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Title: Biodiversity in species, traits and structure determines carbon stocks and uptake in tropical forests

Running title: Biodiversity determines carbon stocks and uptake

Authors:

Masha T. van der Sande[1,2,3*], Lourens Poorter[1], Lammert Kooistra[4], Patricia Balvanera[5], Kirsten Thonicke[6], Jill Thompson[7], Eric J. M. M. Arets[2], Nashieli Garcia Alaniz[8], Laurence Jones[9], Francisco Mora[5], Tuyeni H. Mwampamba[5], Terry Parr[10], and Marielos Peña-Claros[1]

[1] Forest Ecology and Forest Management Group, Wageningen University and Research, PO Box 47, 6700 AA Wageningen, The Netherlands

[2] Wageningen Environmental Research (Alterra), Wageningen University and Research, PO Box 47, 6700 AA Wageningen, The Netherlands

[3] Instituto Boliviano de Investigación Forestal, Km 9 al Norte, El Vallecito, Santa Cruz de la Sierra, Bolivia

[4] Laboratory of Geo-Information Science and Remote Sensing, Wageningen University, P.O. Box 47, 6700 AA Wageningen, The Netherlands

[5] Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Morelia, Mexico.

[6] Earth System Analysis, Potsdam Institute for Climate Impact Research e.V. (PIK), Telegrafenberg A31, D-14473 Potsdam, Germany

[7] Centre for Ecology & Hydrology, Bush Estate, Penicuik, Midlothian, EH26 0QB, UK

[8] CONABIO, National Commission for the Knowledge and Use of Biodiversity, Mexico DF, Mexico

[9] Centre for Ecology and Hydrology, Environment Centre Wales, Deiniol Road, Bangor, LL57 2UW, UK

[10] Centre for Ecology and Hydrology, Lancaster Environment Centre, Library Avenue, Bailrigg, Lancaster, LA1 4AP, UK

[*] Corresponding author:

Masha T. van der Sande

Phone no.: +49 341 9733117

Email: masha.vandersande@idiv.de, masha.vandersande@ufz.de

ABSTRACT

Impacts of climate change require that society urgently develops ways to reduce amounts of carbon in the atmosphere. Tropical forests present an important opportunity, as they take up and store large amounts of carbon. It is often suggested that forests with high biodiversity have large stocks and high rates of carbon uptake. Evidence is, however, scattered across geographic areas and scales, and it remains unclear whether biodiversity is just a co-benefit or also a requirement for the maintenance of carbon stocks and uptake. Here, we perform a quantitative review of empirical studies that analysed the relationships between plant biodiversity attributes and carbon stocks and carbon uptake in tropical forests. Our results show that biodiversity attributes related to species, traits or structure significantly affect carbon stocks or uptake in 64% of the evaluated relationships. Average vegetation attributes (community-mean traits and structural attributes) are more important for carbon stocks, whereas variability in vegetation attributes (i.e. taxonomic diversity) is important for both carbon stocks and uptake. Thus, different attributes of biodiversity have complementary effects on carbon stocks and uptake. These biodiversity effects tend to be more often significant in mature forests at broad spatial scales than in disturbed forests at local spatial scales. Biodiversity effects are also more often significant when confounding variables are not included in the analyses, highlighting the importance of performing a comprehensive analysis, which adequately accounts for environmental drivers. In summary, biodiversity is not only a co-benefit, but also a requirement for short- and long-term maintenance of carbon stocks and enhancement of uptake. Climate change policies should therefore include the maintenance of multiple attributes of biodiversity as an essential requirement to achieve long-term climate change mitigation goals.

Keywords: biodiversity-ecosystem functioning, biomass dynamics, biomass growth, climate change mitigation, functional traits, species diversity, tropical forest

INTRODUCTION

The global increase in emissions of greenhouse gases such as CO_2 has led to rapid changes in climate, occurring at unprecedented rates compared to the last 1300 years (IPCC 2014). Simultaneously, anthropogenic disturbances have resulted in a loss of species diversity, with the current rate of extinctions being at least 1000 times higher than natural extinction rates (De Vos *et al.* 2015). These changes have raised international concerns and stimulated initiatives such as the Kyoto Protocol to reduce emissions and combat climate change, and the Convention on Biological Diversity to conserve and sustainably use biodiversity. During the climate change conference of the United Nations Framework Convention on Climate Change (UNFCCC) in December 2015 in Paris, 196 countries agreed to keep global warming below 2 °C (United Nations 2015). To achieve this goal, countries need to implement effective mitigation strategies.

Tropical forests are particularly important for climate change mitigation and biodiversity conservation initiatives. They are crucial ecosystems of both carbon stocks and biodiversity; they host around 47,000 tree species (Slik *et al.* 2015), store 25% of global terrestrial carbon in plant biomass (Bonan 2008) and account for 34% of gross primary productivity (Beer *et al.* 2010). The Reduced Emissions from Deforestation and forest Degradation (REDD+) policy, UNFCCC's most relevant policy for carbon mitigation in the tropics, recognizes the importance of conserving biodiversity as a co-benefit of conserving carbon to avoid unintended negative effects for biodiversity (Phelps, Webb, *et al.* 2012). The question remains, however, whether biodiversity also directly contributes to, and is thus a

86 requirement for, maintaining carbon stocks and carbon uptake (hereafter termed CSU, where
87 'uptake' mostly refers to biomass growth, see Glossary; Balvanera *et al.* 2006; Díaz *et al.*
88 2009).

89 Various ecological theories predict that biodiversity is a requirement for CSU. Here,
90 we refer to 'biodiversity' as general vegetation attributes, including aspects that represent
91 variability in vegetation attributes (e.g., species and trait diversity) as well as aspects that
92 represent average vegetation attributes (e.g., community-mean trait values and vegetation
93 structure, Glossary, Table 1). The niche complementarity theory (Tilman 1999) predicts that
94 diversity in the number and functioning (i.e., trait diversity or functional diversity) of species
95 should increase resource use efficiency and therefore lead to greater carbon uptake, and
96 hence, greater carbon accumulation over time and larger carbon stocks per area of forest
97 (Chisholm *et al.* 2013). Species diversity may also enhance CSU through facilitation among
98 species (Hooper *et al.* 2005) and through reduced impact of species-specific pathogens
99 (Schnitzer *et al.* 2011). Contrary to these diversity theories, the mass-ratio theory (Grime
100 1998) predicts that the most dominant species and their characteristics, rather than the
101 diversity of species, determine ecosystem processes. In addition to the effects of number and
102 type of species, the structural attributes of the vegetation (such as tree density and plot basal
103 area) and/or environmental conditions (such as climate and soil fertility) also strongly
104 determine CSU (Poorter *et al.* 2015). Finally, the nature of biodiversity-CSU relationships
105 could change across spatial and temporal scales. For example, at short temporal scales, greater
106 redundancy among species – and hence a lower importance of species and trait diversity –
107 may occur than at long temporal scales (Cardinale 2012).

108 Evidence for an effect of biodiversity on CSU has been provided by local-scale
109 experiments and empirical field studies carried out mainly in temperate grasslands or other
110 relatively simple ecosystems (Balvanera *et al.* 2006, Tilman *et al.* 2001, Fraser *et al.* 2015,

111 Paquette & Messier 2011). Furthermore, several reviews have been carried out but these are
112 dominated by results from temperate grasslands (e.g., Hooper *et al.* 2012) or focused on
113 forests in general and are mostly conceptual (e.g., Díaz *et al.* 2009). Yet, evidence from
114 highly diverse and structurally complex tropical forests has only recently become available
115 and is still fragmented (e.g., Bunker *et al.* 2005, Poorter *et al.* 2015). This evidence is
116 therefore insufficient at present to inform on the design and implementation of policies such
117 as REDD+.

118 Here, we perform a quantitative review on empirical studies that evaluate the
119 relationships of tree biodiversity with carbon stocks and uptake (CSU) in tropical forests. We
120 focus on different attributes of biodiversity (taxonomic diversity, trait diversity, community-
121 mean traits, and structural attributes; Table 1) related to community-level vegetation
122 attributes. These attributes describe the average as well as the variability in vegetation
123 attributes. Furthermore, we focus on stocks and uptake separately because they may be driven
124 by different biodiversity attributes. We evaluate how different biodiversity attributes relate to
125 CSU, and how the relationship of biodiversity attributes with CSU is influenced by spatial
126 scale, management intensity, and analytical approach. We then synthesize this information to
127 evaluate under which conditions biodiversity is important for CSU and which ecological
128 theories can explain this. Finally, we provide recommendations on the policy implications of
129 our findings and on the next steps required to improve our understanding of biodiversity-CSU
130 relationships in tropical forests.

131

132

133 **METHODS**

134

135 **Selection of studies**

We searched the literature for peer-reviewed studies as well as yet unpublished studies that were part of the ROBIN-project (Role Of Biodiversity In climate change mitigation, http://robinproject.info/home/) that evaluate biodiversity effects on CSU (see Appendix S1 for details on study selection). We also considered the effect of environment, if reported in the study. As our unit of replication, we used each reported relationship between a biodiversity attribute group or environmental attribute and CSU. Hence, if a study tested the effect of one biodiversity attribute on one component of CSU, then this study yielded one relationship, but if the study tested for multiple biodiversity attributes and/or multiple CSU components, then this study yielded multiple relationships. To increase the number of relationships assessed per group and better understand the role of biodiversity attributes in carbon stocks and the uptake of carbon, we grouped the different measures of CSU into 'carbon stocks' (including above- and belowground carbon or biomass stocks, and soil organic matter or soil carbon) and 'carbon uptake' (including (litter) productivity, (net) growth, and loss through tree mortality) (Appendix S2).

Quantitative review of studies

We found 38 empirical studies that describe 165 relationships between one or more of the four biodiversity attributes and carbon stocks (64 relationships) and/or uptake (101 relationships) in tropical forests (Table 1, and see Appendix S2 and S3 for details about the studies). The studies mainly came from the Neotropics (68%), but also from Africa (8%), Asia (5%) and across multiple continents (18%). For both carbon stocks and uptake, we evaluated whether biodiversity effects were positive, negative, both positive and negative (which can occur when multiple measures of the same biodiversity attribute are tested) or neutral (i.e., not significant). For community-mean trait effects, we did not distinguish

between positive and negative because the relevance of the direction depends on the trait considered (i.e., they were classified as either “significant” or “neutral”).

In many cases, studies used multiple variables within the same biodiversity attribute group to predict CSU (for example, taxonomic richness and Shannon diversity). In these cases, we summarized the multiple variables within one biodiversity attribute group as one relationship in the following way; in case both positive and non-significant effects were found, then we gave the relation a ‘positive’. Similarly, in case both negative and non-significant effects were found, then the relation was given a ‘negative’. Finally, when it showed both positive and negative (and non-significant) relationships, it was given a ‘positive and negative’. We neglected the non-significant effects in these cases because the absolute amount of variables in each biodiversity attribute group may not be representative, as authors will pre-select some variables and/or not report variables that show non-significant effects. The relationship between a biodiversity attribute group and a CSU component was classed as non-significant when all tested effects were not significant. We evaluated the effect of biodiversity attributes on carbon stocks and uptake by calculating percentages of relationships that were significant. Note that ‘biodiversity attributes’ refer both to variability in vegetation attributes (i.e. taxonomic and trait diversity) and to average vegetation attributes (i.e. community-mean traits and structural attributes).

Statistical analyses

Using logistic regression models (with a significance level of 0.05, using the glm function of the stats package of the R software version 3.3.1, R Core Team 2016) we also evaluated whether the probability of a significant relationship between one of the biodiversity attributes and carbon stocks or uptake was statistically different from the probability of a non-significant relationship. For taxonomic diversity, trait diversity and structural attributes we

185 performed three different tests. First, we tested whether biodiversity attributes have, in
186 general, a significant effect on CSU. We did so by testing whether the probability of a
187 significant relationship, either *positive and/or negative*, was statistically different from the
188 probability of a non-significant relationship. Second, we tested whether biodiversity attributes
189 have in general a significant positive effect on CSU. We did so by testing whether the
190 probability of a *positive* relationship was statistically different from the probability of no
191 significant positive relationship (i.e., a neutral or negative relationship). Third, we tested
192 whether biodiversity attributes have in general a significant negative effect on CSU. We did
193 so by testing whether the probability of a significant *negative* relationship was different from
194 no significant negative relationship (i.e., a neutral or positive relationship). The relationships
195 that were both positive and negative (due to multiple indices of the same biodiversity attribute
196 group) were included in test two and three. For community-mean traits and environmental
197 conditions, we only performed the first test (i.e., all significant effects combined).
198 Per test, the relationships that were considered significant were given a '1' (i.e., all
199 significant relationships in test 1, significantly positive ones in test two, and significantly
200 negative ones in test three), while the relationships that were considered non-significant were
201 given a '0'. The intercept of the logistic regression models represents the 'probability',
202 defined as the log of the odds. The log of the odds is the log of the probability of being equal
203 to 1 (i.e., for significant relationships) divided by the probability of being equal to 0 (i.e., for
204 non-significant relationships). If the probability of significant and non-significant relationship
205 is equal, then the odds is 0.5/0.5 = 1, and hence the log odds is log(1) = 0. If the intercept is
206 significantly higher than 0 (i.e., the 2.5% confidence interval (CI) is higher than 0), then there
207 is a significant probability of a significant relationship. If the intercept is significantly lower
208 than 0 (i.e., the 97.5% CI is lower than 0), then there is a significant probability of a non-
209 significant relationship.

To correct for possible differences in precision among studies, we added a weight factor as the square root of the total sampled area (the average plot size multiplied by the number of plots, Appendix S2). For the studies from which we could not reconstruct the plot size, we used the average plot size across the other studies. Because of the variety of analyses and effect sizes used among studies, and because often standard errors were missing, we could not perform a more formal meta-analysis. Details about the analyses are presented in Table 2.

RESULTS & DISCUSSION

We performed a literature review to evaluate how different biodiversity attributes relate to carbon stocks and uptake (CSU) in tropical forests. Generally, taxonomic diversity, community-mean traits and structural attributes were better predictors for CSU than trait diversity (Fig. 1, Table 2), and they were more often significantly related to carbon stocks than carbon uptake. Carbon stocks were most often predicted by community-mean traits and forest structure, and carbon uptake was most often predicted by forest structure and taxonomic diversity, although negative relationships were more common for carbon uptake than for carbon stocks.

Biodiversity–CSU relationships

Carbon stocks were significantly positively related to taxonomic diversity in 42% of the relationships, both positively and negatively in 21% of the relationships (which could occur when multiple indices for taxonomic diversity were tested, Fig. 1), and negatively in only 5% of the relationships, supporting diversity theories such as niche complementarity. However,

these results also indicate that some studies find no relationship or a negative relationship between taxonomic diversity and carbon stocks, suggesting that diversity mechanisms may not universally apply throughout tropical forests. The diversity of trait values only rarely had a positive effect (17%) or both positive and negative effects (33%) on carbon stocks. Trait diversity is a complex measure that is constructed using a variety of traits of which only a subset may be important for CSU (Butterfield & Suding 2013). Probably for this reason, a non-significant effect of trait diversity on CSU was often observed. Carbon stocks were significantly affected by community-mean trait values in 100% of the relationships (Fig. 1), providing support for Grime's mass-ratio theory (Grime 1998). These results were also confirmed by the results of the logistic regressions (Table 2); taxonomic diversity and community-mean traits had significant effects on carbon stocks.

In comparison to carbon stocks, carbon uptake was more often significantly and positively related to taxonomic diversity (53% for uptake vs. 41% for stocks), but less often when including the studies that find both positive and negative relationships (57% vs. 63%). Moreover, carbon uptake was less often significantly related to community-mean traits (47% for uptake vs. 100% for stocks). These results are also supported by the logistic regression models, which showed a significant positive effect of taxonomic diversity on carbon uptake (Table 2) but a non-significant effect of community-mean traits on carbon uptake (Fig. 1, Table 2). In agreement with these results, the studies that present standardized correlation or regression coefficients (β) show that the effect of community-mean traits is strong for carbon stocks (β up to 0.6), and that the effect of species diversity can be strong for both carbon stocks and carbon uptake (β up to 0.3-0.4). Hence, community-mean traits are more important for carbon stocks, whereas taxonomic diversity is important for both carbon stocks and uptake.

Most reviewed studies support the idea that stands with high diversity have higher complementary in resource use and can therefore be more productive and store more biomass, and that stands dominated by tall and dense-wooded trees (as determined by community-mean traits) have higher carbon stocks. Studies that report significant effects of community-mean traits on carbon uptake show that, in most cases, acquisitive trait values (e.g., high specific leaf area) increase carbon uptake (e.g., Finegan *et al.* 2015). However, some studies on sites with stronger limitation of water and/or soil nutrients showed that acquisitive trait values decreased carbon uptake, possibly because such traits result in higher respiration and lower survival rates in harsh conditions, and consequently lead to lower total carbon gain (e.g., Prado-Junior *et al.* 2016, van der Sande, *et al.* in review).

Structural attributes (e.g., tree density and plot basal area, Table 1) had a consistent positive effect on carbon stocks in 78% of the relationships. Structural attributes, often indicating forest density, were positively related to carbon stocks because denser forests may have more and larger stems, and since most carbon is held in stems, this directly increases carbon stocks (e.g., Poorter *et al.* 2015). Although a relationship between structural attributes and carbon stocks is expected because they are used to calculate carbon stocks, it is important to understand the relative importance of structural attributes and biodiversity in determining CSU. Contrary to the positive effect on carbon stocks, structural attributes had mixed effects on carbon uptake; they were positively related to carbon uptake in 44% of the relationships and negatively related in 33% of the relationships. Two mechanisms can possibly explain the positive and negative effects of structural attributes on carbon uptake. On the one hand, a large quantity of leafy vegetation could lead to high productivity because many leaves are available to assimilate carbon (e.g., Peh 2009). On the other hand, large plants and dense vegetation that compete for resources and space could reduce stand-level carbon uptake because less light, water and nutrients are available for growth of other individuals (e.g.,

284 Phillips *et al.* 1994). Structural attributes were significantly positively related to carbon
285 stocks, and significantly related to carbon uptake only when combining all studies that find
286 significant relationships, and was not significantly positively or negatively related to carbon
287 uptake (Fig. 1, Table 2). In agreement with these results, the studies reported generally larger
288 effect sizes of structural attributes for carbon stocks (β up to 0.9) than for carbon uptake (β up
289 to 0.5-0.6).

290 Overall, we found that biodiversity attributes generally better predict carbon stocks
291 than carbon uptake. Carbon stocks are most often significantly related to biodiversity
292 attributes that relate to *average* vegetation attributes (i.e. the community-mean traits and
293 structural attributes), whereas carbon uptake is most often significantly positively related to
294 biodiversity attributes that relate to *variability* in vegetation attributes (i.e. taxonomic
295 diversity). These results also agree with additional recent publications showing that
296 community-mean traits are more important for carbon stocks than taxonomic diversity
297 (Sullivan *et al.* 2017), and that taxonomic diversity is important for carbon uptake (Liang *et*
298 *al.* 2016). The different results of carbon stocks versus uptake also indicate that these are not
299 necessarily positively correlated. An increase in carbon uptake could lead to higher carbon
300 build-up and thus higher stocks (Chisholm *et al.* 2013), but it could also be that dynamic
301 forests with high carbon uptake have a high abundance of fast-growing species with short
302 lifespan and high turnover, which would decrease overall carbon stocks (Keeling & Phillips
303 2007).

304 When combining all biodiversity attributes, then biodiversity had a significant effect
305 on carbon stocks and uptake (Table 2). This indicates that biodiversity in general is important,
306 but that we need to understand better which biodiversity attribute matters for which ecosystem
307 process (e.g., carbon stocks vs. uptake) and under what conditions. Across our studies,
308 environmental variables also had a significant effect on both carbon stocks (82% of the

relationships, Fig. 1, Table 2) and uptake (79%). Where significant, the reviewed studies show that standardized effect size (β) of environmental variables was up to 0.67, indicating that environmental conditions may be at least as important as biodiversity attributes in explaining CSU.

We need to be aware of a possible publication bias due to the fact that studies that find significant effects of biodiversity attributes on CSU may be more often published than studies that find a non-significant relationship. Possible publication bias could be identified by evaluating how the probability of a significant relationship depends on the sample size of the study (in our case the total sampled forest area). Without publication bias, a larger sampled area would increase the probability of finding significant relationships between biodiversity attributes and CSU. For the studies in this review, however, we found no relationship between total sampled area and the probability of significant relationships (Appendix S4), suggesting that the publications may be biased towards studies with significant relationships. To advance science, we advocate moving from a culture in which we only valorise and publish novel papers with spectacular results, to one where we valorise and publish all solid research.

Causes of variation: scale, management intensity and analytical approach

Effects of biodiversity on CSU can depend on factors related to spatial scale, forest management, and the analytical approach used. We therefore evaluated how the biodiversity-CSU relationship depends on these factors. We summarized this only in a descriptive way, as in most cases the sample sizes were too small (see Fig. 2) to do a formal statistical analysis.

Biodiversity-CSU relationship at different spatial scales – Ecological processes operate at different spatial scales (McGill 2010). At local spatial scales (i.e., within one plot or study site) with low variation in abiotic conditions, species-specific interactions may be important, whereas at broader spatial scales (i.e., among multiple sites) with large variation in

environmental conditions, environmental filtering may be more important (Laliberté *et al.* 2009). Therefore, the importance of biodiversity attributes and environmental conditions for CSU may vary with spatial scale. We found that for both carbon stocks and uptake, the effects of taxonomic diversity, vegetation structure and environmental conditions were more often important at broader scales (i.e., all scales beyond local site-studies, e.g. Chisholm *et al.* 2013) than at local scales (e.g., van der Sande *et al.* 2017a, Fig. 2a and b). Effects of community-mean traits on carbon uptake were more often important across sites at regional and global scales than within sites at local scales, whereas community-mean trait effects on carbon stocks were not sensitive to scale. Trait diversity was more often important for stocks and uptake at local scales. It could be, however, that part of the differences between broad and local scales is due to the generally larger sample size and sampled forest area in broad-scale studies (on average 217 ha, compared to 9 ha for local-scale studies). Interestingly, our results do not agree with studies that evaluate different plots sizes, which find stronger relationships in small compared to large plots (Chisholm *et al.* 2013, Poorter *et al.* 2015). This indicates that scale effects depend on the measure of spatial scale considered – extent (used here) or grain size – and that we need studies that explicitly evaluate the role of different measures of scale on biodiversity-CSU relationships. Hence, the scale-dependence of the biodiversity-CSU relationship depends on the biodiversity attribute, but seems to be generally stronger at broader spatial extents and at small grain sizes (e.g. plot size).

Biodiversity-CSU relationship at different management intensities – We hypothesized that biodiversity effects on CSU may be more frequently found in disturbed forests and plantations, where overall diversity and functional redundancy may be lower than in mature forests without recent anthropogenic disturbance (see also Hooper *et al.* 2005). We found, however, that biodiversity was less often significantly related to CSU in plantations and disturbed forests than in mature forests, especially for carbon uptake (Fig. 2c and d). Possibly,

359 the strong differences in light availability among forests with different disturbance intensities,
360 and among plantations with different stem densities, may be so important for CSU that it
361 overwhelms the effect of taxonomic diversity. Alternatively, lower diversity and structural
362 complexity in plantations and disturbed forests could lead to less complementarity and thus
363 lower importance of diversity. Strong diversity effects on CSU have been widely documented
364 by theoretical, experimental, and observational studies mainly in temperate grasslands
365 (Tilman *et al.* 2014). Here, we show that this relationship also applies to tropical plantations,
366 disturbed forests, and especially to mature tropical forests.

367 *Biodiversity-CSU relationship evaluated by different analytical approaches* – The
368 studies included in this review used a range of analytical approaches that are likely to affect
369 the observed biodiversity-CSU relationship. For example, independent effects of biodiversity
370 on CSU can only be evaluated when controlling for possible confounding factors, such as
371 variation in environmental conditions. In the studies reviewed here, biodiversity attributes
372 more frequently affected CSU when analysed separately than when analysed together with
373 other environmental variables, as for example in a multiple regression analysis (Fig. 2e and f).
374 This suggests that some of the biodiversity-CSU relationships are correlative associations
375 rather than causal relationships, although a large part of the relationships still shows effects of
376 biodiversity attributes on CSU when environmental conditions are accounted for (on average
377 83% for stocks and 41% for uptake). Hence, for a full understanding of underlying drivers and
378 independent biodiversity effects on CSU, a more complete and mechanistic framework is
379 needed that includes multiple biodiversity and environmental drivers and their mutual
380 relationships.

381

382 **Synthesis of biodiversity–CSU relationships**

How important is biodiversity for CSU? – A significant relationship between biodiversity attributes and carbon stocks or uptake was observed in 64% of the relationships. Therefore, these results extend the findings from experimental studies and temperate ecosystems that **biodiversity, defined as both the average and variability in vegetation attributes, matter for ecosystem functioning in highly diverse tropical forests**.

Which biodiversity attributes matter for CSU and under what conditions? – Our results indicate that not only species diversity, but a suite of biodiversity attributes (taxonomic and trait diversity, community-mean trait values, and structural attributes, Table 1) are important for CSU. *Variability* in vegetation attributes (species and trait diversity) most often positively related with carbon uptake, whereas *average* vegetation attributes (community-mean traits and structural attributes) most often related with carbon stocks. Variability in vegetation attributes and average vegetation attributes have thus complementary effects on CSU. Our results also indicate that the biodiversity-CSU relationship is stronger at larger spatial scales, possibly because of greater variation in species diversity and other biodiversity attributes across these larger environmental gradients. Furthermore, the biodiversity-CSU relationship was strongest in mature forests, possibly because of higher diversity and structural complexity leading to greater complementarity. These results, however, are based on relatively few studies, indicating that we need more detailed understanding of which biodiversity attributes matter, for which CSU variables, and under what conditions. In summary, **the biodiversity-CSU relationship tends to be weaker in disturbed forests and at local scales, and stronger in mature forests and across larger (e.g. continental) spatial scales.**

Which ecological theories explain biodiversity effects on CSU? – In this study, we evaluated several ecological theories that predict how biodiversity can affect CSU (Table 1), and found that both the quantity (i.e., structural attributes) and also the quality (i.e., taxonomic

or trait diversity or community-mean traits) of the vegetation can affect CSU. The traits of the dominant species were most important for carbon stocks, which is in line with the mass ratio theory (Grime 1998). Taxonomic diversity was most important for carbon uptake, which could be explained by a range of diversity theories (i.e., niche complementarity, facilitation, or dilution of the effects of host specific pathogens). Modelling studies have also shown that, over the long term (Sakschewski *et al.* 2016) and at a large spatial scales (Loreau *et al.* 2003), biodiversity enhances ecosystem resilience in the face of environmental change (the insurance theory, Yachi and Loreau 1999), which assures long-term stability of CSU. Only with sufficient variation of species and ecological strategies in the plant community does the community have the potential to adapt to environmental change, in which the rare species of today could become the dominant species in the future and thus maintain ecosystem functioning over time. Furthermore, remote sensing studies indicate that biodiversity is also important for CSU at larger spatial scales (i.e., beyond single site studies), where variation in environmental conditions and biodiversity attributes increases (e.g., Murray *et al.* 2015). Hence, **our review and modelling studies highlight three mechanistic reasons (diversity, mass-ratio, and insurance effect) that could explain why biodiversity matters for carbon stocks and uptake at multiple spatial and temporal scales**.

What are the next research steps for improving understanding of biodiversity-CSU relationships? – We identify three important steps for further research. First, long-term monitoring of forests that cover a range of spatial scales, environmental conditions and land-use intensities will be necessary for a better understanding of biodiversity-CSU relationships in the face of global change (Balvanera *et al.* 2014). Second, to separate the contributions of biodiversity attributes on CSU from those of environmental conditions, comprehensive and mechanistic analytical frameworks are needed. Such frameworks should aim to disentangle different mechanisms underlying CSU and incorporate possible confounding variables. Third,

433 a suite of complementary approaches, such as experiments, empirical field studies, remote
434 sensing, and modelling can best address the needs for a better understanding of biodiversity-
435 CSU relationships (van der Sande *et al.* 2017b). The mechanisms behind real-world
436 biodiversity-CSU relationships can best be evaluated using empirical data, as presented in this
437 review. To move beyond these predominantly local-scale and short-term studies, we could
438 make additional use of remote sensing to evaluate the biodiversity-CSU relationship at larger
439 spatial scales (e.g., Asner *et al.* 2015), and of ecosystem modelling to explore the relationship
440 at longer temporal scales (e.g., Sakschewski *et al.* 2016). Integrating these approaches will
441 therefore lead to a more complete understanding of biodiversity-CSU relationships at various
442 spatial and temporal scales. Consequently, f**uture research on biodiversity-CSU should**
443 **focus on long-term forest monitoring, the use of comprehensive analytical approaches to**
444 **separate biodiversity from other effects on CSU, and on the combination of empirical,**
445 **remote sensing and ecosystem modelling approaches for a better understanding across**
446 **spatial and temporal scales**.
447
448 **POLICY IMPLICATIONS**
449
450 The findings in this review indicate that different attributes of biodiversity contribute to the
451 long-term conservation of carbon stocks and to the uptake of carbon from the atmosphere.
452 These findings have implications for policies related to biodiversity and carbon conservation
453 in tropical forests. We consider three that are particularly relevant.
454 First, forest-related carbon mitigation policies such as REDD+ would need to **move**
455 **beyond their current position where biodiversity is considered a 'nice to have' (i.e., a co-**
456 **benefit or add-on), towards incorporating biodiversity as a 'must have'**. Explicitly
457 including biodiversity ensures that climate mitigation and adaptation strategies are grounded

458 on ecosystem function, stability and resilience (Christophersen & Stahl 2011, Miles *et al.*
459 2010, Garcia-Alaniz *et al.* 2017), and that biodiversity conservation is not only based on
460 moral and ethical justifications. Moreover, it ensures the consideration of a wider range of
461 biodiversity attributes (e.g. traits versus species richness) in identifying priority areas (Phelps
462 et al 2012). Such an approach to REDD+ in which carbon and biodiversity are explicitly
463 combined could simultaneously protect up to 90% of carbon stocks and more than 90% of
464 biodiversity (Thomas *et al.* 2013).

465 Second, **biodiverse, carbon rich and productive forests should be given priority**
466 **under the REDD+ framework, especially when threatened by degradation or land-use**
467 **change**. Data on both carbon stocks and biodiversity attributes could be used to identify
468 priority REDD+ target areas, allowing alignment of global and national strategies aimed at
469 maximizing biodiversity and carbon conservation (Phelps, Friess, *et al.* 2012). To keep the
470 quantification of biodiversity cost-effective, remote sensing based methods, verified by
471 locally measured biodiversity, can be used to scale to larger areas (Asner 2015, Dutrieux *et al.*
472 in review). At the national scale, countries could prioritize protection of forests rich in carbon
473 and biodiversity in their Nationally Appropriate Mitigation Actions (NAMAs,
474 http://unfccc.int/focus/mitigation/items/7172.php). At the local scale, because policies
475 combining carbon and biodiversity conservation may have higher costs (Phelps, Webb, *et al.*
476 2012), community involvement, strengthening ownership, and the development of pro-
477 conservation local governance could reduce the costs of monitoring for REDD+ and sustain
478 long-term biodiversity and carbon conservation initiatives (Gardner *et al.* 2012).

479 Third, forest-related mitigation efforts should **recognize and incorporate a suite of**
480 **biodiversity attributes as a requirement to maintain and obtain carbon-rich, productive**
481 **and resilient systems**. Despite policy recognition that biodiversity refers to more than just
482 species richness, current forest-related carbon mitigation policies rarely incorporate other

483 measures of biodiversity, such as functional traits and community structure. Global and
484 national efforts to maintain and increase forest cover (through natural regeneration,
485 restoration, and land use systems that enhance tree cover) under national climate protection
486 plans, REDD+, the Bonn Challenge, the 2014 UN Declaration on Forests, and the Paris 2015
487 declaration initiatives could benefit from recognizing a suite of biodiversity attributes. This
488 would not only strengthen the justification for biodiversity considerations in REDD+, but it
489 would also promote a more-encompassing understanding of biodiversity and its role in
490 maintaining ecosystem functions such as carbon stocks and uptake. For example, carbon
491 stocks and uptake could be maximized through the selection of a large variety of species with
492 specific desirable traits, manipulated at a range of spatial scales. However, care should be
493 given to the fact that biodiversity attributes that increase carbon stocks are not necessarily the
494 same as the ones that increase carbon uptake, and that conserving carbon stocks and uptake
495 does not necessarily optimize other ecosystem services, or fully support biodiversity at other
496 trophic levels.
497 Consideration of these policy issues is necessary to realise the full potential of tropical
498 forests to mitigate climate change through optimizing biodiversity.
499

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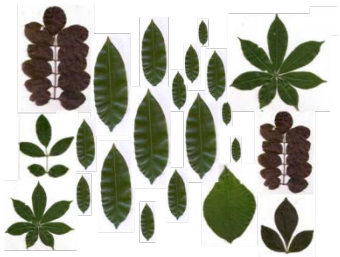
654 **Table 1:** Four biodiversity attributes (taxonomic diversity, trait diversity, community-mean traits, and structural attributes), the ecological

655 theories for which they are a proxy and ways to quantify those attributes. The forest structure diagram is obtained from Richards (1996).

656

Biodiversity attribute	**Taxonomic diversity**	**Trait diversity**	**Community-mean traits**	**Structural attributes**
Pictogram				
Ecological theory	Niche complementarity and insurance	Niche complementarity and insurance	Mass-ratio	Vegetation quantity, vegetation distribution
Examples to quantify biodiversity attributes	Taxonomic richness, Shannon-Wiener index, taxonomic evenness	Coefficient of variation in trait values (e.g., wood density, specific leaf area), multivariate trait richness, multivariate trait evenness	Community-mean traits (e.g., wood density, specific leaf area), trait values of the most dominant species	Basal area per hectare, tree density per hectare, canopy height

657 **Glossary**

Biodiversity	"The variability among living organisms from all sources including terrestrial, marine, and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, among species, and of ecosystems" (Convention on Biological Diversity).
Biodiversity attributes	Taxonomic diversity, trait diversity, community-mean trait values, and vegetation structural attributes (see also Table 1).
Carbon uptake	The fluxes in carbon per unit area per unit time (at the ecosystem level). Examples of positive uptake that are mostly included in this review are: total aboveground biomass increase, and growth of recruiting trees. Tree mortality is a negative flux, but was incorporated in some studies to evaluate the net carbon uptake. In this review, carbon uptake is mostly based on positive fluxes. Carbon uptake can be independent from carbon stocks.
Carbon stocks	The amount of carbon (or biomass) per unit area (at the ecosystem level). This carbon can be based on aboveground living biomass, (fine) root biomass, or soil organic matter.
Community-mean traits	Community average trait values, such as specific leaf area, wood density and leaf nitrogen concentration, often weighted by species' basal area or abundance.
Functional trait	Any measurable characteristic of an individual that is expected to have an effect on one or multiple specific ecosystem processes and is affected by environmental conditions.
Insurance theory	Species respond differently to environmental changes and thus a

	species-rich community insures long-term ecosystem functioning under environmental change (Yachi & Loreau 1999).
Mass-ratio theory	The most dominant species and their traits mostly determine ecosystem processes (Grime 1998). That is, the community-mean (e.g., of trait values, often weighted by species' abundance or basal area) more strongly determines ecosystem processes than diversity (in species or trait values) in the community.
Niche complementarity theory	Species are complementary in their resource acquisition and use. Therefore, high diversity (of species or traits) results in efficient acquisition and use at the community-level, and thus in high carbon stocks and uptake (Tilman 1999).
Remote sensing	Information on biodiversity and CSU obtained from a distance, e.g. by using aircrafts or satellites.
Resilience	The capacity of an ecosystem to return to the pre-condition state following a perturbation, including maintaining its essential characteristics taxonomic composition, structures, ecosystem functions, and process rates (Holling 1973).
Structural attributes	Community-average or community-total values of structural components of the community, such as plot basal area and average stem diameter.
Taxonomic diversity	Variability in species (e.g., the number or diversity) within a community.
Trait diversity (or functional trait diversity)	Variability in trait values within a community. This can be based on multivariate trait diversity and on the variability in individual traits (Table 1).

Table 2: Results from logistic regression models to evaluate the probability of a significant relationship between the attributes and carbon stocks or carbon uptake (CSU) as response variable. If the intercept is significantly positive (i.e., the 2.5% confidence interval (CI) is higher than 0), then the probability of obtaining a significant relationship is significantly higher than the probability of obtaining a non-significant relationship. If the intercept is significantly negative (i.e., the 97.5% CI is lower than 0), then the probability of obtaining a non-significant relationship is significantly higher than the probability of obtaining a significant relationship. An asterisk ('*') indicates the significant intercepts. For taxonomic diversity, trait diversity and structural attributes, we evaluated the probability of any significant relationship (i.e., either positive and/or negative), a positive relationship (+), and a negative relationship (-). For community-mean traits, all biodiversity attributes, and environmental conditions, we only evaluated the probability of any significant relationship. The column 'Effect is true or false' indicates whether the tested prediction is 'true' (i.e. significant positive intercept), is 'false' (i.e. significant negative intercept), or is not significant ('ns'). The relationship of community-mean traits and all biodiversity attributes with stocks have NAs because all reviewed relationships were significant, and of negative structural attributes effects on stocks because no relationships were significantly negative. For sample sizes and percentage significant relationships, see Fig. 2.

Carbon response variable	Biodiversity predictor variable	Intercept	2.5% CI	97.5% CI	Effect is true or false:
Stocks	Taxonomic diversity +/-	1.64*	1.16	2.19	true
	Taxonomic diversity +	1.42*	0.96	1.93	true
	Taxonomic diversity -	-1.46*	-1.97	-1.00	false
	Trait diversity +/-	-2.41*	-3.09	-1.84	false
	Trait diversity +	-0.32	-1.12	0.45	ns
	Trait diversity -	-0.49	-1.31	0.28	ns
	Community-mean traits	NA*	NA	NA	true
	Structural attributes +/-	3.67*	2.40	5.77	true
	Structural attributes +	3.67*	2.40	5.77	true
	Structural attributes -	NA	NA	NA	ns
	All biodiversity attributes	NA*	NA	NA	true
	Environmental conditions	2.00*	1.24	2.94	true
Uptake	Taxonomic diversity +/-	1.42*	1.03	1.84	true
	Taxonomic diversity +	0.94*	0.59	1.30	true
	Taxonomic diversity -	-2.32*	-2.93	-1.80	false

Trait diversity +/-	-2.54*	-3.12	-2.03	false
Trait diversity +	-1.55*	-2.24	-0.95	false
Trait diversity -	-3.08*	-4.54	-2.07	false
Community-mean traits	-0.66*	-1.15	-0.20	false
Structural attributes +/-	1.09*	0.58	1.64	true
Structural attributes +	-0.85*	-1.37	-0.37	false
Structural attributes -	-0.20	-0.67	0.25	ns
All biodiversity attributes	2.74*	2.16	3.44	true
Environmental conditions	1.33*	0.74	1.99	true

675

a) **Carbon stocks** b) **Carbon uptake**

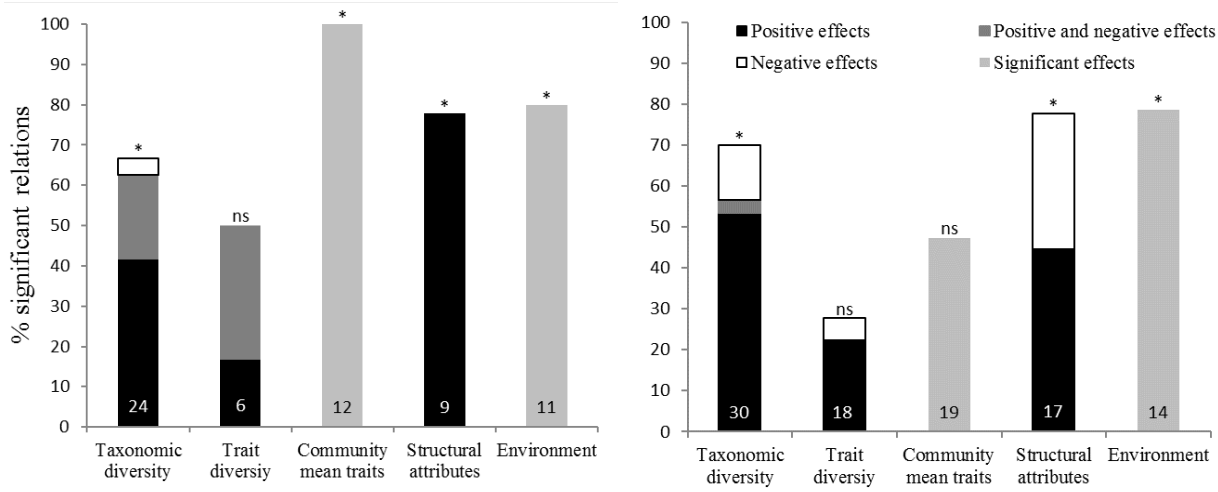


Figure 1: Percentage significant relationships (in the 38 reviewed studies) of biodiversity attributes on (a) carbon stocks and (b) carbon uptake (see Glossary for definition and Appendix S1 for more information). The bars represent the four biodiversity attributes (taxonomic diversity, trait diversity, community-mean traits, and forest structural attributes) and environment. The colours show the % relationships reporting a positive effect (black), negative effect (white), or both positive and negative (dark grey) effects. For community-mean traits and environment, significant effects were not separated into positive and negative (because these are only meaningful when elaborating on the meaning of the variable used); therefore, only the total percentage of significant relations are shown (light grey). The numbers inside each bar represent the total number of relationships evaluated. An asterisk ('*') on top of a bar means that the probability of obtaining a significant relationship (for positive and negative effects together) was statistically higher than the probability of obtaining a non-significant relationship. Conversely, an 'ns' on top of a bar means that the probability of obtaining a non-significant relationship is statistically higher than the probability of obtaining a significant relationship. For details on these statistics, see Table 2.

a) **Carbon stocks** b) **Carbon uptake**

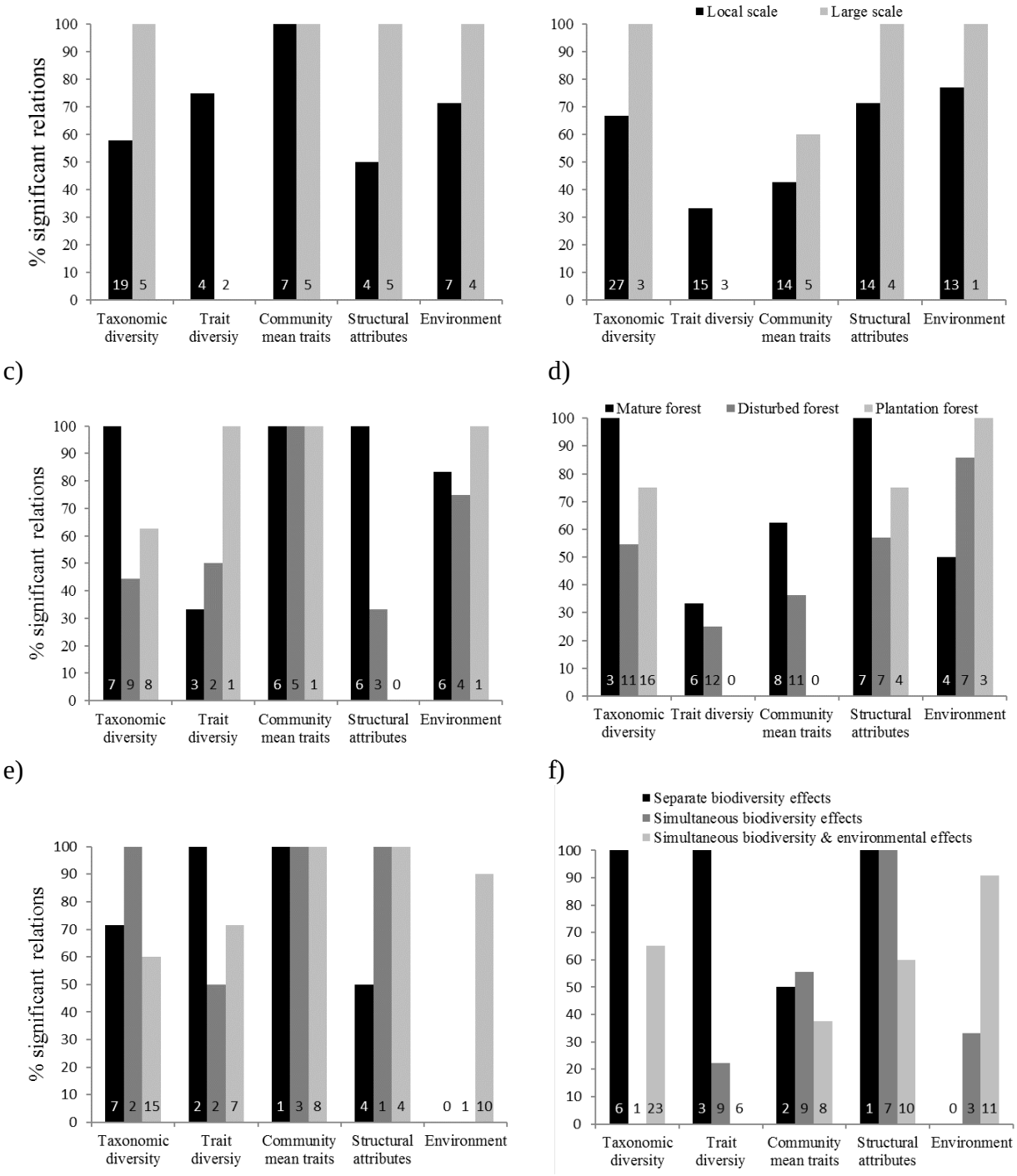


Figure 2: Percentage of relationships showing a *significant* effect of four biodiversity attribute groups (taxonomic diversity, trait diversity, community-mean traits and structural attributes) and environment on carbon stocks (all left panels) and carbon uptake (all right panels) in the 38 reviewed studies. Each pair of graphs shows a different grouping of studies: (a and b) by scale, comparing local and large spatial scale; (c and d) by management intensity, comparing plantation forests, disturbed forests and mature forests; and (e and f) by analytical

framework used in the studies: comparing frameworks that use all biodiversity attributes individually ('Separate biodiversity effects'), multiple biodiversity attributes simultaneously ('Simultaneous biodiversity effects'),and multiple biodiversity attributes and environmental variables simultaneously ('Simultaneous biodiversity & environmental effects'). The numbers in each bar indicate the number of relationships that were evaluated.