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

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A B S T R A C T

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.

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 and Wiersum, 2005; Timko et al., 2010; Shackleton and Pandey, 2014; van Andel et al., 2015; Shackleton et al., 2018). 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 and 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 and Wiersum, 2005; Sills et al., 2011; Shackleton and Pandey, 2014) and for relationships

between ecosystem services and biodiversity (Díaz et al., 2005; Cardinale et al., 2012; 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 (Myers et al., 2000; Corlett, 2016; Asaad et al., 2017; Barlow et al., 2018). It is also assumed that species-rich ecosystems provide a larger quantity and higher quality of ecosystem services (Díaz et al., 2005; Cardinale et al., 2012; 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 (Sheil and Wunder, 2002; Belcher et al., 2005; Belcher and Schreckenberg, 2007; 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 (Peters et al., 1989; Johnston, 1998; 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 (ter Steege et al., 2013, 2019a; Morera-Beita et al., 2019). 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 permanently flooded 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).

2. Material and methods

2.1. 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 previously unpublished data on 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 (Fig. 1) and lie within a minimum rectangular spatial extent of ca. 44 $\times$ 10^3 km2. 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). Hydrology and physiognomy of the vegetation surveys included terra firme forests (n = 138), seasonally flooded 'igapó' forests (n = 70) and permanently flooded 'swamp' forests (n = 79). 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 impressions of 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 and 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
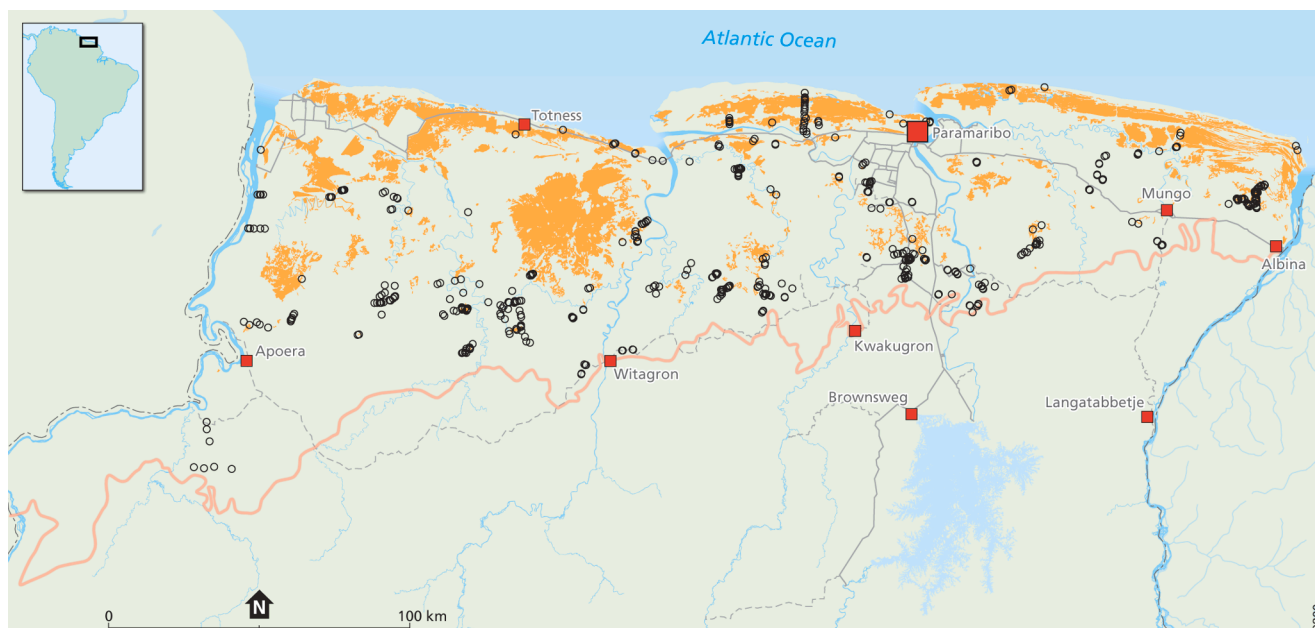
Fig. 1. Map showing the locations of the 287 lowland tropical forest plots (black circles) of the Teunissen dataset in the coastal region of Northern Suriname. The coastal region of Suriname includes the young and old coastal plains and the savanna belt (i.e. the area between the Atlantic Ocean, the 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. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

harvest of NIMOS, SBB and UNIQUE, 2017). More information on the Teunissen database, dataset and digitization is included in Appendix A.

2.2. NTFP abundance

For each plot in the Teunissen database, we calculated the cumulative NTFP abundance ($\sum$ number of stems of NTFP species). The selection of NTFP species included only wild plant species that produce NTFPs that are 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 Appendix B for more information). From the combined list, 58 wild and commercially relevant woody NTFP species were present across the plots (Appendix B, Table B.1). Their cumulative abundance ranged from 0 to 120 stems per 0.04 ha, with a mean of 18.49 (SD 22.78) (See also Appendix C, Table C.1).

2.3. 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, and 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, for each plot 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 (($\sum$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 Appendix C.

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 Appendix C.

2.4. 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 Appendix D.

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 et al., 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 a model including only an intercept (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 Appendix G). 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.

3. Results

3.1. 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 1). However, the relationship explained little variation in NTFP abundance (i.e. 8.8% pseudo-R^2; see Appendix E, Output E.1), indicating that other variables also determined NTFP abundance.

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 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 Appendix E, Table E.1).

Table 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 Appendix E, Output E.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)

3.2. Predicting NTFP abundance with taxonomic and structural diversity indicators

Multiple regression analyses showed that a combination of non-NTFP species richness, Camargo evenness, Simpson diversity, stem density and average maximum diameter with their interactions could optimally significantly explain about one-third, i.e. 37.2%, of the variation in NTFP abundance (pseudo-R^2; Table 2, unrestricted model). The optimized multiple regression model restricted to main variables (i.e. excluding interactions) explained 23.3% of the variation in NTFP abundance (pseudo-R^2; Table 2, restricted model), indicating that interactions between the tested plant diversity indicators explained about one-seventh of the total 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 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 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 variation in NTFP abundance (Table 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 Appendix F, Fig. F.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. <50 stems, the relationship between non-NTFP Camargo evenness and NTFP abundance was positive but at high non-NTFP stem densities, i.e. >50 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 <50 stems), the main effect of non-NTFP Camargo evenness on the NTFP abundance was positive (Table 2, right column).

3.3. 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 being based on at least five samples (Appendix G, Fig. G.1). Most of these floristic clusters also corresponded to a dominant hydrology and physiognomy. 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 Appendix G, 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 < 0.000; Appendix G, Output G.1). Post-hoc Tukey contrasts showed that the mean NTFP abundance differed significantly between the floristic clusters (Appendix G, Output G.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 (Appendix G, Fig. G.2). For example, clusters #1 to #4 had the lowest mean NTFP abundance and clusters #9 to #11 has 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 < 0.000; Appendix G, Output G.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 variation in NTFP abundance, 18.6% more than the same model without floristic clusters (i.e. 55.9% − 37.2% Pseudo-R^2; Appendix G, Output G.4). Similar results were found when we added the floristic clusters as dummy variables to the optimized restricted model (See Appendix G, Outputs G.5 & G.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.

Table 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 Appendix F, Outputs F.1-F.2 and Figures F.1-F.2 for full model details.

Predictor variable	Unrestricted Model			Restricted model			
	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%			

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

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* (Appendix H, Table H.1; species also listed in Table 3).

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 < 0.000; Appendix H, Output H.1; Post-hoc Tukey contrasts shown in Appendix H, Output H.2). The pattern in ranks of mean *E. oleracea* abundance between the floristic clusters resembled that of the ranks of mean NTFP abundance (Appendix H, Output H.2; compare Figs. H.1 to G.2). For example, clusters #9 to #11 had the highest mean *E. oleracea* abundance as well as the highest mean NTFP abundance.

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.

4.1. 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.

4.2. 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; er Steege et al., 2019a, 2019b; 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 forest 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.

4.3. 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 as a considerate part of the variation in NTFP abundance that can be expected for 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 (Peters et al., 1989; Johnston, 1998; van Andel, 2000), it would be expected that NTFP abundance is generally negatively related to the evenness of species abundance. However, in these 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.

4.4. 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; van 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 et al., 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.

4.5. 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 both 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 (Harvey et al., 2010; Asaad et al., 2017), 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 (van Andel et al., 2003, 2007; Shackleton and Pandey, 2014; 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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CRediT authorship contribution statement

G. Steur: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing, Visualization, Funding acquisition. **R.W. Verburg:** Conceptualization, Writing - review & editing, Supervision. **M.J. Wassen:** Writing - review & editing, Supervision, Funding acquisition. **P.A. Teunissen:** Resources. **P.A. Verweij:** Conceptualization, Writing - review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2020.107202.

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