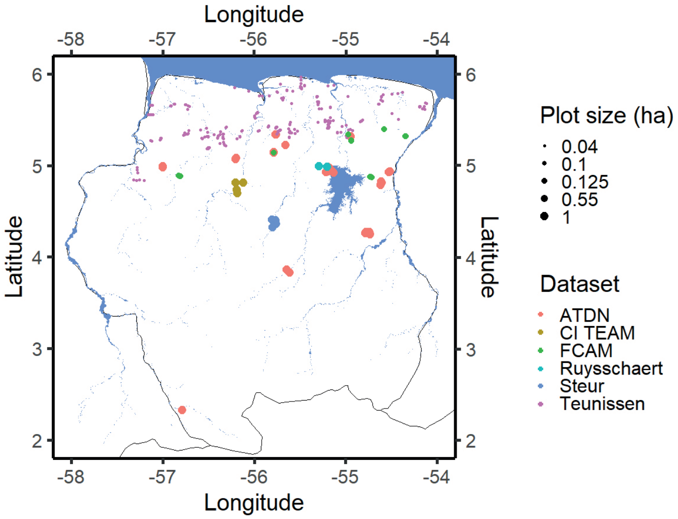

Figure S5.1.2.1. Graphical overview plot locations of different datasets. Border lines (black) drawn according to the ggplot 'maps()' function in R (Becker & Wilks, 1993).

Table S5.1.2.1. Overview of plot data used in this study.

Dataset	Data owners	Plot number and size	Area in Suriname	Reference
Teunissen	Pieter Teunissen and Gijs Steur	276 x 0.04 ha	Coastal area (incl. Savanna belt)	1
Steur	Gijs Steur	6 x 1 ha	Interior (along the Saramacca river)	This study
ATDN	Hans ter Steege, Olaf Banki, Bruce Hoffman, Christopher Baraloto	42 x 1 ha, 1 x 0.55 ha, 2 x 0.1 ha	Savanna belt and bauxite mountains, Interior (along Suriname river and South-Suriname)	2, 3, 4, 5, 6, 7, 8, 9, 10
Ruysschaert	Sofie Ruysschaert	2 x 1 ha	Savanna belt and interior (around Brownsweg)	11
CI TEAM	Tropical Ecology, Assessment and Monitoring Network	4 x 1 ha	Interior (Central Nature Reserve)	12
FCAM	State Forestry Service of Suriname	13 x 0.125 ha	Savanna belt and interior	13

1 Steur, G., Verburg, R. W., Wassen, M. J., Teunissen, P. A., & Verweij, P. A. (2021). Exploring relationships between abundance of non-timber forest product species and tropical forest plant diversity. Ecological Indicators, 121, 107202.

2 Bánki, O. S. (2006) Tree diversity in the vicinity of Kabo: A field report. Ecology & Biodiversity, Utrecht University.

3 Bánki, O. S. (2006) Tree diversity plots in the vicinity of Bitagron: A field report. Ecology & Biodiversity, Utrecht University.

4 Bánki, O. S. (2006) Tree diversity plots on white sand in the Bruynzeel Suriname Houtmaatschappij Kabo Concession: A field report. Ecology & Biodiversity, Utrecht University.

5 Bánki, O. S. (2010) Does neutral theory explain community composition in the Guiana Shield forests? PhD Thesis, Dept. Biology, Utrecht University.

6 Bánki, O. S., ter Steege, H., Jansen-Jacobs, M. J. & Raghoenandan, U. P. D. (2003) Plant diversity of the Nassau Mountains Suriname. Report of the 2003 Expedition. NHN-Utrecht, BBS-Paramaribo.

7 ter Steege, H. B., O. S., van Andel, T. R., Behari-Ramdas, J., Ramharakh, G. (2004b) Plant diversity in the Brownsberg Nature Park, Suriname. Report of the Nov-Dec 2003 expedition. NHN-Utrecht, BBS-Paramaribo, Utrecht.

8 ter Steege, H., Bánki, O.S., Jansen-Jacobs, M., Ramharakh, G. & Tjon, K. (2005) Plant diversity of Lely Mountains, Suriname. Report of the Nov-Dec 2004 Expedition. NHN-Utrecht, BBS-Paramaribo.

9 Hoffman, B. (2009) Drums and arrows: Ethnobotanical classification and use of tropical forest plants by a Maroon and Amerindian community in Suriname, with implications for biocultural conservation. PhD Thesis University of Hawai'i.

10 Baraloto, C., Rebaud, S. Molto, Q., Blanc, L., Fortunel, C., Hérault, B., Dávila, N., Mesones, I., Rios, M., Valderrama, E., Fine, P.V.A. (2011) Disentangling stand and environmental correlates of aboveground biomass in Amazonian forests. Global Change Biology, 17, 8. https://doi.org/10.1111/j.1365-2486.2011.02432.x

11 Ruysschaert, S. (2018). Non-timber forest products in Suriname: diversity, knowledge and use of plants in an Ameridian and Maroon community. PhD Thesis Ghent University. Faculty of Bioscience Engineering, Ghent, Belgium.

12 Linares-Palomino, R. and Wortel, V., 2015-10-28, Vegetation - Trees & Lianas Metadata Version 1.5, VT-20180521030329_3993. www.teamnetwork.org. The Tropical Ecology Assessment and Monitoring (TEAM) Network is collaboration between Conservation International, the Missouri Botanical Garden, the Smithsonian Institution, and the Wildlife Conservation Society, and partially funded by these institutions, the Gordon and Betty Moore Foundation, and other donors.

13 Crabbe, S. (ed.), Somopawito, S., Hanoeman, W., Playfair, M., Tjon, K., Djosetro, M., Pinas, B., Worel, V., Sanches, M., Soetosenojo, A. (2012). Results of Forest Carbon Assessment and Monitoring Project Suriname, period 2010-2011. Technical Report State Forestry Service of Suriname.

S5.1.3 Fieldwork impressions and supplementary data

Figure S5.1.3.1. UPPER: One of our main informants, the market vendor Trees Waterberg, next to her stall in the Vreedzaam market. Photo by Jeffrey Brand. LOWER: Photo of Luc Haverhals, Master student of Utrecht University, measuring plant-based NTFPs for sale on the Vreedzaam market. Photo by Gijs Steur.

Figure S5.1.3.2. Outside the Vreedzaam market around 04:40 A.M. on a Monday in July 2018. harvesters and middle-men are offering NTFPs for wholesale in large white rice bags. Photo by Gijs Steur.

Figure S5.1.3.3. Evidence of bark harvesting of a *Pseudopiptadenia suaveolens* individual. The bark was removed on all sides up to 2 m high, apparently without consequence for its survival. Bark shown in the left picture has started to regenerate. Photos by Gijs Steur.

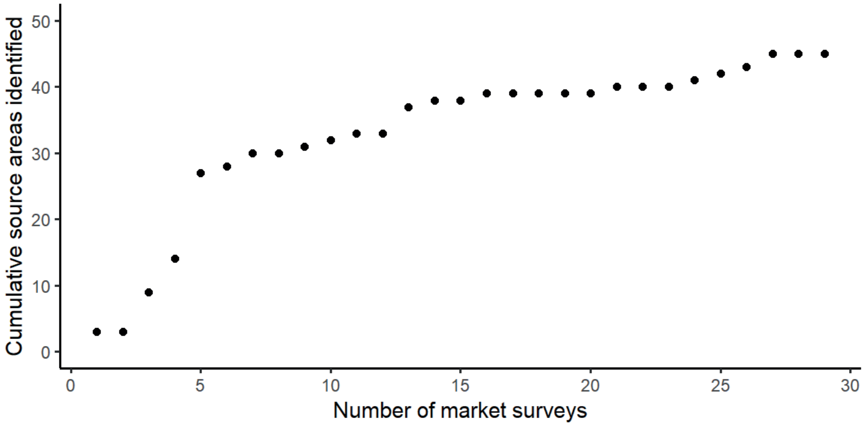

Figure S5.1.3.4. Accumulation curve of source areas (y-axis) across the number of market surveys (x-axis).

Table S5.1.3.1. Surface area of old-growth forest types across Suriname and across the harvest area, based on the Sarvision vegetation map of Suriname (Quiñones & Hoekman, 2011).

Tropical forest type	**Suriname**		**Harvest area**		
Mangrove forests	415 km^2	0.26%	29 km^2	2,895 ha	0.38%
Swamp forests	2,483 km^2	1.55%	298 km^2	29,798 ha	3.88%
Marsh forests	20,979 km^2	13.11%	1,563 km^2	156,310 ha	20.38%
Terra firme forests of the Coastal plains	6,374 km^2	3.98%	1,658 km^2	165,817 ha	21.62%
Terra firme forests of the Savanna belt	7,920 km^2	4.95%	920 km^2	92,054 ha	12.00%
Terra firme forests of the Interior	116,895 km^2	73.04%	3,089 km^2	308,920 ha	40.28%
White sand forests of the Savanna belt	1,670 km^2	1.04%	108 km^2	10,778 ha	1.40%
Mountain forests of the Interior	3,296 km^2	2.06%	3 km^2	308 ha	0.04%
Total	160,032 km^2	100%	7,668 km^2	766,881 ha	100%

Table S5.1.3.2. Mean and standard deviation of NTFP abundance (# stems ha-1) per old-growth tropical forest type. n = number of plots. Colouration per species according to the relative abundance across the forest strata: light green: rare, green: common, dark green: abundant. Below the percentage of total NTFP stems is given per forest type.

NTFP Species	**Mangrove forests**	**Swamp forests**	**Marsh forests**	**Terra firme forests of the Coastal plains**	**Terra firme forests of the Savanna belt**	**Terra firme forests of the Interior**	**White sand forests of the Savanna belt**	**Mountain forests of the Interior**
	n = 3	n = 61	n = 88	n = 52	n = 44	n = 30	n = 53	n = 15
Astrocaryum sciophilum	0 ± 0	0 ± 0	1.1 ± 6.0	6.5 ± 26.4	21.6 ± 51.9	26 ± 40.2	0 ± 0	0 ± 0
Attalea maripa	0 ± 0	0.8 ± 4.2	16.1 ± 22.3	18.7 ± 34.1	0.2 ± 1.5	0.7 ± 1.4	0.9 ± 5.6	0.1 ± 0.3
Carapa guianensis	0 ± 0	5.9 ± 18.1	28.4 ± 49.7	3.7 ± 11.4	0.2 ± 1.5	0.6 ± 1.9	0 ± 0	0.2 ± 0.8
Carapa surinamensis	0 ± 0	1.3 ± 4.6	3.1 ± 11.2	3.3 ± 12.0	0.9 ± 2.9	5.3 ± 8.8	0 ± 0	0.6 ± 2.1
Carapa guianensis + C. surinamensis	0 ± 0	7.4 ± 18.6	31.6 ± 49.5	6.9 ± 16.7	1.4 ± 3.5	6.5 ± 8.7	0 ± 0	0.8 ± 2.8
Copaifera guyanensis	0 ± 0	1 ± 3.5	10.9 ± 26.9	5.2 ± 8.3	0.5 ± 2.1	0.2 ± 0.8	0.2 ± 1.4	0 ± 0
Oenocarpus bacaba	0 ± 0	0 ± 0	1.8 ± 5.6	5.2 ± 10.8	3.4 ± 7	9.2 ± 17.3	0.4 ± 2.7	1.9 ± 2.1
Dipteryx odorata	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.5	0.1 ± 0.3	0 ± 0	0.7 ± 1
Parkia pendula	0 ± 0	0 ± 0	0.02 ± 0.2	0.2 ± 1.4	0.3 ± 1.5	0.2 ± 0.4	0.04 ± 0.2	0.4 ± 0.5
Pseudopiptadenia suaveolens	0 ± 0	0 ± 0	0.01 ± 0.1	0 ± 0	0.2 ± 0.7	1.2 ± 3.2	0 ± 0	1.0 ± 1.3
Spondias mombin	0 ± 0	0.8 ± 5.3	1.7 ± 5.3	0.4 ± 2.8	0 ± 0	0.3 ± 1.5	0 ± 0	0 ± 0
Hymenaea courbaril	0 ± 0	0 ± 0	0.3 ± 1.8	0 ± 0	0 ± 0	0.1 ± 0.2	0 ± 0	0.5 ± 1.1
All species	0 ± 0	10.0 ± 20.3	63.6 ± 58.6	43.1 ± 45.8	27.6 ± 50.7	44.6 ± 43.5	0.8 ± 2.8	5.4 ± 4.6
	0%	5.1%	32.5%	22.0%	14.1%	22.8%	0.8%	2.7%

Table S5.1.3.3. Analysis of variance F-tests for mean NTFP abundance (# stems ha^{-1}) across the eight old-growth forest types (n = 346).

Model	F-statistic	Df1	Df2	p-value	Multiple R-squared
Astrocaryum sciophilum ~ Forest type	7.068	7	338	6.963e-08	0.1277
Attalea maripa ~ Forest type	10.37	7	338	8.512e-12	0.1768
Carapa guianensis ~ Forest type	9.29	7	338	1.574e-10	0.1614
Carapa surinamensis ~ Forest type	1.814	7	338	0.08362	0.03621
Carapa guianensis + C. surinamensis ~ Forest type	10.01	7	338	2.255e-11	0.1717
Copaifera guyanensis ~ Forest type	4.87	7	338	2.992e-05	0.09161
Oenocarpus bacaba ~ Forest type	5.952	7	338	1.515e-06	0.1097
Dipteryx odorata ~ Forest type	12.1	7	338	8.353e-14	0.2004
Parkia pendula ~ Forest type	1.075	7	338	0.3791	0.02178
Pseudopiptadenia suaveolens ~ Forest type	7.153	7	338	5.493e-08	0.129
Spondias mombin ~ Forest type	1.67	7	338	0.1153	0.03344
Hymenaea courbaril ~ Forest type	1.441	7	338	0.1879	0.02897

Table S5.1.3.4. Estimated sustainable NTFP production values per NTFP individual.

NTFP species	NTFP type	Estimated mean production per individual	Sources
Astrocaryum sciophilum	Oil from seeds	On average, a mature individual produces 33 fruits yr^{-1} corresponding to 759 ± 280 g yr^{-1}; ca. 50 kg of fruit is needed for 1 litre of oil; 15.18 ± 5.61 ml yr^{-1}	Mean production of fruit and mean weight of fruit: Kahn & De Granville (1992), Charles-dominique et al. (2003) and interview data. Conversion kg of fruit to L of oil: interview data.
Attalea maripa	Oil from seeds	3(-4) inflorescences per year; 2 infructescences needed for 1 litre of oil; 1.5 L or 1500 ml yr^{-1}	Number of inflorescences per year: Matos et al. (2017), Pires et al. (2016), Shanley et al. (2011) and interview data. Conversion inflorescences to L of oil: interview data.
Carapa guianensis + *Carapa surinamensis*	Oil from seeds	66% of all DBH > 10 cm individuals produce fruit; and individual produces ca. 50 kg of fruit each year; 50 kg of fruit is needed for ca. 3 litres of oil; 412.5 ml yr^{-1}	Average yearly fruit production across all DBH > 10 cm individuals on terra firme and várzea soils: Londres et al. (2017), Plowden, (2004), Shanley et al. (2011), Sist et al. (2014), Tonini et al. (2009), Klimas et al. (2012) and interview data; conversion of kg of fruit to L of oil: Sist et al. (2014) and interview data.
Copaifera guyanensis	Oleoresin	35% of all individuals produce oleoresin each year; Harvest of oleoresin is carried out during 2(-3) weeks, only once each year; An individual produces ca. 50 ml each year; 17.5 ml yr^{-1}	Average yearly oleoresin production: (de Benathar et al. (2020), Newton et al. (2011), Shanley et al. (2011) and interview data. Harvest practices: interview data.
Oenocarpus bacaba	Fruits	2-3 inflorescences per year; one infructescence weighs around 10 kg; average amount of 36.8 kg of fruit per individual per year	Yearly production per individual: Peters et al. (1989a) and interview data.
Dipteryx odorata	Seeds	Usually, an individual produces 1 kg of dried seeds per year, but once every 3-4 years a bulk amount of up to 25kg, thus on average (1+1+1+25/4) 7 kg yr^{-1}; a seed weighs 2.36 g; 2960 seeds yr^{-1}	Production: Pérez & Souto (2011)Estimated mean and interview data

NTFP species	NTFP type	Estimated mean production per individual	Sources
Parkia pendula	Bark	With regeneration, bark can be harvested 1-2 times each year: 1.5 times. Average DBH: 35.7 cm (n = 20)	Bark regeneration: Interview data.
Carapa guianensis + Carapa surinamensis	Bark	With regeneration, bark can be harvested 3-4 times each year: 3 times. Average DBH: 22.9 cm (n = 493)	Bark regeneration: Interview data.
Copaifera guyanensis	Bark	With regeneration, bark can be harvested 3-4 times each year: 3 times. Average DBH: 29.6 cm (n = 154)	Bark regeneration: Interview data.
Dipteryx odorata	Bark	With regeneration, bark can be harvested once each year: 1 time. Average DBH: 47.2 cm (n = 18)	Bark regeneration: Interview data.
Pseudopiptadenia suaveolens	Bark	With regeneration, bark can be harvested 1-2 times each year: 1.5 times. Average DBH: 29.5 cm (n = 39)	Bark regeneration: Interview data.
Spondias mombin	Bark	With regeneration, bark can be harvested once each year: 1 time. Average DBH: 26.1 cm (n = 25)	Bark regeneration: Interview data.
Hymenaea courbaril	Bark	With regeneration, bark can be harvested once each year: 1 time. Average DBH: 49.4 cm (n = 12)	Bark regeneration: Interview data.

Table S5.1.3.5. Estimated number of stems per species for each forest type in the harvest area and for the total harvest area. Per forest type the number of stems was estimated by first calculating the mean abundance per ha (including standard deviation, SD), second multiplying the mean with the relative surface area of the forest stratum. Estimated number of stems per forest type were summed to provide the estimated number of stems for the total harvest area.

NTFP species	**Mangrove forests**	**Swamp forests**	**Marsh forests**	**Terra firme forests of the Coastal plains**	**Terra firme forests of the Savanna belt**	**Terra firme forests of the Interior**	**White sand forests of the Savanna belt**	**Mountain forests of the Interior**	**Total harvest area**
	(3 plots) (2,895 ha)	(61 plots) (29,798 ha)	(88 plots) (156,310 ha)	(52 plots) (165,817 ha)	(44 plots) (92,054 ha)	(30 plots) (308,920 ha)	(53 plots) (10,778 ha)	(15 plots) (308 ha)	(346 plots) (766,881 ha)
Astrocaryum sciophilum	0 ± 0	0 ± 0	179,401 ± 940,413	1,084,188 ± 4,379,535	1,987,534 ± 4,781,848	8,031,934 ± 12,416,067	0 ± 0	0 ± 0	11,283,057 ± 14,038,857
Attalea maripa	0 ± 0	24,425 ± 125,188	2,513,391 ± 3,481,446	3,093,124 ± 5,659,240	20,921 ± 138,777	205,947 ± 431,829	10,168 ± 60,766	41 ± 108	5,868,018 ± 6,661,274
Carapa guianensis + *C. surinamensis*	0 ± 0	219,821 ± 554,545	4,937,970 ± 7,731,156	1,147,963 ± 2,777,337	127,621 ± 319,019	2,018,281 ± 2,692,781	0 ± 0	246 ± 873	8,451,903 ± 8,668,607
Copaifera guyanensis	0 ± 0	29,309 ± 104,716	1,699,870 ± 4,206,991	860,973 ± 1,373,278	41,843 ± 193,965	72,081 ± 252,450	2,034 ± 14,805	0 ± 0	2,706,110 ± 4,438,153
Oenocarpus bacaba	0 ± 0	0 ± 0	287,752 ± 871,711	860,973 ± 1,783,196	309,637 ± 648,219	2,852,366 ± 5,337,535	4,067 ± 29,610	592 ± 663	4,315,387 ± 5,731,493
Dipteryx odorata	0 ± 0	0 ± 0	0 ± 0	0 ± 0	8,369 ± 43,578	41,189 ± 106,808	0 ± 0	205 ± 301	49,763 ± 115,356
Parkia pendula	0 ± 0	0 ± 0	3,552 ± 33,325	31,888 ± 229,947	25,106 ± 140,891	61,784 ± 125,681	407 ± 2,074	123 ± 156	122,860 ± 299,393
Pseudopiptadenia suaveolens	0 ± 0	0 ± 0	1,776 ± 16,663	0 ± 0	16,737 ± 63,631	381,002 ± 989,222	0 ± 0	304 ± 417	399,820 ± 991,407
Spondias mombin	0 ± 0	24,425 ± 156,688	268,214 ± 828,115	63,776 ± 459,894	0 ± 0	92,676 ± 452,785	0 ± 0	0 ± 0	449,090 ± 1,061,528
Hymenaea courbaril	0 ± 0	0 ± 0	53,287 ± 285,270	0 ± 0	0 ± 0	20,595 ± 78,376	0 ± 0	144 ± 347	74,026 ± 295,840
All species	0 ± 0 (0%)	297,979 ± 605,810 (0.884%)	9,945,215 ± 9,166,533 (29.493%)	7,142,884 ± 7,598,960 (21.183%)	2,537,767 ± 4,671,827 (7.526%)	13,777,857 ± 13,447,340 (40.86%)	16,676 ± 80,145 (0.049%)	1,656 ± 1,409 (0.005%)	33,720,033 ± 18,568,787 (100%)

Table S5.1.3.6. Estimated potential NTFP supply (including standard deviation, SD) for each NTFP per forest stratum within the harvest area. Per forest stratum the potential supply was estimated by calculating the mean potential supply per ha and multiplying this with the relative surface area of the forest stratum. Estimated potential supply per forest type were summed to provide the estimated potential supply for the harvest area (harvestable NTFP supply).

NTFP species	**NTFP supply unit**	**Mangrove forests**	**Swamp forests**	**Marsh forests**	**Terra firme forests of the Coastal plains**	**Terra firme forests of the Savanna belt**	**Terra firme forests of the Interior**	**White sand forests of the Savanna belt**	**Mountain forests of the Interior**	**Total harvest area**
		(3 plots)	(61 plots)	(88 plots)	(52 plots)	(44 plots)	(30 plots)	(53 plots)	(15 plots)	(346 plots)
		(2,895 ha)	(29,798 ha)	(156,310 ha)	(165,817 ha)	(92,054 ha)	(308,920 ha)	(10,778 ha)	(308 ha)	(766,881 ha)
Astrocaryum sciophilum	L oil yr^{-1}	0 ± 0	0 ± 0	2,723 ± 14,275	16,458 ± 66,481	30,171 ± 72,588	121,925 ± 188,476	0 ± 0	0 ± 0	171,277 ± 213,110
Attalea maripa	L oil yr^{-1}	0 ± 0	36,637 ± 187,782	3,770,087 ± 5,222,169	4,639,686 ± 8,488,861	31,382 ± 208,165	308,921 ± 647,743	15,252 ± 91,149	62 ± 163	8,802,026 ± 9,991,910
C. guianensis + *C. surinamensis*	L oil yr^{-1}	0 ± 0	90,676 ± 228,750	2,036,913 ± 3,189,102	473,535 ± 1,145,652	52,643 ± 131,595	832,541 ± 1,110,772	0 ± 0	102 ± 360	3,486,410 ± 3,575,800
Copaifera guyanensis	L oleoresin yr^{-1}	0 ± 0	,513 ± 1,833	29,748 ± 73,622	15,067 ± 24,032	732 ± 3,394	1,261 ± 4,418	36 ± 259	0 ± 0	47,357 ± 77,668
Oenocarpus bacaba	kg Fruit yr^{-1}	0 ± 0	0 ± 0	10,589,282 ± 32,078,955	31,683,792 ± 65,621,608	11,394,636 ± 23,854,445	104,967,084 ± 196,421,275	149,676 ± 1,089,655	21,778 ± 24,414	158,806,249 ±210,918,929
Dipteryx odorata	kg Seed yr^{-1}	0 ± 0	0 ± 0	0 ± 0	0 ± 0	58,580 ± 305,045	288,326 ± 747,656	0 ± 0	1,438 ± 2,104	348,343 ± 807,494
Parkia pendula	m^2 bark yr^{-1}	0 ± 0	0 ± 0	31,607 ± 296,496	30,054 ± 216,720	25,338 ± 135,166	263,297 ± 736,110	621 ± 3,270	335 ± 619	351,251 ± 833,676
C. guianensis + *C. surinamensis*	m^2 bark yr^{-1}	0 ± 0	764,250 ± 2,051,040	21,069,965 ± 34,126,285	4,598,203 ± 11,300,883	518,661 ± 1,377,304	8,057,364 ± 9,757,137	0 ± 0	1,186 ± 4,292	35,009,630 ± 37,331,203
Copaifera guyanensis	m^2 bark yr^{-1}	0 ± 0	128,910 ± 526,835	9,718,640 ± 24,842,698	3,937,023 ± 7,391,867	78,872 ± 365,615	355,633 ± 1,136,632	19,167 ± 139,535	0 ± 0	14,238,244 ± 25,952,302
Dipteryx odorata	m^2 bark yr^{-1}	0 ± 0	0 ± 0	0 ± 0	0 ± 0	33,797 ± 214,411	119,005 ± 340,573	0 ± 0	528 ± 716	153,329 ± 402,445
Pseudopiptadenia suaveolens	m^2 bark yr^{-1}	0 ± 0	0 ± 0	3,800 ± 35,649	0 ± 0	51,405 ± 186,800	1,225,056 ± 2,988,967	0 ± 0	597 ± 856	1,280,858 ± 2,995,011
Spondias mombin	m^2 bark yr^{-1}	0 ± 0	24,554 ± 150,851	468,741 ± 1,629,364	40,071 ± 288,960	0 ± 0	167,962 ± 726,645	0 ± 0	0 ± 0	701,328 ± 1,813,586
Hymenaea courbaril	m^2 bark yr^{-1}	0 ± 0	0 ± 0	234,370 ± 1,474,083	0 ± 0	0 ± 0	30,280 ± 115,288	0 ± 0	434 ± 1,125	265,084 ± 1,478,585

Figure S5.1.3.4. Left: two standard market units of 'krapa oli', oil made from the seeds of *Carapa guianensis* and/or *C. surinamensis*, as sold at the Vreedzaam market in July 2018. Note the slight difference in oil density: the oil of the right bottle contains less water. Photo by Gijs Steur. Right: a basket and a 0.5 L tin can of 'kumbu siri', the fruit of *Oenocarpus bacaba*, as observed to be sold at the Vreedzaam market between 2017-2018. The tin can is used as standard market unit. Photo taken from https://www.stopandstare.nl/ultieme-reistips-om-suriname-te-ervaren/ in July 2021.

Table S5.1.3.7. Estimated harvestable NTFP supply vs. the sales volumes on the Vreedzaam market.

NTFP type	**NTFP species**	**Harvestable NTFP supply**		**Sales volumes Vreedzaam market**		**Percentage sales volume to harvestable NTFP supply (%)**
Oil	*Astrocaryum sciophilum*	171,277	L yr^{-1}	112	L yr^{-1}	0.06539115
Oil	*Attalea maripa*	8,802,026	L yr^{-1}	600	L yr^{-1}	0.00681661
Oil	*Carapa guianensis + C. surinamensis*	3,486,410	L yr^{-1}	1,600	L yr^{-1}	0.04589248
Oleoresin	*Copaifera guyanensis*	47,357	L yr^{-1}	800	L yr^{-1}	1.68929620
Fruit	*Oenocarpus bacaba*	158,806,249	kg yr^{-1}	1,509	kg yr^{-1}	0.00095021
Seed	*Dipteryx odorata*	348,343	kg yr^{-1}	28	kg yr^{-1}	0.00803805
Bark	*Parkia pendula*	351,251	m^{2} yr^{-1}	726	m^{2} yr^{-1}	0.20668980
Bark	*Carapa guianensis + C. surinamensis*	35,009,630	m^{2} yr^{-1}	221	m^{2} yr^{-1}	0.00063125
Bark	*Copaifera guyanensis*	14,238,244	m^{2} yr^{-1}	379	m^{2} yr^{-1}	0.00266184
Bark	*Dipteryx odorata*	153,329	m^{2} yr^{-1}	17	m^{2} yr^{-1}	0.01108727
Bark	*Pseudopiptadenia suaveolens*	1,280,858	m^{2} yr^{-1}	636	m^{2} yr^{-1}	0.04965421
Bark	*Spondias mombin*	701,328	m^{2} yr^{-1}	26	m^{2} yr^{-1}	0.00370725
Bark	*Hymenaea courbaril*	265,084	m^{2} yr^{-1}	606	m^{2} yr^{-1}	0.22860678
					average	0.17841716

Figure S5.1.3.5. UPPER: six standard market units of 'tonka siri', the seed of *Dipteryx odorata*, as sold at the Vreedzaam market in in February 2017. Photo by Jeffrey Brand. LOWER: five standard market units of 'kwatakama buba', the bark of *Parkia pendula*, as sold at the Vreedzaam market in March 2018. A ruler of 30 cm is shown on next to most left bark. Photo by Gijs Steur.

Table S5.1.3.8. PEstimated potential economic value of harvestable NTFP supply per NTFP, showing the value for each and across all old-growth forest types in the harvest area.

NTFP type	**NTFP species**	**Mangrove forests**	**Swamp forests**	**Marsh forests**	**Terra firme forests of the Coastal plains**	**Terra firme forests of the Savanna belt**	**Terra firme forests of the Interior**	**White sand forests of the Savanna belt**	**Mountain forests of the Interior**	**Across the harvest area (sum)**	
Oil	*Astrocaryum sciophilum*	0	0	145,913	881,808	1,616,532	6,532,656	0	0	917,6909	USD/yr
Oil	*Attalea maripa*	0	990,870	101,964,860	125,483,811	848,753	8,354,990	412,509	1,666	23,805,7459	USD/yr
Oil	*Carapa guianensis + C. surinamensis*	0	2,479,633	55,701,559	12,949,319	1,439,593	22,766,721	0	2,780	9,533,9605	USD/yr
Oleoresin	*Copaifera guyanensis*	0	21,298	1,235,243	625,642	30,406	52,379	1,478	0	196,6446	USD/yr
Fruit	*Oenocarpus bacaba*	0	0	117,944,380	352,896,932	126,914,487	1,169,132,837	1,667,100	242,569	176,879,8305	USD/yr
Seed	*Dipteryx odorata*	0	0	0	0	4,181,606	20,581,531	0	102,613	2486,5750	USD/yr
Bark	*Parkia pendula*	0	0	108,999	103,643	87,380	908,010	2,142	1,155	121,1329	USD/yr
Bark	*Carapa guianensis + C. surinamensis*	0	2,810,426	77,481,958	16,909,272	1,907,307	29,629,872	0	4,363	12,874,3198	USD/yr
Bark	*Copaifera guyanensis*	0	565,557	42,638,012	17,272,670	346,030	1,560,249	84,088	0	6,246,6606	USD/yr
Bark	*Dipteryx odorata*	0	0	0	0	482,601	1,699,343	0	7,536	218,9480	USD/yr
Bark	*Pseudopiptadenia suaveolens*	0	0	16,321	0	220,769	5,261,283	0	2,562	550,0935	USD/yr
Bark	*Spondias mombin*	0	153,909	2,938,128	251,173	0	1,052,805	0	0	439,6015	USD/yr
Bark	*Hymenaea courbaril*	0	0	957,117	0	0	123,655	0	1,772	108,2544	USD/yr
SUM		0	7,021,693	401,132,490	527,374,272	138,075,463	1,267,656,333	2,167,317	367,016	2,343,794,584	USD/yr
Surface area per forest type (ha)		2,896	29,798	156,310	165,817	92,054	308,921	10,778	308	766,882	ha
USD/ha/yr		0	236	2,566	3,180	1,500	4,103	201	1,191	3,056	USD/ha/yr

Table S5.1.3.9. REstimated realizedeconomic value of harvestable NTFP supply per NTFP, showing the value for each and across all old-growth forest type in the harvest area.

NTFP type	NTFP species	Mangrove forests	Swamp forests	Marsh forests	Terra firme forests of the Coastal plains	Terra firme forests of the Savanna belt	Terra firme forests of the Interior	White sand forests of the Savanna belt	Mountain forests of the Interior	Across the harvest area (sum)	
Oil	*Astrocaryum sciophilum*	0	0	96	579	1,062	4,291	0	0	6,028	USD/yr
Oil	*Attalea maripa*	0	68	6,951	8,554	58	570	28	0	16,229	USD/yr
Oil	*Carapa guianensis* *+ C. surinamensis*	0	1,138	25,563	5,943	661	10,448	0	1	43,754	USD/yr
Oleoresin	*Copaifera guyanensis*	0	360	20,867	10,569	514	885	25	0	33,220	USD/yr
Fruit	*Oenocarpus bacaba*	0	0	1,121	3,353	1,206	11,109	16	2	16,807	USD/yr
Seed	*Dipteryx odorata*	0	0	0	0	336	1,654	0	8	1,998	USD/yr
Bark	*Parkia pendula*	0	0	225	214	181	1,876	4	2	2,502	USD/yr
Bark	*Carapa guianensis* *+ C. surinamensis*	0	18	490	107	12	187	0	0	814	USD/yr
Bark	*Copaifera guyanensis*	0	15	1,136	460	9	42	2	0	1,664	USD/yr
Bark	*Dipteryx odorata*	0	0	0	0	53	188	0	1	242	USD/yr
Bark	*Pseudopiptadenia suaveolens*	0	0	8	0	110	2,611	0	1	2,730	USD/yr
Bark	*Spondias mombin*	0	6	108	9	0	39	0	0	162	USD/yr
Bark	*Hymenaea courbaril*	0	0	2,190	0	0	283	0	4	2,477	USD/yr
SUM		0	1,604	58,754	29,788	4,201	34,183	76	21	128,627	USD/yr
Surface area per forest type (ha)		2,896	29,798	156,310	165,817	92,054	308,921	10,778	308	766,882	ha
USD/ha/yr		0	0.05	0.38	0.18	0.05	0.11	0.01	0.07	0.17	USD/ha/yr

Table S5.1.3.10. Kendall's tau correlations between the percentage of harvestable NTFP supply sold at the Vreedzaam market ('percentage supply sold'), NTFP abundance in the harvest area, harvestable NTFP supply, the sales volume on the Vreedzaam market, the NTFP forest exit price and market price on the Vreedzaam market. First number is Kendall's tau, second is its p-value. Significant p-values, i.e. $p < 0.05$, are highlighted in bold. Number of samples: n = 10 for NTFP forest exit price, n = 13 for all other variables.

	Percentage supply sold		NTFP abundance in harvest area		Harvestable NTFP supply		Sales volumes		NTFP Forest Exit price	
Percentage supply sold										
NTFP abundance in harvest area	-0.1961	0.3574								
Harvestable NTFP supply	**-0.6410**	**0.0023**	0.3530	0.0976						
Sales volumes	0.2051	0.3290	0.2223	0.2970	0.1538	0.4641				
NTFP Forest Exit price	0.1798	0.4725	0.3219	0.2051	-0.2697	0.2812	0.2247	0.3692		
NTFP Market price	0.1282	0.5418	0.1961	0.3574	-0.2308	0.2721	-0.1026	0.6255	**0.5843**	**0.0196**

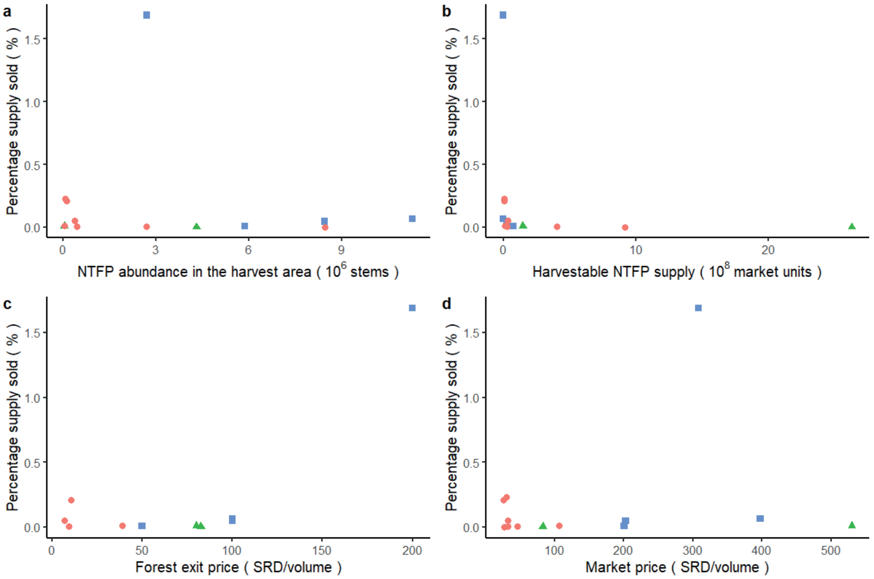

Figure S5.1.3.6. Scatter plots of the percentage of harvestable NTFP supply sold at the Vreedzaam market ('percentage supply sold'; y-axis) against NTFP abundance in the harvest area (panel a), harvestable NTFP supply (panel b), forest exit price (panel c) and market price at the Vreedzaam market (panel d). Red circles are bark-based NTFPs, green triangles are fruit-based NTFPs, and blue squares are oil-based NTFPs.

Table S5.1.3.11. Mean forest exit price, mean market price and percentage forest exit price of the market price, per NTFP unit in USD. Mean shown with standard deviation (SD) where available.

NTFP type	**NTFP species**	**Forest exit price (mean ± SD)**		**n**	**Market price (mean ± SD)**		**n**	**% Forest exit price of market price**
Oil	*Astrocaryum sciophilum*	13.5	USD L^{-1}	1	53.6 ± 2.1	USD L^{-1}	21	25.2%
Oil	*Attalea maripa*	6.7	USD L^{-1}	1	27.0 ± 4.2	USD L^{-1}	20	24.8%
Oil	*Carapa guianensis + C. surinamensis*	13.5 ± 0	USD L^{-1}	2	16.6 ± 0.9	USD L^{-1}	83	81.4%
Oleoresin	*Copaifera guyanensis*	26.9	USD L^{-1}	1	41.5 ± 20.8	USD L^{-1}	13	64.8%
Fruit	*Oenocarpus bacaba*	NA[a]	USD kg^{-1}	-	11.1	USD kg^{-1}	1	NA
Seed	*Dipteryx odorata*	10.8	USD kg^{-1}	1	71.3	USD kg^{-1}	1	15.1%
Bark	*Parkia pendula*	1.4 ± 0.7	USD m^{-2}	7	3.4 ± 1.1	USD m^{-2}	51	40.6%
Bark	*Carapa guianensis + C. surinamensis*	NA[b]	USD m^{-2}	-	3.7 ± 0.8	USD m^{-2}	5	NA
Bark	*Copaifera guyanensis*	1.3	USD m^{-2}	1	4.4 ± 0.8	USD m^{-2}	4	29.7%
Bark	*Dipteryx odorata*	5.2	USD m^{-2}	1	14.3	USD m^{-2}	1	36.4%
Bark	*Pseudopiptadenia suaveolens*	0.9 ± 0.8	USD m^{-2}	2	4.3 ± 2.8	USD m^{-2}	51	20.9%
Bark	*Spondias mombin*	NA[b]	USD m^{-2}	-	6.3	USD m^{-2}	1	NA
Bark	*Hymenaea courbaril*	NA[b]	USD m^{-2}	-	4.1 ± 0.9	USD m^{-2}	26	NA
						average		37.7%

[a] Fruit of *Oenocarpus bacaba* was sold by the harvesters themselves, i.e. without intermediaries.

[b] The forest exit price of *Carapa spp.*, *Spondias mombin*, and *Hymenaea courbaril* bark were not recorded as these were not encountered in wholesale during the field work.

S5.1.4 Analysis of annual gross revenue and monetary costs of value chain actors

Although we recorded costs of harvest, processing, transport and marketing, it was not possible to attribute costs to specific NTFPs. For example, harvesters seldomly harvested or transported only one NTFP, market vendors never sold only one NTFP, and both harvesters and market vendors varied in the NTFPs they harvested or sold at the Vreedzaam market. To gauge the relative importance of costs, we quantified the revenues and costs per actor and relating these two. For this comparison, we assumed that all sold NTFPs on the market were harvested by harvesters and not by market vendors. This approach yields the maximum costs.

S5.1.4.1 Harvesters

We carried out interviews with 20 harvesters of plant-based NTFPs, including 6 walks-in-the-woods. On the basis of this, we concluded that most harvesters of plant-based NTFPs focused on gathering plant-based NTFPs only, as opposed to also gathering animal-based NTFPs. To our knowledge, maroon harvesters do not collect mushroom-based NTFPs. On the basis of the mode of operation, we classified harvesters of plant-based NTFPs as being either a 'generalist' or a 'specialist'. Here, generalists typically gathered a large range of plant species, collecting plant species in an opportunistic manner, i.e. without a detailed search or collect strategy. By contrast, specialists gathered a smaller range of plant species, collecting plant species with a detailed search and collect strategy, for example collecting specific plant species at specific quantities on the basis of a set order by a market vendor. The selected 13 NTFPs in this study were typically collected by specialists, who only went to the market when they had collected a volume of NTFPs with an estimated gross revenue value of at least 65 USD (500 SRD). According to the harvest frequency, some harvesters went to the Vreedzaam market only once per month, while other went each weekend. This range of activities amounted to a maximum annual gross revenue of between 780 – 3,120 USD (6,000 – 24,000 SRD per year; 50 active weeks). This range in gross revenue reached beyond the gross revenue based on the minimum wage in Suriname from 2017 up to July 2018. The minimum wage up to July 2018 was 0.7982 USD per hour (6.14 SRD per hour). Assuming 8 working hours a day, 5 days a week, and working 50 weeks in the year, this amounts an annual minimum wage gross revenue of 1596.4 USD per year.

Harvesting costs

All harvesters used a machete to harvest plant-based NTFPs. In 2018 a machete costed around 8.45 – 9.1 USD (65 – 70 SRD) and lasted 1 to 3 years under general use (including both harvest and other use). This amounted to a maximum annual cost of between 8.45 – 9.1 USD. During harvest NTFPs were commonly transported using large white rice bags, where harvesters could carry up to two full rice bags. Such large white rice bags costed around 0.65 USD (5 SRD) and these bags lasted 1 to 4 years. This amounted to a maximum annual cost of 1.3 USD. Based on the previous costs, a harvesters endured a maximum annual harvest cost of between 9.75 – 10.4 USD, between 0.31 – 1.33% of the annual gross revenue values (9.75 – 10.4 vs 780 – 3,120 USD).

Processing costs

Harvesters stated that the oils made of the fruit of *Astrocaryum sciophilium* ('tjo tjo oli'), *Attalea maripa* ('maripa oli') and *Carapa* spp. ('krapa oli') required considerable processing after harvest, costing mainly time and attention (See also van Andel & Ruysschaert, 2011, and van den Boog et al., 2018, for descriptions of NTFP processing). For oil made from the fruit of *A. sciophilum*, the hard fruit was first broken using a mortar and pestle and then boiled to let the seeds exude its oil. The thin layer of oil that develops on top of the boiling water was then removed from the water, and baked until it got a characteristic black colour. The process from fruit to blackish oil took about a day, during which the processer needed to regularly check the progress. For oil made from the fruit of *A. maripa*, first the fleshy mesocarp was removed, after which the exposed seed was dried in the sun for a period of one to two months. During this drying a constant vigilance is required to prevent the seed becoming wet during rain spells. After drying, the seeds were broken using a hammer, exposing the white kernel, which was then boiled for several hours. The thin layer of whitish oil that developed on top of the boiling water was then removed and baked until it got a yellow to brownish colour. Social rules dictated that oil from *A. sciophilum* and *A. maripa* could only be made in a traditional wooden hut, in which the seeds were boiled and the oil was baked by a woman in menopause. We only observed these huts in the harvest area around the Upper Suriname river and Upper Saramacca river. Interviewees indicated that such traditional huts could no longer be found in use in area near the capitol. This was in line with our observation that all *tjo tjo oli* that was offered for wholesale at the Vreedzaam market appeared to be sourced from the interior of Suriname, not from the area near to the capital. Last, for oil made from the fruit of *Carapa spp.*, the capsule seeds were first boiled for several hours and then left to rot for two to three weeks. When red mould would form on the seeds, the seeds were broken using a mortar and pestle, and pried open using a knife. The inner seed paste was then removed and frequently kneaded by hand to force out most of the oil. This kneading could take up to 3 weeks. The boiling and baking involved for the oils made from *A. sciophilium*, *A. maripa* and *Carapa* spp. was carried out using ordinary cooking equipment, using fuel wood.

All of the other selected NTFPs required negligible amounts of processing: the seeds of *Dipteryx odorata* needed to be removed from the fruit and set to soak in an alcohol-rich fluid for 24 hours, the tapped olreoresin of *Copaifera guyanensis* sometimes required some filtering to remove unwanted material; the fruit of *Oenocarpus bacaba* often needed to be manually plucked from its infructescence. Harvested bark required no further processing after harvest. In sum, we concluded that further processing of harvested NTFPs indebted no considerable monetary costs, only for some NTFPs indebting a considerable time-investment.

Processing of oils generally required two big pots, which costed around 26 USD each (200 SRD), and lasted approximately four years. This amounted to a maximum annual cost of 0.08 USD. We excluded the monetary costs of firewood as our interviews and observations suggested that fire wood which was freely and relatively easily accessible around the villages. Based on this cost, harvesters endured a maximum annual processing cost of 0.08 USD, between 0.002 – 0.01% of the annual gross revenue values (0.08 USD vs 780 – 3,120 USD).

Market transport costs

Transport costs to the market were dependent on the distance to the market and the number of items transported. Plant-based NTFPs were commonly transported in large white rice bags, but the costs of these have been included in the harvest costs, see under S1.4.1.1. Across all recorded source areas, costs of a return trip with 1 to 10 large white rice bags cost between 0.585 – 58.5 USD (4.5 – 450 SRD). However, most interviewed harvesters and middle-men came from source areas that were within 4 traveling hours and usually took 2 large white rice bags of harvested NTFPs with them. As most harvesters and middle-men visited the market either once per week or once per month, this amounted to costs of between 159.25 – 559 USD per year for most of the harvesters. This represented between 5.1 – 71.7% of the annual gross revenue values (159.25 – 559 USD annual transport costs vs 780 – 3,120 USD annual gross revenues). Note that potential private transport costs, such as the use of private boats or cars, have been excluded, as data on this subject was not recorded.

S5.1.4.2 Market vendors

Interviews with our main informants at the market vendors indicated that the average weekly gross revenues of market vendors varied between 54.6 – 78 USD in 2018 (420 - 600 SRD), depending on the size of the stand and relative success of the business. The relative success of the business seemed to vary according to the quality of the goods and the knowledge of the vendor, for example the freshness of herbal NTFPs and the knowledge about potential applications of NTFPs. The estimated weekly gross revenues amounted to an annual gross revenue of between 2,730 – 3,900 USD. This range was entirely reached beyond the annual minimum wage gross revenue of 1596.4 USD per year.

Market stand costs

Operating one meter of market stall costed 0.26 USD per month in 2018 (2 SRD). All market vendors operated between 1 to 3 meters of market stall. This amounted to potential costs of market stalls of between 3.12 – 9.36 USD per year, representing 0.0008 – 0.0034% of the annual gross revenues.

All of our included NTFPs had relatively long shelf-lives of up multiple years, except for the fruit of *Oenocarpus bacaba*, which perished within three days after harvest. On the basis of observations, we estimated that about 1/3 of the volume *Oenocarpus bacaba* fruit that was marketed each week was not sold because it perished. The value of the perished fruit of *Oenocarpus bacaba* represented between 0.08 – 0.34% of the annual gross revenue values (3.12 – 9.36 USD annual marketing costs vs 2,730 – 3,900 USD annual gross revenues).

Inside a tropical forest, Suriname, gazing upwards. Photo by Gijs Steur.

6

Synthesis

6.1 Recapitulating the focus and approach of this thesis

Natural ecosystems are being degraded and lost at an alarming rate, and this is threatening the world's biodiversity and the ecosystem services that are essential to our quality of life. In response, there has been an increasing momentum to focus conservation efforts on protecting ecosystem services. Central to this movement are the assumed positive relationships between biodiversity and ecosystem services: if ecosystem services are protected, biodiversity will be preserved as well. However, despite evidence of positive relationships in general biodiversity-ecosystem service assessments, it remains unclear how plant diversity is related to ecosystem services in tropical forests. This thesis focuses on the relationships between plant diversity and three ecosystem services (carbon storage, timber provisioning and non-timber forest product (NTFP) provisioning) in old-growth tropical forests.

In the General Introduction (**Chapter 1**), a preliminary assessment was made of the current state of knowledge of these relationships, identifying three major knowledge gaps: 1) incomplete and fragmented evidence of the alleged relationships, 2) lack of knowledge of how spatial scale aspects of plot size and geographical extent influence these relationships, and 3) lack of knowledge of the linkages between the stock, potential supply and flow of these three ecosystem services. Therefore, in **Chapter 2**, the empirical evidence from across the tropics was assessed in a systematic review of the literature. On the basis of the evidence found, a meta-analysis was carried out to shed light on how plant diversity is related to these three ecosystem services, and to assess the potential influence of plot size and geographical extent on these relationships. From the systematic review and meta-analysis, it became clear that not all aspects had been adequately studied in the literature and that further analyses were needed to arrive at general conclusions on particular relationships. In **Chapter 3**, the effect of geographical extent in the form of environmental heterogeneity was further analysed for the relationship between woody species richness (i.e. the richness of tree and arborescent palms) and the stock component of the three ecosystem services. Using a large dataset of previously published tropical forest plots, relationships were analysed across and within multiple forest types and biogeographical strata of the Guiana Shield region and entire Amazonia. In **Chapters 4 and 5**, the relationships between plant diversity and NTFP provisioning were further analysed for tropical forests in Suriname, focusing on the linkages between NTFP stock, potential supply and flow. First, in **Chapter 4**, the relationships between woody plant diversity and NTFP abundance (i.e. the abundance of NTFP producing species) were analysed, using newly digitised tropical forest plots. Second, in **Chapter 5**, the linkages between NTFP abundance, potential supply and flow were studied using a newly developed conceptual framework. This framework was operationalised with the case of commercial trade of plant-based NTFPs in Suriname, using both newly and previously censused tropical forest plots as well as data collected during interviews and walks-in-the-woods with harvesters.

In this thesis chapter, the results of these research chapters (2 to 5) are synthesised in order to answer the following four research questions:

RQ 1: *How are taxonomic, structural and functional plant diversity related to the stock and flow components of carbon storage, timber provisioning and NTFP provisioning in tropical forests?*
RQ 2: *How is plant diversity related to multiple ecosystem services in tropical forests, such as carbon storage, timber provisioning and NTFP provisioning?*
RQ 3: *What are the effects of the spatial scale aspects of plot size and geographical extent on the observed relationships between plant diversity and carbon storage, timber provisioning and NTFP provisioning in tropical forests?*
RQ 4: *What are the relationships between plant diversity and the stock, potential supply and use of tropical forest NTFPs?*

These four research questions are addressed in succession in the following four sections (sections 6.2 to 6.5). This is followed by a discussion of the implications for tropical forest conservation (section 6.6), a reflection on the main aim of this thesis (6.7) and recommendations for future research (6.8).

6.2 How are taxonomic, structural and functional plant diversity related to the stock and flow components of carbon storage, timber provisioning and NTFP provisioning in tropical forests? (RQ1)

Plants are the primary producers and the habitat engineers of tropical forests, exhibiting variation in taxonomic, functional and structural dimensions and forming the main component of the aboveground biomass. It may be expected that taxonomic, functional and structural plant diversity show relationships to the three biomass-based ecosystem services of carbon storage, timber provisioning and NTFP provisioning in old-growth tropical forests (Chapter 1, section 1.1). In particular, hypotheses such as the 'niche complementarity' (Tilman et al., 1997), 'insurance' (Yachi & Loreau, 1999) and 'selection effect' hypotheses (Tilman et al., 1997) suggested positive relationships (See Table 6-1,). The systematic review of Chapter 2 assessed the empirical evidence in the literature for such relationships. As it was expected that relationships between plant diversity and ecosystem services could differ between the stock and flow components of the service, the evidence was also assessed per stock and flow component.

Table 6-1. Three popular hypotheses in the literature on biodiversity-ecosystem service relationships that predict positive relationships between plant diversity and biomass-based ecosystem services.

Niche complementarity hypothesis	Plant communities with a higher biodiversity will have a higher variation in species traits, and will thus be able to better utilise limited available resources. This would result in increased productivity, which can in turn result in higher aboveground biomass. After Tilman et al. (1997).
Insurance hypothesis	Biodiverse communities contain species that can complement each other in productivity, providing higher resilience against environmental fluctuations. This enables biodiverse communities to maintain a high rate of productivity across time, and ultimately, a higher aboveground biomass. After Yachi & Loreau (1999).
Selection effect hypothesis	Biodiverse communities have a higher chance of including specific species or traits from the larger species pool that are highly productive, which can result in a higher aboveground biomass. After Tilman et al. (1997).

Although various methods had been used to assess the relationships found in the systematic review, including different plant diversity indicators, plot sizes and geographical extents, clear patterns could still be observed for relationships between plant diversity and carbon storage (Chapter 2, Table 2-1). These relationships are summarised in Figure 6-1. The empirical evidence illustrated that taxonomic and structural plant diversity indicators show mainly positive relationships to carbon storage, whereas functional plant diversity indicators show a mixture of both positive and negative relationships. These findings are in line with the assessment of the relationships between plant diversity and carbon storage across multiple tropical vegetation types by van der Sande et al. (2017), who pooled findings for old-growth forests, secondary forests and plantations. The positive relationships concerning taxonomic and functional plant diversity that were found are in line with hypotheses such as the 'niche complementarity', 'insurance' and 'selection effect' hypotheses. It is likely that the positive relationship between structural plant diversity and carbon storage are mainly caused by structural collinearity, as most structural plant diversity indicators included structural aspects that were also used to calculate the amount of carbon storage, for example mean stand density (# stems ha^{-1}) and mean basal area (m^2 ha^{-1}). In the empirical evidence of relationships between plant diversity and carbon storage also negative relationships were observed. This prompted me to take a closer look at how plot size and geographical extent may affect the observed plant diversity-ecosystem service relationships; this is discussed in section 6.4.

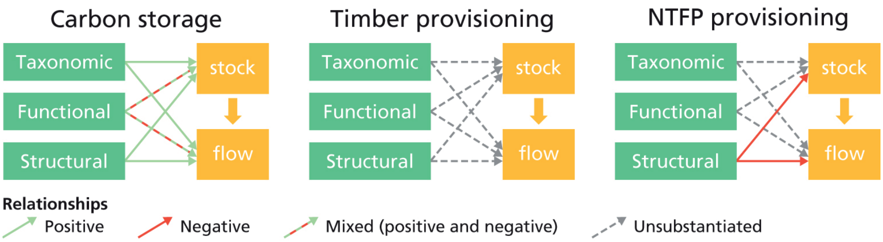

Figure 6-1. Summary of the observed general relationships of taxonomic, functional and structural plant diversity (green boxes) with the stock and flow components (yellow boxes) of the ecosystem services of carbon storage, timber provisioning and non-timber forest product (NTFP) provisioning in old-growth tropical forests. Based on reported empirical findings in the literature (review of 1,082 papers, see Chapter 2). A solid green arrow indicates that generally positive relationships were observed, a solid green-red arrow indicates generally mixed relationships (including both positive and negative), and a solid red arrow indicates generally negative relationships. Dashed grey arrows indicate that there was insufficient evidence to substantiate patterns.

Unfortunately, for the ecosystem services of timber provisioning and NTFP provisioning, too few relationships were reported to substantiate generic patterns (Figure 6-1). The tentative evidence showed mainly non-significant relationships, whereas only for NTFP provisioning, several negative relationships were found with structural plant diversity indicators. These are in line with the negative relationship I found between structural plant diversity and NTFP abundance (a proxy for NTFP stock) in Suriname in Chapter 4, and this suggests competition effects such as for light, space and/or water between NTFP- and non-NTFP-producing species. In addition, in Chapter 4, evidence was found of negative relationships between taxonomic plant diversity and NTFP abundance, which seem to contrast with hypotheses such as the 'niche complementarity' and 'insurance' hypotheses. Although on the basis of the findings of Chapter 4 it is not possible to substantiate general patterns for the relationships of taxonomic and structural plant diversity with NTFP stock, the findings illustrate that taxonomic and structural plant diversity may show different relationships to NTFP provisioning than to carbon storage.

Interestingly, the empirical evidence from the literature also suggested that relationships between plant diversity and carbon storage, timber provisioning and NTFP provisioning in general did not differ considerably between the stock and flow components (Figure 6-1). For carbon storage, there is sufficient evidence to conclude that relationships with stock and flow are similar in direction and frequency of significance. These findings are mostly in line with the review by van der Sande et al. (2017), with the exception of how structural plant diversity is related to carbon flow. Our review showed mainly positive relationships to carbon flow, whereas the review by van der Sande et al. (2017) found a mixture of both negative and positive relationships. This discrepancy may be caused by the fact that van der Sande et al. (2017) also included relationships from secondary tropical forests and tropical plantations, which are expected to differ in their vegetation structure when compared to old-growth tropical forests. The similarity between the relationships observed in Chapter 2 between plant diversity and carbon stock on the one hand and between plant diversity and carbon flow on the other suggest that the same dimensions of plant diversity are relevant for high carbon stocks and carbon flows; high taxonomic and structural diversity are associated to high carbon stocks and flows. For timber and NTFP provisioning, there was unfortunately too little evidence to assess and generalise any differences between stock and flow components. To my knowledge, such differences have not been assessed before. For NTFP provisioning, I investigated the relationships between plant diversity and both stock and flow components in Suriname in Chapters 4 and 5, which are discussed in section 6.5.

In conclusion, the empirical evidence from the literature includes support for both positive and negative relationships between plant diversity and carbon storage, timber provisioning and NTFP provisioning in old-growth tropical forests. For carbon storage, there is ample support that taxonomic, functional and structural plant diversity show mainly positive relationships to both carbon stock and carbon flow, in line with the 'niche complementarity', 'insurance' and 'selection effect' hypotheses. Nevertheless, several contradicting negative relationships were identified that deserve further attention in research. For timber and NTFP provisioning, additional analyses are needed to draw up general patterns. The findings in Chapter 4 suggest that relationships of structural and taxonomic plant diversity with NTFP abundance can show a direction that is different from that of the relationships of structural and taxonomic plant diversity with carbon stock.

6.3 How is plant diversity related to multiple ecosystem services in tropical forests, such as carbon storage, timber provisioning and NTFP provisioning? (RQ 2)

Conceptually, biodiversity could underpin multiple ecosystem services simultaneously, potentially supporting bundles of ecosystem services (Bennett et al., 2015; Duncan et al., 2015; C. Raudsepp-Hearne et al., 2010). Previously, this had not been adequately assessed for plant diversity-ecosystem service relationships in old-growth tropical forests (Chapter 1, section 1.4). In Chapter 2, it became clear that plant diversity-ecosystem service relationships in old-growth tropical forests can differ across plot sizes and geographical extents, but that the effect of geographical extent had not been systematically analysed (see also section 6.4). This means that previous findings on how plant diversity is related to specific ecosystem services in old-growth tropical forests are not necessarily comparable. Therefore, in Chapter 3, I systematically related plant diversity to multiple ecosystem services in old-growth tropical forests, using a set plot size (i.e. 1 ha) and a set geographical extent (i.e. a regional extent). Specifically, I related woody species richness to carbon stock, timber stock and NTFP abundance in terra firme forests and white sand forests across the Guiana Shield biogeographical region.

The analyses in Chapter 3 showed that woody species richness was consistently positively related to carbon stock, showing a positive relationship in terra firme forests, the dominant forest type, and for most of the biogeographical subregions of the Guiana Shield. By contrast, woody species richness was not frequently related to timber stock and NTFP abundance, showing only one or no significant relationship in the four subregions of the Guiana Shield. Although woody species richness was positively related to timber stock in terra firme forests, it only showed significant relationships in one of the four subregions. Woody species richness only showed a significant, but negative, relationship to NTFP abundance in white sand forests. A positive relationship between woody species richness and carbon stock across the Guiana Shield region confirms previous findings at regional spatial scales (Aldana et al., 2017; Chapter 2) and is in line with hypotheses such as the 'niche complementarity', 'selection effect' and 'insurance' hypotheses (Tilman et al., 1997; Yachi & Loreau, 1999). The non-significant relationships between woody species richness and NTFP abundance across all forest types contradict the finding of a significant negative relationship across all forest types in Northern Suriname in Chapter 4, but it is likely that the latter negative relationship was biased by the inclusion of flooded forests. In Chapter 4, a large sample of flooded forests was included and flooded forests have generally low woody species richness and high NTFP abundance (Johnston, 1998; Peters, Balick, et al., 1989; van Andel, 2000).

In contrast to the relationship between species richness and carbon stock, no mechanism had been proposed in the literature on how species richness would influence commercial timber stock and NTFP abundance, and these relationships had not been tested before. On the basis of the findings in this thesis, it was postulated in Chapter 3 that timber stock and NTFP abundance are driven by variation in species floristic composition, rather than by species richness. For services such as timber and NTFP provisioning, the presence of specific subsets of species is relevant; in other words, not all species provide perceived valuable timber or NTFPs. For example, in Chapter 4, it was found that variation in commercially relevant NTFP abundance in Suriname tropical forests was driven by what I named 'NTFP oligarchs', a particularly small selection of NTFP producing species (NTFP species) with high abundances. For commercially relevant timber stock, it is commonly known that timber species that are highly marketed tend to include more abundant than rare species. As the presence and relative abundance of species tends to vary across floristic regions in Amazonia, where, for example, certain species are dominant in particular forest types and biogeographical regions (ter Steege et al., 2013; 2019a), it may be expected that timber stock and NTFP abundance are determined by floristic composition. In support of this, it was found in Chapter 4 that floristic composition was indeed a stronger predictor of NTFP abundance than species richness.

In conclusion, there is evidence that woody species richness can show both similar and dissimilar relationships to the three studied ecosystem services in old-growth tropical forests. For carbon stock and timber stock, positive relationships were found with woody species richness, suggesting the existence of ecosystem service bundles of both high carbon stocks and timber stocks in species-rich tropical forests. However, as only carbon stock was robustly positively related to species richness, the occurrence of a service bundle of both high carbon and timber stock remains questionable. Previous authors have suggested that multiple mechanisms, including those described under the 'niche complementarity', 'selection effect' and 'insurance' hypotheses, might act simultaneously in providing a positive effect of species richness on tropical forest carbon stock (e.g. Poorter et al., 2015). However, to my knowledge, this has not been systematically analysed. For timber stock and NTFP abundance, their relationships to species richness may be expected to differ according to tropical forest regions, varying across floristic compositions and socio-economic factors such as demand. Species richness can only be used as a rough surrogate for plant diversity in general, for example because it excludes measures of species abundances and is not systematically positively associated with structural diversity (Isbell et al., 2017; Pascual et al., 2021; Chapter 1, section 1.3); as a result, questions currently remain on how the full spectrum of plant diversity is related to carbon stock, timber stock and NTFP abundance in old-growth tropical forests.

6.4 What are the effects of the spatial scale aspects of plot size and geographical extent on the observed relationships between plant diversity and carbon storage, timber provisioning and NTFP provisioning in tropical forests? (RQ 3)

There has been increasing awareness that spatial scale and related aspects such as the plot size and geographical extent can influence biodiversity-ecosystem service relationships (Chisholm et al., 2013; Isbell et al., 2017; Scheiner et al., 2011). Here, the plot size is the unit of sampling, and the geographical extent is the study area or the geographical area over which samples are compared. Effects of plot size and geographical extent could explain why contradictory relationships have been found in different studies (Chisholm et al., 2013; Isbell et al., 2017; Scheiner et al., 2011; Chapter 1, section 1.5). In Chapter 2, I concluded that the effects of plot size could not explain all contradictory findings for plant diversity-carbon stock relationships that have been reported in the literature. Previous large-scale analyses suggested that plant diversity and carbon stocks were only positively associated when relatively small plot sizes of <1 ha were used, while mainly non-significant relationships were found when plots of 1 ha were used (Poorter et al., 2015; Sullivan et al., 2017). However, my systematic review in Chapter 2 identified several studies that found a relatively strong positive association between woody species richness and carbon stock while using a plot size of 1 ha (Aldana et al., 2017; Con et al., 2013; Gonzalez et al., 2014). Moreover, the meta-analysis of taxonomic richness-carbon relationships from across the tropics in Chapter 2 revealed a significant positive correlation, regardless of the large variation in plot size (varying between 0.04 to 1 ha; Chapter 2, Figure 2-1).

The meta-analysis of Chapter 2 also indicated that the geographical extent included in the comparison could moderate the association between woody species richness and carbon stock, independently of the plot size used. My analysis showed that the strength of the positive correlation between taxonomic richness and carbon stock was negatively related to the geographical extent included in the comparison, where the strength of the positive association was strongest between local and regional scales, but became almost zero at continental and intercontinental scales (Chapter 2, Figure 2-3). Although previous studies on the relationship between woody species richness and carbon stock in tropical forests have suggested that geographical extent could moderate relationships (e.g. Sullivan et al., 2017; van der Sande et al., 2017), such effects had not been quantified before. In the discussion of Chapter 2, it was postulated that the observed negative effect of geographical extent on the species-carbon relationship could be explained by the increasing amount of environmental heterogeneity that was included in the comparison. With increasing geographical extent there is a higher chance that an increasing amount of environmental heterogeneity is included, which can influence both plant diversity and ecosystem service values.

In support, my analyses of the species-carbon relationship across different forest types and biogeographical strata at a regional and a continental spatial scale in Chapter 3 illustrated that the influence of environmental heterogeneity on the species-carbon relationship increased with spatial scale and ultimately obscured the relationship. For instance, although the species-carbon relationship differed between the biogeographical subregions across the Guiana Shield, the relationship was only to a minor degree affected by the environmental heterogeneity represented by the subregions, remaining significantly positive across the regional spatial scale of the Guiana Shield. Yet, at the continental spatial scale of entire Amazonia, the relationship became non-significant and even weakly negative, while being either significantly positive or showing a non-significant positive trend in each of the biogeographical regions of Amazonia separately (Chapter 3, Figure 3-3). The pattern within and across Amazonian biogeographical regions resembled a 'Simpson's paradox': a statistical phenomenon where a relationship is found in subgroups but disappears or changes direction when the subgroups are aggregated

(Simpson, 1951). Only when the variation in carbon stock among the biogeographical regions was accounted for, did the relationship across Amazonia remain positive.

It remains currently unclear how the differences in carbon stock between the biogeographical strata can be explained. As the biogeographical regions used in the analyses of Chapter 3 were recognised according to differences in substrate history, geological age and floristic composition, it is likely that the observed differences in carbon stock are influenced by multiple factors. For example, the substrate history (the history of geomorphic processes such as weathering and flooding) and geological age of the biogeographical regions have been related to differences in soil fertility and tree stem mortality (Johnson et al., 2016; Quesada et al., 2011, 2012), while multiple spatial gradients in floristic composition identified across the Amazon biogeographical regions coincide with a spatial gradient in wood density (Chave et al., 2006; Phillips et al., 2019; ter Steege et al., 2006). A complex interplay of multiple historical and environmental factors could also explain why previous similar analyses of the species-carbon relationships at continental scales found contrasting results while accounting for different selections of specific environmental factors (Poorter et al., 2015; Sullivan et al., 2017).

In conclusion, evidence was found that both plot size and geographical extent can moderate the relationships between plant diversity and ecosystem services in old-growth tropical forests. This illustrates that both spatial scale aspects can be important in explaining contradictory findings between biodiversity and ecosystem services in general. The effects of plot size on plant diversity-ecosystem service relationships have previously been shown to be solely effects of sampling (e.g. Chisholm et al., 2013; Poorter et al., 2015; Sullivan et al., 2017); however, the effects of geographical extent had not been analysed before. In Chapter 3, I illustrated how geographical extent could affect the plant diversity-ecosystem service relationships by introducing an increasing amount of environmental heterogeneity. However, the relationship between geographical extent and environmental heterogeneity needs to be further analysed to conclude how geographical extent can moderate relationships. It may be expected that a larger geographical extent will always lead to a higher sampled environmental heterogeneity, as biodiversity and ecosystem services vary across spatial scale. However, it is likely that environmental variation will only moderate biodiversity-ecosystem service relationships if a considerate amount of variation in either biodiversity or ecosystem service is sampled, which may only happen at larger spatial scales such as the regional or continental. For the relationships between woody species richness and carbon stock at the continental spatial scale, the variation in carbon stock across environmental heterogeneity as represented by biogeographical regions caused a Simpson's paradox. Further research is needed to elucidate how environmental heterogeneity may cause the differences in carbon stock among the biogeographical regions and how other relationships of plant diversity and ecosystem services in tropical forests are affected by environmental heterogeneity.

6.5 What are the relationships between plant diversity and the stock, potential supply and use of tropical forest NTFPs? (RQ 4)

Ecosystem services delivery is determined by a complex interplay of ecological and socio-economic factors, but there is a general lack of knowledge about how this interplay influences ecosystem service stock, potential supply and flow (Bennett et al., 2015; Costanza et al., 2017; Mace et al., 2012). This limits the generalisation of biodiversity-ecosystem service relationships across other areas and the assessment of the extent to which the use of an ecosystem service (i.e., the flow) does not negatively affect the (future) stock (Bennett et al., 2015; Duncan et al., 2015; Hein et al., 2016). In this thesis, I took a closer look at the relationships between plant diversity and NTFP provisioning, which had been studied incompletely (Chapter 1, section 1.6). Specifically, I investigated the relationships between plant diversity and commercially relevant NTFP stock, potential supply and flow in the old-growth tropical forests of Suriname. I did so in two steps. First, in Chapter 4, the relationships between plant diversity and commercially relevant NTFP abundance (a proxy for NTFP stock) were analysed across a gradient of flooded and non-flooded tropical forests. This was followed in Chapter 5 by addressing how the NTFP abundance and potential supply of 13 commercially relevant plant-based NTFPs were related to the volumes sold on the market.

In Chapter 4, I found that a combination of taxonomic and structural plant species diversity indicators could explain over half (> 55%) of the observed variation in commercially relevant NTFP abundance across the Surinamese tropical forests. Across tropical forests, woody species diversity and evenness showed positive relationships to NTFP abundance, while woody species richness and stem density showed negative relationships. The negative relationship between woody species richness and NTFP abundance was in contrast with the more generic positive relationship between species diversity and aboveground biomass on the basis of the 'niche complementarity', 'insurance' and 'selection effect' hypotheses. However, as also discussed in section 6.3 of this chapter, NTFP abundance is likely to be determined by species floristic composition rather than species richness. The notion that NTFP abundance is primarily driven by floristic composition was supported by the finding of NTFP oligarchs (e.g. Chapter 4, Table 4-3) that were associated with specific floristic compositions. The existence of NTFP oligarchs is similar to the existence of 'stem oligarchs' for carbon stock at the regional scale and 'hyperdominants' at the continental scale (Fauset et al., 2015; Morera-Beita et al., 2019). The negative relationship between stem density and NTFP abundance is in line with the negative relationships between structural plant diversity and NTFP abundance in the systematic review of Chapter 2, and is likely to be an effect of the competition for light, space and/or water (see also section 6.3 of this chapter).

With the help of the theoretical framework developed in Chapter 5, NTFP abundance per forest type was linked to the potential NTFP supply and NTFP volumes sold on at the market. The framework describes the relationships between NTFP abundance, potential NTFP supply and market sales volumes by addressing the relevant ecological and socio-economic factors that determine ecosystem service delivery, which were identified using data from literature and fieldwork (Chapter 5, Figure 5-1). The framework illustrates that commercial NTFP provisioning is determined by a multitude of ecological and socio-economic factors. For example, ecologically, NTFP abundances significantly varied across the different Surinamese tropical forest types, and although a high NTFP abundance was generally positively related to high NTFP potential supply, the production factor of the species also played an important role (i.e. how much NTFP supply a NTFP species individual could produce; Chapter 5, Figure 5-3). In addition, socio-economic factors such as institutional constraints, marginal costs and profits of harvest, and societal demand, determined the share of the potential NTFP supply that was actually harvestable (harvestable NTFP supply) and how much harvestable NTFP supply was actually sold on the market. In line with expectations, this led to the finding that a high NTFP abundance (NTFP stock) did not always lead to a high NTFP flow. In particular, although the flow of NTFPs is inherently derived from NTFP abundance, flow was not significantly associated to NTFP abundance; I found that the percentage of harvestable NTFP supply that was sold at the market (an indicator of the NTFP flow; see Chapter 5, Table 5-5), was not significantly correlated to NTFP abundance.

In addition to quantifying how NTFP abundance was linked to potential supply and flow, I found no evidence that current harvest (flow) of the 13 considered NTFPs leads to a long-term reduction in their NTFP abundances in the forests. There was evidence of local overharvesting of only one species (i.e. the palm *Oenocarpus bacaba*), for which several of my co-authors and I observed locally reduced population sizes in specific forest types. The finding of generally ecologically sustainable use of plant-based NTFPs in Suriname was in line with previous assessments (Ruysschaert, 2018; van Andel & Havinga, 2008; van den Boog et al., 2018). In addition, I found evidence that the harvesters of the included NTFPs receive a reasonable income from the commercial trade in NTFPs. I estimated that most harvesters earned gross revenues from selling NTFPs around or above the minimum wage level. These two lines of evidence (no evidence of long-term negative harvest effects and indications of a reasonable income) suggest that currently, the marketing of plant-based NTFP sourced from old-growth tropical forests in Suriname could in principle provide an incentive for the local stakeholders to 'keep forests standing'.

In conclusion, I found evidence of significant relationships between plant diversity and NTFP abundance, but these do not necessary reflect relationships between plant diversity and NTFP provisioning. The findings of Chapter 5 suggest that socio-economic circumstances mainly determine which plants will be harvested, thus determining which subset of plant diversity is relevant for NTFP provisioning. In addition, I found evidence that the NTFP flow for commercial use can be ecologically sustainable in terms of stable NTFP stocks while also providing sufficient economic incentive to conserve tropical forests. However, these findings cannot be readily generalised across other tropical forest areas, because this requires information on both harvestable NTFP supply and use (flow) for those other areas. Although this had been suggested before by various authors (e.g. Belcher & Schreckenberg, 2007; Godoy et al., 1993; Sheil & Wunder, 2002), as far as I know Chapters 4 and 5 are the first studies that have quantified the linkages between the stock, potential supply and flow of NTFPs, illustrating the relevance of both ecological and socio-economic factors. Unfortunately, much remains unknown about how the relevant socio-economic factors that determine NTFP provisioning can be predicted. This means that detailed (field) studies will be needed to assess the use and value of NTFP provisioning for other tropical areas.

6.6 Implications for tropical forest conservation

As stated in the General Introduction, there is an increasing momentum to put ecosystem services forward as a focal point of conservation efforts, under the assumption that biodiversity will then also be conserved (Guerry et al., 2015; Mace, 2014; Chapter 1, section 1.1). For tropical forests, most contemporary conservation approaches focus on designating protected areas (Barlow et al., 2018; Morales-Hidalgo et al., 2015), either to conserve iconic or endemic landscapes and species, or to conserve high carbon stocks (Barlow et al., 2018; Harvey et al., 2010; Myers et al., 2000; Phelps et al., 2012; Watson et al., 2014). In light of this, three main implications for tropical forest conservation can be identified from this thesis.

1. Protecting carbon-rich tropical forests is likely to protect many woody species, but not necessarily high stocks of timber or NTFPs.

In Chapters 2 and 3, evidence was found of a consistent positive association between woody species richness and carbon stock across the tropics. This positive relationship supports potential win-win scenarios for conservation approaches that focus on protecting forests with high biodiversity or high carbon stocks. In particular, the relatively strong positive relationship between woody species richness and carbon stock up to regional spatial scales should be relevant for most national conservation policies. The extent of most tropical countries covers regional spatial scales, and the associated strong relationship represents an effective way of conserving both carbon stocks and many woody species. In this way, protected areas and policies that are implemented at a national scale, such as REDD+ (Phelps et al., 2012), can be used to help conserve tropical forests that contain large amounts of carbon stock and high concentrations of woody species as well. In contrast to the consistent positive relationship between woody species richness and carbon stock, the findings of my thesis suggest that commercially relevant timber stocks and NTFP abundances are not consistently related to woody species richness. In Chapters 3 and 4, only incidental relationships were observed for specific forest types and biogeographical subregions, and it is likely that these were caused by their specific floristic composition. This means that most contemporary conservation approaches will not automatically conserve important timber stocks or NTFP abundances, and that additional conservation measures are needed if such stocks are to be protected.

2. Some tropical forests with important timber and NTFP provisioning may be safeguarded in multiple use protected areas or indigenous territories

As timber and NTFP often play an important role in local livelihoods and national economies, I suggested in Chapters 3 and 4 that it is promising to include timber and/or NTFP stocks in multiple use protected areas and/or indigenous territories, such as the extractive reserves in Brazil (Barlow et al., 2018). Although forests with high timber and NTFP stocks are not necessarily species-rich, these forests might still contain important plant diversity which can then be conserved. For instance, a meta-analysis of protected areas has shown that local communities can be relatively successful in combining the harvesting of biological resources while at the same time achieving biological conservation (Oldekop et al., 2016). However, it is important to note that these conservation measures are only feasible for forests that are being used now or are usable in the foreseeable future. If stocks are not used or cannot be used, for example because they are too far way or are not accessible due to institutional constraints, then such stocks can be expected to have little to no value to stakeholders, increasing the risk that stakeholders do not protect or conserve them. In Chapter 5 (and the references in that chapter), I noted that local communities in tropical forests mainly use the forests nearby habitation to harvest timber and NTFPs (Ramirez-Gomez et al., 2016, 2017; van den Boog et al., 2018; Chapter 5). This suggests that the conservation measures mentioned above can only be effectively established for a limited geographical area. In practice, the spatial delineation of potential multiple use protected areas or indigenous territories could be established by using Participatory Mapping, identifying the tropical forests that are used or provide important values to local stakeholders in collaboration with the local community (Ramirez-Gomez et al., 2015, 2016, 2017). Analyses of the relationships between plant diversity and ecosystem services as used in this thesis could then help to identify which plant diversity is relevant and needs to be incorporated in the management.

3. Commercial use of tropical forest NTFPs can be ecologically sustainable, providing an economic incentive to keep forests standing

In line with the 'conservation-through-use paradigm', it has been suggested that the cash-income received by local stakeholders from the commercial trade of NTFPs sourced from tropical forests may function as an incentive to keep these forests standing (Kusters et al., 2006; E. Marshall et al., 2006; A. C. Newton, 2008). Under this paradigm, commercial NTFP provisioning could be considered ecologically sustainable when at least 1) the economic value received by local stakeholders was adequality high, and 2) harvesting would not lead to a reduction in natural populations (Kusters et al., 2006; A. C. Newton, 2008). In Chapter 5, evidence was found that supports both criteria under the current harvesting and sales practices of plant-based NTFPs in Suriname. We found that harvesters were likely to earn reasonable gross revenues compared to the national minimum wage, and that most of the harvest of plant-based NTFPs did not have clear long-term negative effects on the plant populations involved or the tropical forests surrounding them. For Suriname, this suggests that the use of NTFPs can provide a win-win situation by contributing to local livelihoods and conservation of old-growth tropical forests. As discussed in Chapter 5, if the effective conservation of tropical forest by commercial NTFP use is supported by further assessment, capturing this use in national management strategies could help to safeguard the continuous use of NTFPs in Suriname for future generations.

It is important to note that not all NTFPs are eligible to contribute to the conservation of old-growth tropical forests. For example, in Suriname many plant-based NTFPs are sourced from secondary vegetation and tropical savannas (e.g. van Andel & Havinga, 2008), and it is expected that many animal-based NTFPs from old-growth tropical forests are unsustainably exploited (e.g. van Andel et al., 2003; van den Boog et al., 2018; Verheij, 2019). In addition, local demand may vary across tropical areas, affecting the sustainability of plant-based NTFPs sourced from old-growth tropical forests. In Suriname, the demand for local plant-based NTFPs is relatively low due to a small human population size and little international trade. By contrast, in other tropical countries local demand is sometimes much higher and there is sometimes considerable international trade. For example, Brazilian cities such as Belem and Manaus have a much higher demand for forest products and are involved in international trade of large volumes of products such as açaí fruit and Brazil nuts (van Andel et al., 2003). Therefore, it is always important first to carry out an assessment of the local ecology, current demand and potential future demand before considering the commercialisation of NTFPs.

6.7 Seeing the forest through the trees

One of the aims of this thesis was to 'see the forest through the trees'. What I mean by this is that I aimed to discern overall patterns in relationships between plant diversity and ecosystem services in tropical forests from the various details, and assess the relevance of these overall patterns for tropical forest conservation. In this thesis, I have seen many 'trees': relationships between plant diversity, carbon storage, timber provisioning and NTFP provisioning, spanning taxonomic, functional and structural plant diversity and ecosystem service stock and flows. Despite the many different 'trees' and limited time, I was able to 'see' (distil) a few 'forests': concrete findings that can contribute to effective and efficient tropical forest conservation approaches. However, I expect that many more 'forests', meaning relevant relationships between plant diversity and ecosystem services, are still hidden, and these require more scientific attention. For example, due to data limitations I have only addressed tree and arborescent plant diversity, thus excluding herbs, lianas and vines. Although the latter growth forms are not likely to have great relevance for carbon storage or timber provisioning, they are known to produce valuable plant-based NTFPs. In addition, the findings in this thesis have indicated that there can be relevant relationships between structural plant diversity and multiple ecosystem services, but a systematic assessment is currently lacking. In general, most scientific attention has been given to relationships between plant diversity and the ecosystem service of carbon stock, while relationships with the relevant ecosystem services of timber and NTFP provisioning remain less studied. This is also the case for important regulating services, such as climate regulation and water purification, or important cultural services, such as sacred sites for forest-dwelling communities. Nevertheless, I expect that not all plant diversity will be equally relevant for ecosystem service-based conservation measures. For example, timber and NTFP provisioning are driven by subsets of plants, and these subsets are likely to change across space and time due to differences in environmental and socio-economic circumstances. This means that not all plant species at a given time are equally important for these ecosystem services. Regardless, I think there is a great need to further elucidate the relationships between plant diversity and ecosystem services in tropical forests. Only when more knowledge of these relationships becomes available can we assess the full potential of ecosystem services to contribute to tropical forests conservation. It is likely that a combination of ecosystem service-based and other conservation approaches will be needed to help safeguard the treasure troves of biodiversity that tropical forests represent.

6.8 Recommendations for future research

During the research for this thesis, I gained insights that might be relevant in further studying the relationships between plant diversity and ecosystem services in tropical forests as well as the relationships between biodiversity and ecosystem services in general. From the insights provided in the research chapters, I here distil three main recommendations.

1. Address the relationships of plant diversity with ecosystem services other than carbon storage and include ecosystem service flow

In the systematic review of Chapter 2 it became clear that amongst the three ecosystem services of carbon storage, timber provisioning and NTFP provisioning, most attention had been given to carbon storage. Although I found that woody species richness is likely not related to timber provisioning and NTFP provisioning, other types of plant diversity might be. For example, in this thesis significant relationships of the Shannon diversity of woody species and the stem density were found with both carbon stock and NTFP abundance (Chapters 2 and 4). Based on the many different plant diversity indicators that have been successfully related to carbon stock (Chapter 2), there is ample reason to believe that significant relationships of plant diversity with timber and NTFP provisioning can be found. Increasing the number of comparisons of how plant diversity is related to timber provisioning and NTFP provisioning will enable the testing of the postulated hypothesis concerning floristic composition described in section 6.3, and possibly the generation of new hypotheses. In addition, in the systematic review it became clear that most attention has been given to the stock component of ecosystem services. Yet, as I stated in the General Introduction, it is likely that the flow component of ecosystem services is strongly influenced by socio-economic factors, which could theoretically weaken, nullify or even change the direction of relationships between plant diversity and the stock component of ecosystem services (Chapter 1, section 1.2). For instance, in Chapters 4 and 5, I found evidence that relationships between plant diversity and NTFP abundance were likely to be nullified by socio-economic factors such as accessibility and demand (see also section 6.5). The finding of such moderating effects may have large implications for the effectiveness of ecosystem-service based conservation approaches that also aim at protecting plant diversity.

2. Include comparisons with commonly used plant diversity indicators

From the systematic review in Chapter 2 it became clear that for some plant diversity dimensions, many different indicators have been used. Less than half of the seventy unique plant diversity indicators that were reported in the literature were used more than twice, and only five were used sufficiently frequently to allow a meta-analysis (Chapter 2, Table 2-2). In particular, the functional dimension of plant diversity has been approximated by a myriad of scarcely used indicators (Chapter 2, Appendix S4). Moreover, in some cases, the differences between functional indicators were not directly apparent. For example, functional composition can be measured by the Community Weighted Mean (CWM), but the CWM can include different weights (e.g. the number of individuals or the relative contribution to biomass) and the chosen weight was not always explicitly stated in studies. Therefore, to facilitate meaningful comparisons in the future, a consensus should be agreed upon regarding the construction and use of common indicators. For example, for plant functional traits there is a handbook that provides standardised measurements (Pérez-Harguindeguy et al., 2016), which could form the basis of such a consensus. Preferably, publications should use the common indicators agreed upon to test relationships or, at least, include these indicators in tests provided in the supplementary material (appendices).

3. Check for effects of environmental heterogeneity by applying environmental stratification

In Chapter 3, I investigated the effect of environmental heterogeneity on the relationship between plant diversity and ecosystem services. I found that the effects of environmental heterogeneity can obscure relationships and become stronger with an increasing spatial scale. For instance, in the relationships between woody species richness and carbon stock, accounting for variation in carbon stock across different biogeographical subregions of the Guiana Shield did not impact the overall relationship (i.e. no strong effect of environmental heterogeneity), whereas accounting for the variation across the different biogeographical regions of Amazonia did (i.e. a strong effect). Such moderation effects at the continental spatial scale have previously not been detected because it is likely that previous studies did not adequately stratify their data. Therefore, I recommend to always check whether environmental heterogeneity has an impact on the relationships between plant diversity and ecosystem services by applying environmental stratification of the data.

Plant life along a stream in the tropical forest, Suriname. Photo by Gijs Steur.

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Sunset across the Brokopondo lake, Suriname. Photo by Lieke Guinée.

English Summary

Nederlandse samenvatting

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About the author

ENGLISH SUMMARY

Questions about relationships between plant diversity and ecosystem services in tropical forests

Natural ecosystems are home to the largest share of the Earth's biodiversity and deliver essential 'ecosystem services': goods and services that benefit our wellbeing. However, under the ever-increasing human pressure that marks the Anthropocene, natural ecosystems are being degraded and lost at an alarming rate. Despite our efforts to protect natural ecosystems and their biodiversity, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES, 2019) reported dramatical declines. Since the 1970s, 47% of all natural ecosystems have decreased in either extent or environmental quality and a considerable part of the estimated local biodiversity has been lost, 20% on average. As a consequence, 78% of monitored ecosystem services have been deteriorating as well, putting life on Earth under further pressure and threatening human well-being. In response, ecosystem services are increasingly becoming the focal point of conservation efforts. Under the assumption that ecosystem services and biodiversity are positively linked, protecting ecosystem services would protect biodiversity as well. However, although studies have reported positive relationships for certain ecosystems such as temperate grasslands, for tropical forests these relationships are not yet clear. Tropical forests are among the most species-rich biomes on the planet while also providing many important ecosystem services such as carbon storage, timber provisioning and the provisioning of non-timber forest products (NTFPs; products such as foods, medicines and cultural totems). As tropical forests are under increasing pressure of deforestation and degradation, the relationships between biodiversity and ecosystem services need to be elucidated. If positive relationships between biodiversity and ecosystem services are absent or rare, ecosystem service-based conservation measures cannot be expected to simultaneously contribute to biodiversity conservation. In such cases, the focus of conservation efforts will be need to be adapted to also protect biodiversity. Therefore, this thesis aimed to explore the relationships between plant diversity and three selected ecosystem services of old-growth tropical forests that are related to the aboveground biomass: carbon storage, timber provisioning and NTFP provisioning.

In the General Introduction (**Chapter 1**), three hypotheses were introduced that predict a higher plant diversity to be associated to a higher amount of aboveground biomass: the 'niche complementarity', 'insurance' and 'selection effect' hypotheses. In line with these hypotheses, a higher plant diversity would result into a higher amount of biomass-based ecosystem services such as carbon storage, timber provisioning and NTFP provisioning. Although there has been considerable support for positive plant diversity-biomass relationships in grasslands and non-tropical forests and plantations, the evidence for positive relationships between plant diversity and carbon storage, timber provisioning, and

NTFP provisioning in old-growth tropical forests remains inconclusive. This thesis focused on three main knowledge gaps. First, plant diversity consists of multiple dimensions, such as a taxonomic, structural and functional dimension, and ecosystem services have a stock and a flow component. However, previous studies have used a variety of methods, in which only a limited part of the spectrum of possible relationships between these dimensions of plant diversity and components of ecosystem services have been addressed. Second, previous studies suggest that the outcome of the tested relationship may be dependent on spatial scale, including variation in sample plot size and the geographical extent of the study area. Yet, these spatial scale effects need to be further clarified and quantified. Third and last, ecosystem service delivery is characterized by a complex interplay of ecological factors influencing their stock and potential supply on the one hand, and socio-economic factors determining their flow (use) on the other. Yet few studies on old-growth tropical forests have studied this in an integrated way. To fill the three aforementioned knowledge gaps, this thesis identified the following four research questions:

RQ 1: *How are taxonomic, structural and functional plant diversity related to the stock and flow components of carbon storage, timber provisioning and NTFP provisioning in tropical forests?*
RQ 2: *How is plant diversity related to multiple ecosystem services in tropical forests, such as carbon storage, timber provisioning and NTFP provisioning?*
RQ 3: *What are the effects of the spatial scale aspects of plot size and geographical extent on the observed relationships between plant diversity and carbon storage, timber provisioning and NTFP provisioning in tropical forests?*
RQ 4: *What are the relationships between plant diversity and the stock, potential supply and use of tropical forest NTFPs?*

To answer these research questions, this thesis featured original research in the form of four research chapters (chapters 2-5). In **Chapter 2**, a systematic review and meta-analysis of the empirical evidence in the pantropical literature was carried out to identify the state of knowledge on the studied relationships and specify knowledge gaps. These knowledge gaps were then further addressed in the following three research chapters (chapter 3-5) using 'primary' plot data (as opposed to the 'secondary' data of Chapter 2 taken from the literature). **Chapter 3** featured an analysis of the relationships between the richness of tree and arborescent palm species, hereafter 'woody species richness', and the selected three ecosystem services in old-growth tropical forests. It analysed these relationships across and within different biogeographical strata, including biogeographical regions and subregions, and on multiple spatial scales, including the Guiana Shield and all of Amazonia. In this chapter, plant species richness was used as a proxy for plant diversity in a broad sense, including taxonomic, structural and functional dimensions. Because less was known about how tropical forest NTFPs are delivered under the interplay of both ecological and socio-economic factors, chapter 4 and 5 focused on NTFP provisioning in Suriname as case-study. **Chapter 4** focused on the ecological factors influencing variation in NTFP stocks, whereas **Chapter 5** studied the NTFP flow influenced by ecological and socio-economic factors. In this last chapter, a theoretical framework was developed to conceptualize the NTFP flow in relation to both ecological and socio-economic factors.

Relationships between plant diversity in a broad sense and stock and flow components of services (RQ 1)

Old-growth tropical forests are rich in plant diversity while also storing carbon and providing timber and NTFPs. As plant diversity has taxonomic, functional and structural dimensions and ecosystem services have a stock and a flow component, **Chapter 2** analysed how these different dimensions of plant diversity and components of ecosystem services are related to these three ecosystem services across the tropics. The systematic review of 1081 papers from across the tropics showed that a wide range of methods and indicators has been used to study such relationships. Much scientific attention has been given to relationships between plant diversity and carbon storage, while the relationships with timber provisioning and NTFP provisioning have hardly been studied. For carbon storage, taxonomic and structural plant diversity indicators showed mainly positive relationships, while functional plant diversity indicators showed a mixture of both positive and negative relationships. The positive relationships between plant diversity and carbon storage were in line with the predictions of the hypotheses such as the 'niche complementarity', 'insurance' and 'selection effect' hypotheses, but the mix of positive and negative relationships that was discovered was surprising. Relationships of plant diversity with stock and flow components of carbon storage were found to be similar. For timber provisioning and NTFP provisioning, the systematic review found that the number of reported relationships was too small to be able to substantiate generic patterns. These preliminary findings suggest that taxonomic and structural plant diversity have different relationships with timber and NTFP provisioning in comparison to carbon storage, and that relationships differ between stock and flow components. In answer to the research question, this thesis concluded that although positive relationships between plant diversity and carbon storage were frequently reported across the tropics, the finding of negative relationships requires further study. In addition, this thesis illustrates an important knowledge gap regarding how timber and NTFP provisioning are related to plant diversity.

Relationships between species richness and multiple ecosystem services simultaneously (RQ 2)

Conceptually, plant diversity could have similar relationships with carbon storage, timber provisioning and NTFP provisioning, in line with the concept of 'bundles' of ecosystem services, services that are positively related with each other. However, as found in Chapter 2, previous studies have used different methods involving different plant diversity indicators and most attention has been given to carbon storage only. This raised the question how particular plant diversity is related to the combination of aforementioned three ecosystem services in old-growth tropical forests. In the analyses of **Chapter 3,** woody species richness was used as a proxy for plant diversity, where it showed both similar and dissimilar relationships to the stock component of the aforementioned three ecosystem services in tropical forests of the Guiana Shield. Positive relationships were found between species richness, carbon stock and timber stock, suggesting an ecosystem service bundle of carbon and timber stocks in species-rich tropical forests. However, as only carbon stock was consistently positively related to species richness across multiple biogeographical subregions of the Guiana Shield, the occurrence of a general service bundle of both high carbon and timber stock remains questionable. The positive relationship between species richness and carbon stock was in line with the predictions of the 'niche complementarity', 'insurance' and 'selection effect' hypotheses. The precise mechanisms underlying this relation was not a focus of this thesis. No consistent relationships were found between species richness, timber stock and NTFP abundance. Instead, results showed that timber and NTFP stocks varied across subregions for which the relationship was tested. This was probably due to differences in floristic composition and socio-economic factors such as demand. In answer to the research question, this thesis found no evidence for general carbon storage, timber provisioning and/or NTFP provisioning bundles in old-growth tropical forests. At the spatial scale of the Guiana Shield, woody species richness and carbon stock of old-growth tropical forests were positively related.

Effects of plot size and geographical extent on relationships (RQ 3)

Theoretically, relationships between plant diversity and the aforementioned three ecosystem services in tropical forests could be affected by spatial scale aspects such as plot size and geographical extent, potentially resulting in contradictory relationships as found across different studies. However, as such effects had been incompletely studied, **Chapter 2** looked into the question what the effects of plot size and geographical extent are on the relationships between plant diversity and the aforementioned three ecosystem services in tropical forests. The systematic review presented in this chapter found evidence for a moderating effect of plot size. At small plot sizes (< 1 ha) relationships between plant diversity and carbon stock were frequently significantly positive while at large plot sizes (1 ha) they were mostly non-significant. However, the follow-up meta-analysis in this chapter also showed that this did not explain all contradictory findings in the literature. The results suggested that relationships are moderated by geographical extent as well: woody species richness was significantly positively related to carbon stock, but while the relationship was strongly positive at local to regional spatial scales, it became weaker and almost zero at continental and intercontinental scales. In the analyses of **Chapter 3**, it was illustrated how geographical extent can moderate relationships due to the amount of environmental heterogeneity that is sampled. Per biogeographical region of Amazonia, species richness was positively related to carbon stock. However, when all regions were lumped and analysed together, creating a larger geographical extent, the relationship became negative. This pattern resembled a known statistical paradox called a 'Simpson Paradox' and reflected differences in carbon stock between biogeographical regions. Only when the differences in carbon stock between the regions were compensated for, the relationships did become positive. In answer to the research question, this thesis provides novel evidence that both plot size and geographical extent can moderate the relationships between plant diversity and ecosystem services in old-growth tropical forests. Further research is needed to elucidate how patterns in environmental heterogeneity may cause the differences in carbon stock among the biogeographical regions and how relationships between plant diversity and other ecosystem services in tropical forests are affected by environmental heterogeneity.

Influence of ecological and socio-economic factors on NTFP provisioning (RQ 4)

Plant-based NTFP provisioning is determined by a complex interplay of ecological and socio-economic factors, such as the production of particular plant species, access and transport by harvesters, and demand for the specific product. In this way, the use of an ecosystem service (i.e., the flow) partly determines the relationships between plant diversity and an ecosystem service, while also potentially affecting the (future) stock. As there is a general lack of knowledge about this interplay, the question remains what the relationships are between plant diversity on the one hand and the NTFP stock (species abundance), their potential supply and flow (use) on the other. In **Chapter 4**, it was found that a combination of taxonomic and structural plant diversity indicators could explain over half (> 55%) of the observed variation in commercially relevant NTFP stock across the Surinamese tropical forests. In particular, NTFP stock was for a large part determined by a select few plant species with high abundances, coined 'NTFP oligarchs', which were associated with specific floristic compositions found in forest types. However, with the help of the theoretical framework developed in **Chapter 5**, the NTFP stock was found to be unrelated to NTFP flow, suggesting that forest types with high NTFP stocks are not necessarily more intensively used. Last, Chapter 5 found no evidence of systematic overharvesting of NTFP stock in Suriname, while NTFP harvesters received a reasonable income from selling the NTFPs to the market in Paramaribo, compared to the national minimum wage. This suggests that currently, the marketing of plant-based NTFPs sourced from old-growth tropical forests in Suriname could in principle provide an incentive for the local stakeholders to 'keep forests standing'. In answer to the research question, this thesis identified significant relationships between plant diversity and NTFP stock (abundance), but also showed for the first time that the relevant plant diversity indicators are unlikely to be related to NTFP flow (use). The newly developed theoretical framework illustrates that socio-economic factors, such as overall demand, costs related to harvest, transport and processing, and social harvest rules, determine which plants will be harvested, thus determining which subset of plant diversity is relevant for NTFP provisioning. In addition, this thesis provides evidence supporting the 'conservation-through-use-paradigm' by finding that the NTFP flow for commercial use can be ecologically sustainable in terms of stable NTFP stocks while also providing sufficient economic incentive to conserve tropical forests. Although it remains unclear which socio-economic factors are relevant for other tropical areas, the developed theoretical framework can be used elsewhere to shed light on the different components of NTFP flows.

Seeing the forest through the trees

This thesis was intended to 'see the forest through the trees': to discern overall patterns in plant diversity-ecosystem services relationships in tropical forests, and discuss their implications for tropical forest conservation. This thesis distilled three 'forest patterns' in the synthesis in **Chapter 6**. First, as a consistent positive relationship between woody species richness and carbon stock was found across and within Amazonia, protecting carbon-rich tropical forests is likely to protect concentrations in woody species diversity. However, such forests would not necessarily protect large stocks of timber or NTFPs. Second, tropical forests with important timber- and NTFP-producing plant species were often found near forest dwelling communities and therefore, such forests would benefit from conservation through multiple use protected areas, indigenous territories, or other forms of community protected area management. Third and last, in Suriname the commercial use of plant-based NTFPs provided a reasonable income to harvesters while the standing stocks did not show signs of systematic negative impacts. This suggests that the commercial use of tropical forest NTFPs can be ecologically sustainable, providing an economic incentive to keep forests standing. The author of this thesis expects that many more 'forest patterns' are still hidden, requiring further scientific attention. Only when more knowledge of relationships between plant diversity and ecosystem services becomes available can we assess the full potential of ecosystem service-based conservation efforts to contribute to tropical forests conservation. The author expects that it is likely that a combination of ecosystem service-based and other conservation approaches will be needed to help safeguard the treasure troves of biodiversity that tropical forests represent.

NEDERLANDSE SAMENVATTING

Vragen over relaties tussen plantendiversiteit en ecosysteemdiensten in tropische bossen

Natuurlijke ecosystemen huisvesten het grootste deel van de mondiale biodiversiteit en leveren essentiële 'ecosysteemdiensten': ze leveren goederen en diensten die bijdragen aan ons welzijn. Natuurlijke ecosystemen worden echter met een schrikbarende snelheid aangetast en vernietigd onder de alsmaar toenemende menselijke druk die het Antropoceen kenmerkt. Ondanks onze pogingen om natuurlijke ecosysteemdiensten en hun biodiversiteit te beschermen, blijkt uit een recent rapport van het Intergouvernementeel Platform voor Biodiversiteit en Ecosysteemdiensten (IPBES, 2019) dat er dramatische afnames zijn. Sinds de jaren 1970 is 47% van alle natuurlijke ecosystemen achteruitgegaan in omvang of kwaliteit en hierbij is gemiddeld 20% van de lokale biodiversiteit verloren gegaan. Als gevolg daarvan zijn 78% van alle gemonitorde ecosysteemdiensten achteruitgegaan, wat het leven op aarde verder onder druk zet en ons welzijn bedreigt. Als reactie hierop focust natuurbescherming steeds vaker op ecosysteemdiensten. Want, onder de aanname dat ecosysteemdiensten en biodiversiteit positief aan elkaar gekoppeld zijn, zou het beschermen van ecosysteemdiensten ook moeten leiden tot het beschermen van biodiversiteit. Maar alhoewel eerdere onderzoeken positieve verbanden hebben gevonden voor bepaalde ecosystemen zoals graslanden, blijft het onduidelijk wat de relaties zijn in tropische bossen. Tropische bossen behoren tot de meest soortenrijke biomen van de aarde terwijl ze ook veel belangrijke ecosysteemdiensten leveren, zoals koolstofopslag, hout en niet-houtbosproducten ('*NTFP's*'; producten zoals voedsel, medicijnen en producten van cultureel belang). Aangezien tropische bossen onder toenemende druk staan van ontbossing en degradatie is het belangrijk dat de relaties tussen biodiversiteit en ecosysteemdiensten opgehelderd worden. Als er weinig positieve relaties zijn, kan niet verwacht worden dat natuurbescherming die gericht is op ecosysteemdiensten ook zal leiden tot het behoud van biodiversiteit. In dergelijke gevallen zal de focus van natuurbescherming verlegd moeten worden om ook biodiversiteit te beschermen. Daarom richt dit proefschrift zich op het verkennen van relaties tussen plantendiversiteit en drie geselecteerde belangrijke ecosysteemdiensten in volgroeide tropische bossen die gerelateerd zijn aan de bovengrondse biomassa: koolstofopslag, houtvoorziening en NTFP-voorziening.

In de Algemene Inleiding (**Hoofdstuk 1**) werden drie hypothesen geïntroduceerd die voorspellen dat een hogere plantendiversiteit geassocieerd is met een grotere hoeveelheid bovengrondse biomassa: de 'niche-complementariteit', 'verzekering'en 'selectie-effect' hypothesen. In overeenstemming met deze hypothesen zou een grotere plantendiversiteit resulteren in een grotere hoeveelheid van ecosysteemdiensten die gerelateerd zijn met de bovengrondse biomassa, onder andere koolstofopslag, houtvoorziening en NTFP-voorziening. Hoewel er aanzienlijke steun is gevonden voor positieve relaties tussen plantendiversiteit en biomassa in graslanden en niet-tropische bossen en plantages, blijft het bewijs voor positieve relaties tussen plantendiversiteit en koolstofopslag, houtvoorziening en NTFP-voorziening in volgroeide tropische bossen niet overtuigend. Dit proefschrift richtte zich op drie belangrijke kennishiaten. Ten eerste bestaat plantendiversiteit uit meerdere dimensies, zoals een taxonomische, structurele en functionele dimensie, en hebben ecosysteemdiensten een voorraad- (‘*stock*’) en een stroomcomponent (‘*flow*’). Eerdere studies verschillen in methoden, waar een beperkt deel van het spectrum van mogelijke relaties tussen deze dimensies van plantendiversiteit en componenten van ecosysteemdiensten is onderzocht. Ten tweede suggereren eerdere studies dat de uitkomst van geteste relaties afhankelijk kan zijn van de ruimtelijke schaal waarop ze getoetst worden, zoals door de schaalaspecten plotgrootte (grootte van het steekproefoppervlak; ‘*plot size*’) en geografische omvang (de geografische omvang van het studiegebied; ‘*geographical extent*’). De effecten van deze twee ruimtelijke schaalaspecten moeten echter verder worden verkend en gekwantificeerd. Ten derde en tot slot, wordt de levering van ecosysteemdiensten gekenmerkt door een complex samenspel van enerzijds ecologische factoren die hun voorraad en potentieel aanbod beïnvloeden, en anderzijds sociaaleconomische factoren die hun stroom (het gebruik) bepalen. Toch zijn er maar weinig studies over volgroeide tropische bossen die dit samenspel op een geïntegreerde manier hebben bestudeerd. Om de drie kennishiaten te adresseren, zijn in dit proefschrift de volgende vier onderzoeksvragen onderzocht:

OV 1: *Hoe is taxonomische, structurele en functionele plantendiversiteit gerelateerd aan de voorraad- en stroomcomponenten van koolstofopslag, houtvoorziening en NTFP-voorziening in tropische bossen?*

OV 2: *Hoe is plantendiversiteit gerelateerd aan meerdere ecosysteemdiensten tegelijkertijd in tropische bossen, namelijk koolstofopslag, houtvoorziening en NTFP-voorziening?*

OV 3: *Wat zijn de effecten van de ruimtelijke schaalaspecten plotgrootte en geografische omvang op de waargenomen relaties tussen plantendiversiteit en koolstofopslag, houtvoorziening en NTFP-voorziening in tropische bossen?*

OV 4: *Wat zijn de relaties tussen plantendiversiteit en de voorraad, het potentiële aanbod en het gebruik van tropische bos-NTFP’s?*

Om deze onderzoeksvragen te beantwoorden is er voor dit proefschrift nieuw wetenschappelijk onderzoek uitgevoerd in vier hoofdstukken (hoofdstukken 2 tot en met 5). In **Hoofdstuk 2** is een systematische review en meta-analyse uitgevoerd op basis van empirisch bewijs uit de pantropische literatuur om de stand van kennis over de bestudeerde relaties te bepalen en kennishiaten te specificeren. Deze kennishiaten zijn vervolgens verder onderzocht in de daaropvolgende drie onderzoekshoofdstukken (hoofdstukken 3 tot en met 5) met behulp van ‘primaire’ plotdata (in tegenstelling tot ‘secundaire’ data uit de literatuur zoals in hoofdstuk 2). **Hoofdstuk 3** bevat een analyse van de relaties tussen de rijkdom aan boom- en boompalmsoorten, hierna ‘bomensoortenrijkdom’ genoemd, en de geselecteerde drie ecosysteemdiensten in volgroeide tropische bossen. Deze relaties zijn geanalyseerd tussen en binnen verschillende biogeografische strata, namelijk biogeografische regio’s en subregio’s, en op meerdere ruimtelijke schalen, namelijk het Guyanaschild en geheel Amazonia. In dit hoofdstuk werd de bomensoortenrijkdom gebruikt als een proxy voor plantendiversiteit in brede zin, inclusief taxonomische, structurele en functionele dimensies. Omdat er minder bekend was over hoe NTFP’s uit tropische bossen worden geleverd onder het samenspel van ecologische en sociaaleconomische factoren, concentreren hoofdstuk 4 en 5 zich op de NTFP-voorziening in Suriname als casus. **Hoofdstuk 4** richt zich op de ecologische factoren die de variatie in NTFP-voorraden beïnvloeden, terwijl **Hoofdstuk 5** de NTFP-stroom (het gebruik) bestudeert die wordt beïnvloed door zowel ecologische als sociaaleconomische factoren. Voor dit laatste hoofdstuk werd een theoretisch raamwerk ontwikkeld om de NTFP-stroom in relatie tot de ecologische en sociaaleconomische factoren te conceptualiseren.

Relaties tussen plantendiversiteit in brede zin en de voorraad- en stroomcomponenten van diensten (OV 1)

Volgroeide tropische bossen zijn rijk aan plantendiversiteit terwijl ze ook koolstof opslaan en hout en NTFP’s leveren. Aangezien plantendiversiteit taxonomische, functionele en structurele dimensies heeft en ecosysteemdiensten een voorraad- en een stroomcomponent hebben, analyseert **Hoofdstuk 2** hoe deze verschillende dimensies en componenten verband houden met de drie genoemde ecosysteemdiensten over heel de tropen. De systematische review van 1081 artikelen toont aan dat een breed scala aan methoden en indicatoren is gebruikt om dergelijke relaties te bestuderen. Er blijkt veel wetenschappelijke aandacht te zijn besteed aan relaties tussen plantendiversiteit en koolstofopslag, terwijl relaties met houtvoorziening en NTFP-voorziening nauwelijks zijn onderzocht. Met koolstofopslag lieten taxonomische en structurele indicatoren voor plantendiversiteit voornamelijk positieve relaties zien, terwijl functionele indicatoren een mix van zowel positieve als negatieve relaties lieten zien. De gevonden positieve relaties tussen plantendiversiteit en koolstofopslag waren in lijn met de voorspellingen volgend uit hypothesen zoals de ‘niche-complementariteit’, ‘verzekering’ en ‘selectie-effect’-hypothesen, maar de in kaart gebrachte negatieve relaties waren verrassend. Relaties van plantendiversiteit met respectievelijk de voorraad- en de stroom component van koolstofopslag waren vergelijkbaar met elkaar. Voor houtvoorziening en NTFP-voorziening bleek het aantal gerapporteerde relaties te klein om generieke patronen te kunnen onderscheiden. De voorlopige bevindingen suggereren dat taxonomische en structurele plantendiversiteit andere relaties hebben met hout- en NTFP-voorziening vergeleken met koolstofopslag, en dat de relaties met plantendiversiteit verschillen tussen de voorraad-en stroomcomponent. In antwoord op de onderzoeksvraag concludeerde dit proefschrift dat alhoewel er vaak positieve relaties tussen plantendiversiteit en koolstofopslag in volgroeide tropische bossen worden gerapporteerd, de mix van aangetroffen positieve en negatieve relaties verder onderzoek vereist. Bovendien illustreert dit proefschrift dat er een belangrijke kennislacune bestaat over hoe hout en NTFP-voorziening zich verhouden tot de plantendiversiteit.

Relaties tussen soortenrijkdom en meerdere ecosysteemdiensten tegelijkertijd (OV 2)

Conceptueel gezien zou plantendiversiteit vergelijkbare relaties kunnen hebben met koolstofopslag, houtvoorziening en NTFP-voorziening, in lijn met het concept van 'ecosysteemdienstenbundels': ecosysteemdiensten die positief met elkaar samenhangen. Echter, zoals gevonden in Hoofdstuk 2, eerdere studies hebben verschillende methoden gebruikt met verschillende indicatoren voor plantendiversiteit en de meeste aandacht is besteed aan koolstofopslag. Dit riep de vraag op hoe specifieke plantendiversiteit zich verhoudt tot de combinatie van bovengenoemde drie ecosysteemdiensten in volgroeide tropische bossen. In de analyses van **Hoofdstuk 3** werd de bomensoortenrijkdom gebruikt als benadering voor de algehele plantendiversiteit, waar het zowel vergelijkbare als ongelijke relaties met de voorraadcomponent van de bovengenoemde drie ecosysteemdiensten in de bossen van het Guyanaschild vertoonde. Tussen de soortenrijkdom, koolstofvoorraad en houtvoorraad werden een aantal positieve relaties gevonden die suggereren dat er een ecosysteemdienstenbundel zou bestaan van koolstof- en houtvoorraden in soortenrijke tropische bossen. Omdat de soortenrijkdom in meerdere biogeografische subregio's van het Guyanaschild alleen consequent positief gerelateerd was aan de koolstofvoorraad, blijft het echter twijfelachtig of er een generieke ecosysteemdienstenbundel van hoge koolstof- en houtvoorraden bestaat. De positieve relatie tussen soortenrijkdom en koolstofvoorraad was in lijn met de voorspellingen volgend uit de 'nichecomplementariteit', 'verzekering' en 'selectie-effect' hypothesen. De precieze mechanismen die aan de positieve relatie ten grondslag liggen, waren echter geen onderdeel van dit proefschrift. Tussen soortenrijkdom, houtvoorraad en de abundantie van NTFP-producerende soorten werden geen consistente relaties gevonden. In plaats van consistente relaties met soortenrijkdom toonden de resultaten aan dat hout- en NTFP-voorraden variëren met de subregio waarvoor de relatie werd getest. Dit patroon wordt waarschijnlijk veroorzaakt door verschillen in floristische samenstelling en sociaaleconomische factoren zoals de vraag naar producten. In antwoord op de onderzoeksvraag vond dit proefschrift geen bewijs voor algemene ecosysteemdienstenbundels van koolstofopslag, houtvoorziening en/of NTFP-voorziening in volgroeide tropische bossen. Op de ruimtelijke schaal van het Guyanaschild waren alleen de bomensoortenrijkdom en de koolstofvoorraad in volgroeide tropische bossen systematisch positief gerelateerd.

Effecten van plotgrootte en geografische omvang op relaties (OV 3)

In theorie zouden relaties tussen plantendiversiteit en de eerdergenoemde drie ecosysteemdiensten in tropische bossen kunnen worden beïnvloed door de ruimtelijke schaalaspecten plotgrootte en de geografische omvang van het studiegebied. Hierdoor zouden tegenstrijdige bevindingen in de literatuur verklaard kunnen worden. Omdat dergelijke effecten echter onvolledig onderzocht zijn, wordt in **Hoofdstuk 2** ingegaan op de vraag wat de effecten van plotgrootte en geografische omvang zijn op de relaties tussen plantendiversiteit en de eerdergenoemde drie ecosysteemdiensten in tropische bossen. De systematische review die in dit hoofdstuk wordt gepresenteerd leverde bewijs voor een modererend effect van de plotgrootte. Bij kleine plotgroottes (< 1 ha) waren de relaties tussen plantendiversiteit en koolstofvoorraad vaak significant positief, terwijl ze bij grote plotgroottes (1 ha) meestal niet significant waren. Uit de daarop volgende meta-analyse in dit hoofdstuk bleek echter ook dat het modererend effect van plotgrootte niet alle tegenstrijdige bevindingen uit de literatuur verklaarde. Daarentegen suggereerde de meta-analyse dat relaties ook worden gemodereerd door de geografische omvang: de bomensoortenrijkdom was significant positief gerelateerd aan de koolstofvoorraad, maar hoewel deze relatie sterk was op lokale tot regionale ruimtelijke schalen werd deze zwakker en bijna nul op continentale en intercontinentale schalen. In de vervolganalyses van **Hoofdstuk 3** is geïllustreerd hoe de geografische omvang relaties tussen plantendiversiteit en ecosysteemdiensten zou kunnen modereren door de hoeveelheid bemonsterde milieuheterogeniteit. Voor elke biogeografische regio van Amazonia bleek de soortenrijkdom positief gerelateerd aan de koolstofvoorraad. Als echter alle regio's samen worden genomen en geanalyseerd, hierdoor een grotere geografische omvang creërend, word de relatie negatief. Dit patroon leek op een bekende statistische paradox die een ‘Simpson-paradox’ wordt genoemd, en resultaten lieten zien dat deze paradox wordt veroorzaakt door koolstofvoorraadverschillen tussen de regio’s. Pas toen de verschillen in gemiddelde koolstofvoorraad tussen de regio’s werden verrekend, werd de relatie weer positief. In antwoord op de onderzoeksvraag levert dit proefschrift nieuw bewijs dat zowel plotgrootte als de geografische omvang relaties tussen plantendiversiteit en ecosysteemdiensten in volgroeide tropische bossen kunnen modereren. Verder onderzoek is nodig om op te helderen hoe patronen in milieuheterogeniteit de koolstofvoorraadverschillen tussen de biogeografische regio’s kunnen veroorzaken en hoe relaties tussen plantendiversiteit en andere ecosysteemdiensten in tropische bossen kunnen worden beïnvloed door milieuheterogeniteit.

Invloed van ecologische en sociaaleconomische factoren op de voorziening van NTFP’s (OV 4)

De voorziening van plantaardige NTFP’s wordt bepaald door een complex samenspel van ecologische en sociaaleconomische factoren zoals de productie van planten, de toegang van - en het transport door oogsters, en de vraag naar het product. Sociaaleconomische factoren bepalen het gebruik van een ecosysteemdienst (de stroom), beïnvloeden daardoor de relaties tussen plantendiversiteit en de ecosysteemdienst maar daarmee mogelijk ook de (toekomstige) voorraad van de dienst. Aangezien er een algemeen gebrek aan kennis bestaat over het samenspel van ecologische en sociaaleconomische factoren bij ecosysteemdiensten, is de vraag wat de relaties zijn tussen plantendiversiteit, de NTFP-voorraad (abundantie van NTFP producerende soorten), het potentiële NTFP-aanbod, en het daadwerkelijke NTFP-gebruik (de stroom). In **Hoofdstuk 4** werd gevonden dat een combinatie van taxonomische en structurele plantendiversiteitsindicatoren meer dan de helft (> 55%) van de waargenomen variatie in de commercieel relevante NTFP-voorraad in de Surinaamse tropische bossen kon verklaren. In het bijzonder werd de NTFP-voorraad voor een groot deel bepaald door een select aantal plantensoorten met hoge abundanties, die als 'NTFP-oligarchen' werden bestempeld. Hun aanwezigheid bleek sterk geassocieerd te zijn met specifieke floristische samenstellingen die waren gerelateerd aan verschillende bostypen. Echter, met behulp van het theoretische raamwerk dat is ontwikkeld in **Hoofdstuk 5** bleek dat de NTFP-voorraad niet gerelateerd was aan de NTFP-stroom, suggererend dat bostypen met hoge NTFP-voorraden niet noodzakelijkerwijs intensiever worden gebruikt. Ten slotte vond Hoofdstuk 5 geen bewijs van systematische overexploitatie van de plantaardige NTFP-voorraad in Suriname, terwijl oogsters van deze NTFP's een redelijk inkomen ontvingen met de verkoop aan de markt in Paramaribo in vergelijking met het nationale minimumloon. Dit suggereert dat het op de markt brengen van plantaardige NTFP's afkomstig uit volgroeide tropische bossen in Suriname in principe een stimulans zou kunnen zijn voor de lokale belanghebbenden om de 'bossen overeind te houden' (*'keeping forests standing'*). In antwoord op de onderzoeksvraag ontdekte dit proefschrift significante relaties tussen plantendiversiteit en de NTFP-voorraad (de abundantie van NTFP producerende soorten), maar het toonde ook voor het eerst aan dat de relevante plantendiversiteitsindicatoren waarschijnlijk niet systematisch gerelateerd zijn aan de NTFP-stroom (het gebruik). Het nieuw ontwikkelde theoretische raamwerk illustreert dat sociaaleconomische factoren, zoals de totale vraag naar het product, de kosten in verband met de oogst, het transport en de verwerking, en aanwezige sociale oogstregels bepalen welke planten zullen worden geoogst, en uiteindelijk zo bepalen welk deel van de aanwezige plantendiversiteit relevant is voor de NTFP-voorziening. Bovendien levert dit proefschrift ondersteuning voor het 'behoud-door-gebruik-paradigma' ('*conservation-through-use-paradigm*') door enerzijds bewijs te vinden dat de NTFP-stroom voor commercieel gebruik ecologisch duurzaam kan zijn in termen van stabiel blijvende NTFP-voorraden, terwijl het anderzijds ook voldoende economische prikkels biedt aan belanghebbenden om tropische bossen te behouden. Alhoewel het onduidelijk blijft welke sociaaleconomische factoren relevant zijn voor andere tropische gebieden, kan het ontwikkelde theoretische raamwerk elders worden toegepast om de relevante componenten van NTFP-stromen te identificeren.

Door de bomen het bos zien

Dit proefschrift richtte zich op het ‘door de bomen het bos zien’ in de relaties tussen plantendiversiteit en ecosysteemdiensten: het vinden van generieke patronen en de implicaties hiervan voor het behoud van tropische bossen. In de synthese van **Hoofdstuk 6** werden drie relevante ‘bospatronen’ ontwaard. Ten eerste, aangezien er (alleen) een consistente positieve relatie werd gevonden tussen bomensoortenrijkdom en koolstofvoorraad in de tropische bossen van Amazonia is het aannemelijk dat het beschermen van koolstofrijke tropische bossen ook hoge concentraties van boom- en boompalmsoorten beschermt, maar niet noodzakelijkerwijs ook grote voorraden hout of NTFP’s. Ten tweede, aangezien tropische bossen met belangrijke hout- en NTFP-producerende plantensoorten zich vaak bleken te bevinden in de buurt van lokale gemeenschappen die in het bos wonen, zou de bescherming van dergelijke bossen baat kunnen hebben bij het instellen van gebruiksrechten voor lokale gemeenschappen, bijvoorbeeld in de vorm van een gemeenschapsbos of inheems grondgebied. Ten derde en als laatste, zorgt het commerciële gebruik van plantaardige NTFP's in Suriname voor een redelijk inkomen voor oogsters terwijl er geen tekenen van systematische negatieve effecten op de NTFP-voorraden werden gevonden. Dit suggereert dat het commerciële gebruik van tropische bos-NTFP's ecologisch duurzaam kan zijn en in die vorm een economische stimulans zou kunnen vormen om bossen overeind te houden. Tot slot verwacht de auteur van dit proefschrift dat er nog veel meer ‘bospatronen’ verborgen zijn die verdere wetenschappelijke aandacht behoeven. Alleen wanneer meer kennis over de relaties tussen plantendiversiteit en ecosysteemdiensten wordt ontsloten kunnen we het volledige potentieel van natuurbescherming gericht op ecosysteemdiensten beoordelen op haar merites voor het behoud van tropische bossen. De auteur acht het waarschijnlijk dat een combinatie van op ecosysteemdiensten gebaseerde - en andere vormen van natuurbescherming nodig zal zijn om de schatkamer van biodiversiteit die het tropische bos vertegenwoordigt, te kunnen beschermen.

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2016. I remember the first time arriving at Suriname, Zanderij airport (PBM). During the last few minutes of the descent, the green carpet lining Suriname has turned into a dense field of broccoli heads. The broccoli heads differ slightly in their height, the colour of their foliage, the width of their crown. I suddenly realize that most of these slightly different broccoli individuals are likely to represent unique palm or tree species. Lacking any field identification experience at the time, the thought strikes me: "How am I ever going to carry out successful research about the plant diversity in these tropical forests If I cannot even recognize a single tree or palm species – let alone the other plants growing in these forests?!". Fast forward six years later. I am working as a curator of plant diversity at the Utrecht University Botanic Gardens, tasked with identifying all sorts of tropical (and non-tropical) plant species from all over the world. Clearly, I managed to pick up some experience along the way and the research has come to a good end (this PhD Thesis being the proof of the pudding).

I am immensely grateful for the opportunity to carry out this PhD research. I have learned an uncountable number of skills and have enjoyed an inexpressible number of experiences. For example, I value the chance to have spent many months in the literal awe-inspiring tropical forests of the Guiana Shield, getting to know the plants and other beings living in and around them. Or the freedom to become really experienced with programming in R and with ecological statistics. I could not have thought that I would even like these two subjects! Above all, I need to thank the Dutch tax payer for indirectly financing the bulk of this research and thereby helping me gain my valuable experiences. I will try to recompense them by putting my newly acquired skill and expertise to good use.

This thesis would not have been possible without the encouragement, help and shared experiences of others. With the risk of forgetting to mention some of these people, I would like to take the opportunity to acknowledge and thank them, where possible in their native language.

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ABOUT THE AUTHOR

Gijs Steur was born in 1986. He attended high school at the Goese Lyceum in Goes, Zeeland, the Netherlands, with the idea of becoming a teacher. After graduating just above average for his senior general secondary education (HAVO) exam in 2003, he decided he actually would like to know more about the system of the world, or 'biology in general'. On the advice of his biology teacher, he started to pursue academic training in biology. To bridge the knowledge gap he had let grow in the previous years, he restarted school following a pre-university education (VWO), graduating with presentable marks in 2005. During his first year of the Bachelor programme of Biology at Utrecht University between 2005-2006 he was thinking of perhaps pursuing 'something' in ethology. However, the many interesting plant courses, his active involvement in the Utrecht Biologists Association (UBV), and numerous teaching jobs in the curriculum of Biology, ultimately set out a different course. Between 2010 and 2013, during his Master of Science programme at Utrecht University, he played around with the idea with pursuing a career in nature conservation or ecology. At the same time, he helped to develop several courses concerning plants and their diversity, including an introductory course on the Dutch flora and a course on plant diversity and nature conservation. After graduating cum laude in 2013, he started as a teaching and research assistant at the Copernicus Institute of Sustainable Development. At the Copernicus Institute, he consolidated his interests in plant diversity and nature conservation in the form of ecosystem services. In 2016 he won a personal grant at the Dutch Research Council (NWO) and Utrecht University funded Graduate Programme 'Nature Conservation, Management and Restoration' to start his PhD research on the relationships between plant diversity and ecosystem services in tropical forests. In 2020, he continued his research at the Utrecht University Botanic Gardens, working as a curator and as a teacher and researcher on plant diversity and ecosystem services, where he has finished this thesis.