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Review Paper

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

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ABSTRACT

This paper 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 paper 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.

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; Millennium Ecosystem Assessment, 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; Millennium Ecosystem Assessment, 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, Norris, & Fitter, 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, Schmid, & Balvanera, 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). 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). This is relevant as plant diversity is expected to show strong relationships with the provisioning of ecosystem services because it

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represents the primary producers and the building blocks of all terrestrial ecosystems, including tropical forests. 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, 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, Willis, & Field, 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 biodiversity-ecosystem service 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 varying administrative units which differ in spatial scale, such as national parks, provinces and nations boundaries (Malinga, Gordon, Jewitt, & Lindborg, 2015; 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 in 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 quantitative statistical analysis of the effects of geographical extent on specific relationships between plant diversity indicators and ecosystem services in tropical forests.

This paper 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 paper 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-analyses 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. 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;

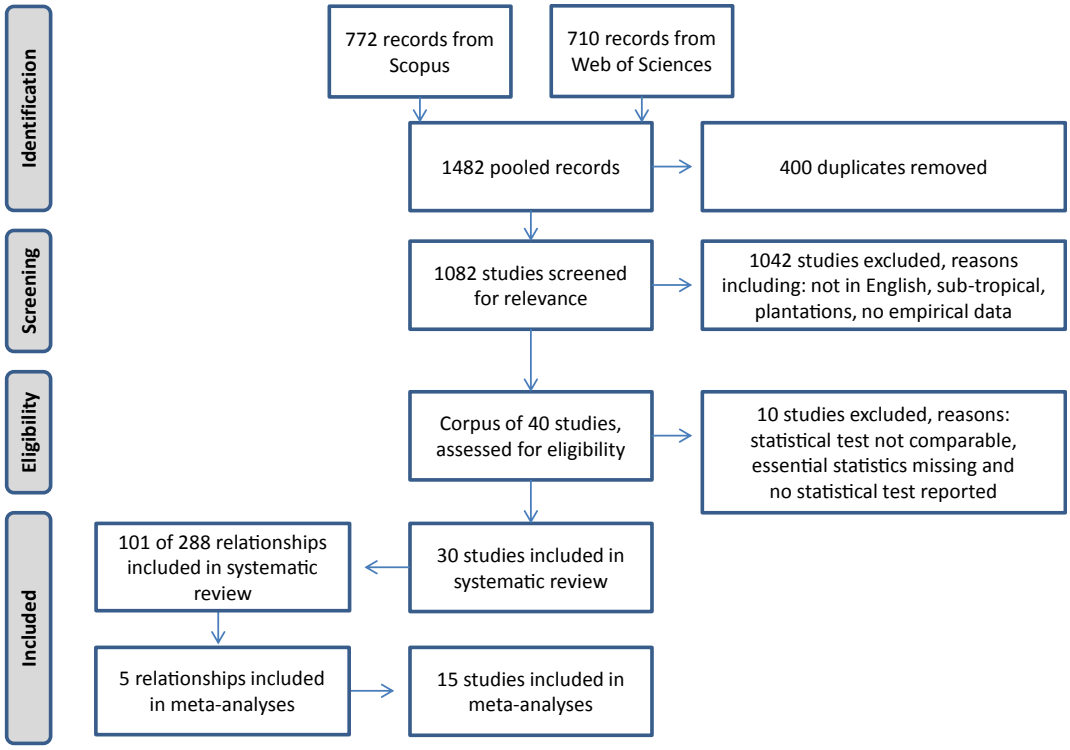

Fig. 1. PRISMA information flow diagram of the systematic review and meta-analysis (after Moher et al., 2009).

Fig. 1 shows the flow of information; Fig. S1.2 in Appendix S1 shows an infographic of the methods used in the systematic review and meta-analyses; Appendix S1.7 shows the PRISMA checklist for this study.

2.1. 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 Fig. S1.1). We managed and screened records in the programme R (R Core Team, 2018), with package 'stringr' (Wickham, 2018). We selected only peer-reviewed articles and excluded non-English records based on the meta-information provided by the search engines. Of the 1082 records, 27, i.e. 2.5%, were not written or not partly written in English. To check the eligibility of the records, we downloaded the full texts with the R package '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 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 having been clear cut. On the basis of the scoping information, we summarized that the forests that we 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 were selectively logged (either presently by local communities or, in most cases, had been 14 to 22 years ago) to forests that had been regenerating after having been 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 Appendix S2.

This process resulted in a corpus of 40 relevant studies for which data was extracted and stored separately by two authors 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 Appendix S1); (3) the type of statistical analysis and outcome; and (4) the spatial covariables, including the plot size (here either the grain size or the focal scale, i.e. the area size to which the samples were standardized prior to analysis, both in ha) and the geographical extent (the area that encompasses the plots compared in a relationship, in km^2; after Whittaker, 2010; Scheiner et al., 2011; see Fig. S1.2 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 Appendix S1 for more information on data extraction, storage and pre-analysis). The corpus database is available as a separate Excel file in Appendix S4.

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 binomial t-tests under the pragmatic assumption that outcomes were independent of each other. Specifically, for each relationship 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, or the other way around. 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.

2.2. 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 Appendix S5). 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 reported 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 or 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 available r to avoid double counting of data 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), in variance between effect sizes within each study (level 2), and in 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). The amount of heterogeneity among overall effect sizes was tested using the Q-statistic.

2.3. 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 (after Knapp and Hartung, 2003) to determine 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.

2.4. Sensitivity analyses

For all meta-analysis models we analysed the sensitivity of the model 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 meta-analyses were carried out using the R package 'metafor' (Viechtbauer, 2010). Additional visual output was created by using the packages 'gmodels', 'ggrepel' and 'ggplot2' (Slowikowski, 2018; Warnes, Bolker, Lumley, & Johnston, 2018; Wickham, 2016). More information on the meta-analyses and sensitivity analyses is included in Appendix S1.

3. Results

3.1. 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 1). Only 1 study covered all three ecosystem services. In these 30 studies, carbon stock was quantified as biomass or carbon 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 (9 and 1 out of the 27 studies, respectively). Timber stock was quantified as the volume of timber tree species that had a diameter at breast height larger than 45 cm (m^3 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 abundance 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-

Table 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.

Plant diversity dimension	Ecosystem service and aspect											
	Carbon				Timber				Non-Timber Forest Products			
	Stock		Flow		Stock		Flow		Stock		Flow	
	27 source studies		3 source studies		1 source study		1 source study		3 source studies		3 source studies	
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

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 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 to be found by to chance (highlighted in bold in Table 1; See Appendix S5 Table S5.1). 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 stock 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.

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 S5.2). A relatively large number of functional indicators were used compared to the number of taxonomic and structural indicators (37 vs 13 and 16, respectively). Further analysis showed that the 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

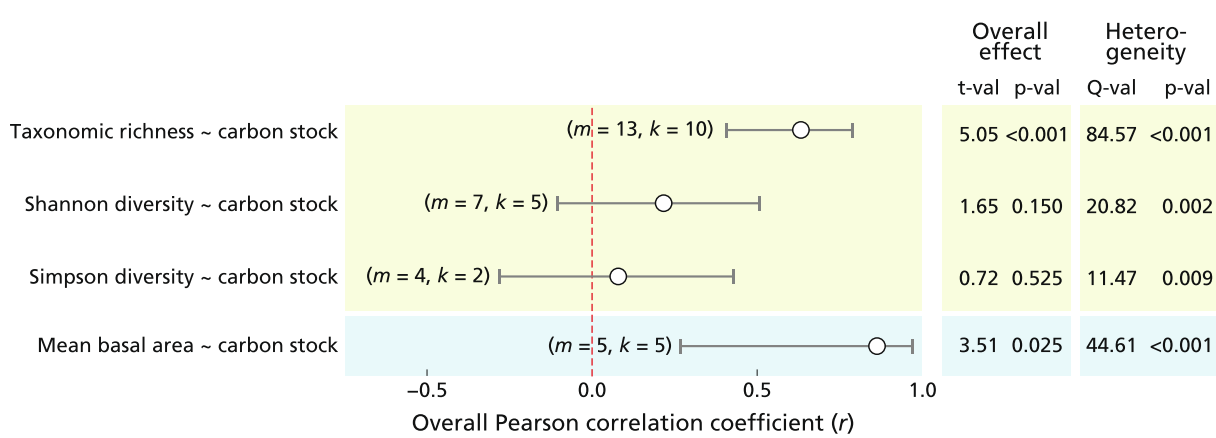

Fig. 2. Overall effect sizes back-transformed to overall Pearson correlation coefficients (white circles) with their 95% confidence intervals (grey bars) for the five relationships in tropical forests for which a sufficient dataset was available. Shown in brackets are the number of effect sizes used, '*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 to 3 decimals).

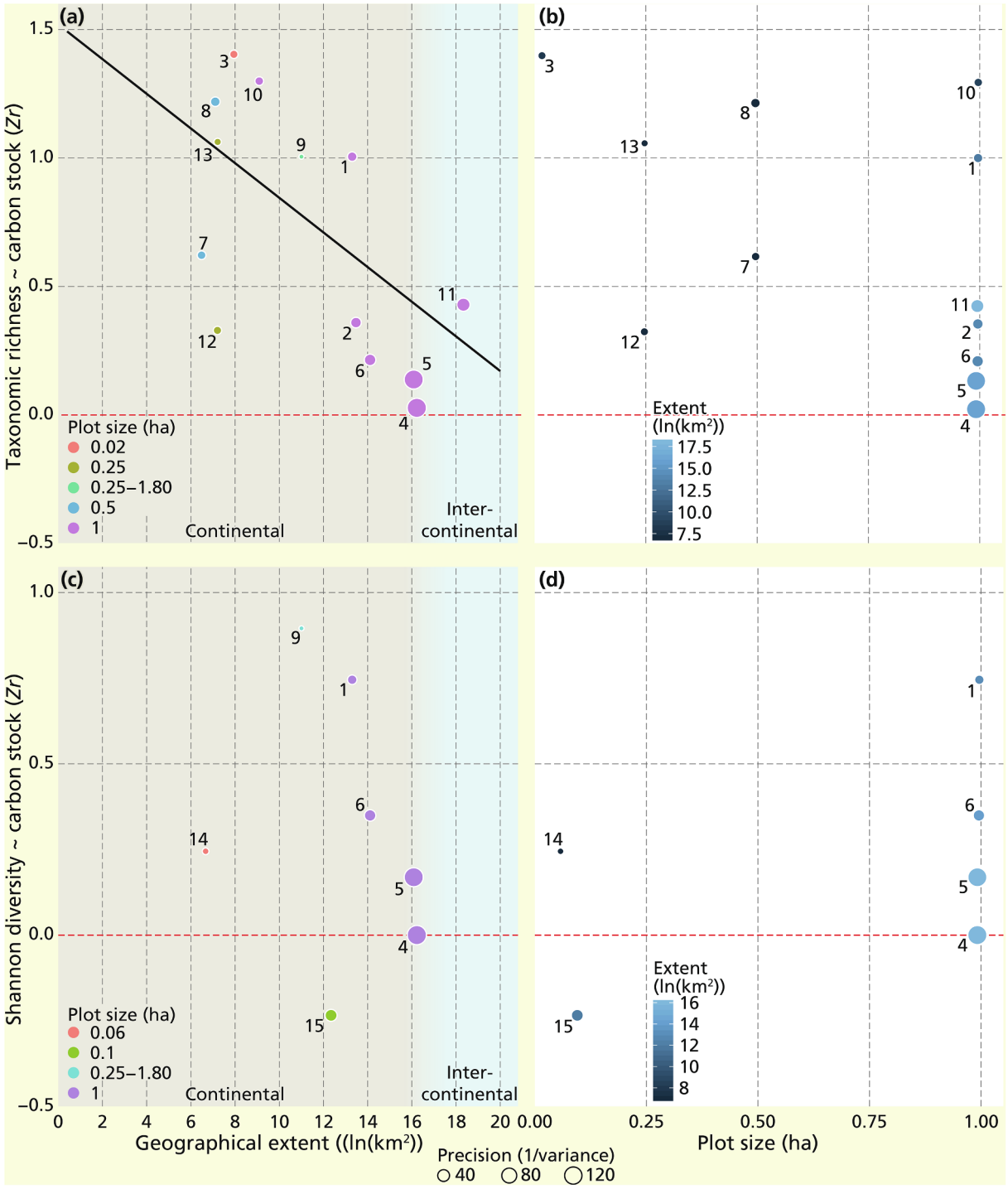

Fig. 3. Effect sizes (*Zr*, Z-transformed Pearson correlation coefficients) of the relationships between tree taxonomic richness and carbon stock in tropical forests against ln-transformed geographical extent (in km^2; $m = 13$; panel a) and plot size (in ha; $m = 12$; panel b), and the relationships 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 geographical extents up to the continental scale; the light blue area in the graph represents geographical extents at inter-continental scales. In panel a, the significant linear relationship between ln-transformed geographical extent and effect sizes is shown with a black line.

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 S5.3). Although most relationship subsets showed uniform directions, most subsets were also too small to make generalizations (i.e. 14 subsets had two samples, 3 had three samples and 6 had four samples).

3.2. 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 subsets 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 correcting for 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 Appendix S6). 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 (Fig. 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 Appendix S6). However, the relationship between mean stand density and carbon stock was 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 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 Appendix S6, S6.1.8).

In all three statistically robust relationships we detected significant heterogeneity (Fig. 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 Appendix S6).

3.3. 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 (102.5×10^6 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 Fig. 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 not affected by the impacts of potential publication bias (analyses given in Appendix S6). The moderating effect of the geographical extent appears to be strongest in study area sizes up to approximately 1×10^6 km^2 (this corresponds to a ca. 14 ln-transformed geographical extent or a Euclidian distance between plots of 1000 km; see Fig. S6.1.4 and Fig. 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 Fig. 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 Fig. 3c and d).

4. Discussion

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

The meta-analysis of 13 outcomes of the correlation between carbon stock and tree taxonomic richness sourced from 10 studies across the tropics yielded a robust positive correlation. 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 1×10^6 km^2 (i.e. regional scales), even though at these extents floristic composition and carbon stocks can show significant variation with abiotic variables (Guitet, Pélissier, Brunaux, Jaouen, & Sabatier, 2015; Poorter et al., 2015; Slik et al., 2013). For example, it has been shown that at geographical extents of approximately 0.6×10^6 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 around 54×10^3 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 to statistically quantify the effect of geographical extent on the relationship between tropical forest carbon stock and tree taxonomic richness. Although previous studies have suggested that geographical extent may have a significant effect on the aforementioned relationship, the specific effect had not been quantified (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 1.5×10^6, 11.4×10^6 and 13.1×10^6 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). This positive correlation decreases with increasing ln-transformed geographical extent, which approaches zero at extents of about 1×10^6 km^2 (regional scales) and above (continental to pan-tropical scales). However, 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.

Because our meta-analyses were limited by data availability, for example by the restriction to only linear relationships and a lack of access to the primary data, it was not possible to directly investigate the variables underlying the observed pan-tropical relationship between tree species richness and carbon stock and explain the positive correlation or the effect of geographical extent. Nevertheless, it is possible to synthesize potential explanations on the basis of the literature. 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 (1.5×10^6 to 13.1×10^6 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. $\geq$ 0.5 ha, see Fig. 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 (i.e. < 0.5 ha; 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*; Appendix 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 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 the relationships concerning Shannon and Simpson diversity, 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 positive correlation 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, Godoy, Turner, & Harvey, 2011; Harvey, Dickson, & Kormos, 2010; Scharlemann et al., 2010). However, up to now findings of such win-win situations have been limited because maps that identify areas of spatial overlap at scales finer than the global scale are currently not available and because 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, Webb, & Adams, 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.

4.2. 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 S5.3). 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 considerable 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 (Appendix S4). 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 that were 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%, it can be expected that including relevant non-English terms in search queries will 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 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. 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.

4.3. 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.

5. Data statement

The corpus database used in the meta-analyses is provided in the Supporting Information.

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Author contributions

G.S. prepared the database and P.A.V. double coded the database. G.S. analysed the data with input from P.A.V. and R.W.V. G.S. drafted the manuscript, and all authors commented on the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoser.2020.101107.

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