Functional trait diversity is a stronger predictor of multifunctionality than dominance: Evidence from an Afromontane forest in South Africa

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ABSTRACT

Studies on how biodiversity influences ecosystem multifunctionality (EMF) help elucidate ecological mechanisms (e.g. niche complementarity and selection) underlying provision of multiple ecosystem services. While it is acknowledged that biodiversity contributes to EMF, the relative importance of functional traits diversity (niche complementarity) and dominance (selection effects) for EMF needs further investigation. To address this gap, we analysed how tree species diversity influences EMF, using data on species functional traits (specific wood density, specific leaf area and maximum plant height) and four ecosystem functions (carbon storage, habitat quality, forage provision and rockfall protection) in an Afromontane forest in South Africa. We tested the hypotheses that (i) trait diversity rather than dominance would link species richness to EMF; and (ii) diversity rather than species richness effects would increase with the level of EMF. For all possible scenarios of EMF indices, functional trait diversity metrics, especially functional divergence and functional richness correlated positively with EMF. On the other hand, functional dominance also influenced EMF, but played limited role in mediating EMF response to species richness, when compared with functional diversity. Results further revealed that total diversity effects, not species richness effect, generally increased with the level of EMF. In summary, we show that species richness does not fully capture the functional contribution of different species. Compared to dominance, trait diversity had significant advantage in explaining biodiversity-EMF relationship, stressing a greater role of niche complementarity as mechanism underpinning delivery of multiple functions. We argue that functional dominance reflects more the competitive dominance of traits and species within a given community and therefore is more likely to have greater effects on single functions than on multifunctionality.

1. Introduction

The increasing rate of ecosystem degradation (Achard et al., 2002; Foley et al., 2007; Turner, 1996) added to the ongoing decline of ecosystem service delivery (De Groot et al., 2002; McMichael et al., 2005; Zarandian et al., 2016) have placed the debate on relationship between biodiversity and ecosystem functions and services high on research agendas (Kremen, 2005; MEA, 2005; Thompson et al., 2011). Although it has been widely acknowledged that biodiversity losses have a negative influence on the ecosystem functioning and the services delivered (Balvanera et al., 2006; Cardinale et al., 2012; Gamfeldt et al., 2013),

the current understanding of the mechanisms underlying the ecological processes is still limited (Paquette and Messier, 2011; Vilà et al., 2013), and several aspects are still subject of the scientific discussion (Balvanera et al., 2014; Lasky et al., 2014). Two well-debated mechanisms have been offered to explain the role of biodiversity in ecosystem functioning: selection effects or sampling effects (Huston, 1997) and niche complementarity/facilitation effects (Hector et al., 1999) (Box 1). Understanding these mechanisms is important to develop management strategies for safeguarding of both biodiversity and ecosystem services (Bhaskar et al., 2014; Cardinale et al., 2012) for current and future human well-being.

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Box 1

Niche complementarity and selection effects hypotheses

Niche complementarity and selection effects hypotheses are the two most common proposed mechanisms to explain diversity effects on ecosystem functioning (Hector et al., 1999; Loreau and Hector, 2001; Tilman et al., 1997). The selection effect hypothesis assumes that in ecosystem with higher diversity, there is a higher probability of the occurrence of dominant species or traits that influence ecosystem functioning. The niche complementarity hypothesis suggests that highly diverse ecosystems allow for a greater variety of functional traits with a likelihood of complementary structures, which provide opportunities for a more efficient resource utilization, thereby increasing ecosystem functions. An illustrative example of both hypotheses in forest ecosystems is that forest biomass and productivity can increase due to a few highly productive and dominant species (selection effects), or a better performance of all the species (e.g. shade and light demanding or deep and flat rooting species) through increased resource use efficiency (niche complementarity). Recent studies showed that both mechanisms can support the effects of diversity on ecosystem functioning through competitive exclusion (selection effects) and complementary use of resources by competitors (niche complementarity) (Carroll and Nisbet, 2015; Fargione et al., 2007; Mensah et al., 2016a; Mensah et al., 2018a).

Diversity metrics

Diversity is a multifaceted concept with different dimensions (and metrics) of biological variability, e.g., taxonomic dimension (species richness, Shannon diversity, Pielou evenness, Simpson index, etc.), structural dimension (structural diversity, or size class based diversity), functional dimension (trait-based diversity and dominance metrics such as functional richness, functional evenness, functional divergence, and functional dispersion, Rao quadratic entropy, trait community weight mean), phylogenetic dimension (referring to the minimum total length of all the phylogenetic branches required to span a given set of taxa on the phylogenetic tree). A review of these measures can be found in Magurran (1988) and Mouchet et al. (2010).

Although the role of biodiversity in ecosystem functioning and service delivery is being increasingly debated (Cardinale et al., 2012; Gamfeldt et al., 2013; Hector et al., 1999; Isbell et al., 2011), a majority of studies focused on individual ecosystem function such as biomass production and carbon storage (but see Jing et al., 2015; Lohbeck et al., 2016; Maestre et al., 2012; Wang and Banzhaf, 2018, for rare examples of case studies on multiple ecosystem functions). As pointed out by Trogisch et al. (2017) and Wang and Banzhaf (2018), biodiversity–ecosystem functioning research should study overall ecosystem functioning based on the simultaneous assessment of multiple functions and services, allowing complex interactions among organisms with tight interconnections of above- and belowground systems. Further, compared to artificial and grassland ecosystems, less effort has been devoted to highly complex dynamic systems such as forest ecosystems, especially in Africa, where vegetation diversity and complexity are unique. In addition, experimental research on the relationships between biodiversity and multiple ecosystem functions in forests began only in the last two decades (Scherer-Lorenzen et al., 2005), and little is known about how diversity metrics (see Box 1) other than species richness would affect ecosystem multifunctionality (EMF). Therefore, observational studies on biodiversity and EMF in multifunctional framework are still needed for a better understanding of the synergies and trade-off between functions and the role of species richness and associated diversity components in influencing multiple ecosystem functions.

A recurrent conclusion in the few diversity and EMF studies is that biodiversity effects increase with the level of EMF (Gamfeldt et al., 2008; Hector and Bagchi, 2007; Lefcheck et al., 2015; Zavaleta et al., 2010). In most of these studies, authors concluded that the magnitude

of the effect of biodiversity on EMF increased with increasing number of functions. In other words, as more functions are considered, greater species diversity is required to sustain these functions simultaneously. Species that are functionally unique will likely provide a specific function; species that are to some extent functionally equal are likely to contribute the same ecosystem function; therefore, all else being equal, a variety of functionally different species would provide a variety of functions, and it follows that adding functionally different species in a given ecosystem should increase the level of EMF. However, the effects of diversity on multiple ecosystem functions are not straightforward as in the case of single functions because multiple trophic groups coexist, and the functional effects of these trophic groups complement or oppose each other (Balvanera et al., 2014; Connor et al., 2016; Duffy et al., 2007; Jing et al., 2015; Naeem et al., 2000). For instance, conserving biodiversity and specifically less dense wood species with larger leaf area (acquisitive species) may increase biomass productivity and carbon storage (Hanif et al., 2019; Staples et al., 2019), without much impact on plant floral resources and pollination (Mensah et al., 2017b). That is to say, biodiversity importance may increase if functions of interest are fulfilled by functionally different species. Furthermore, whether diversity effects on EMF increase with the number of functions might also depend on the set of diversity metrics used. Species richness as the fundamental diversity metric used in most biodiversity studies, does not always reflect the whole functional spectrum relevant for specific functions. To determine whether biodiversity importance may increase with level of EMF, analytical methods should be undertaken beyond species richness and integrate functional traits based diversity, and test for ecological mechanisms underlying EMF (Huang et al., 2019; Le Bagousse-Pinguet et al., 2019).

Findings from biodiversity and EMF studies are reported mainly for biodiversity experiments based on communities of competing species, and it remains unclear whether these results are applicable to natural ecosystems especially forest ecosystems with great trophic complexity (Tilman et al., 2014). In this study, we investigated how tree species diversity influences EMF in an Afromontane natural forest ecosystem, which presents a specific case of complex dynamic system different from artificial and grassland ecosystems where many of diversity-EMF studies have been conducted. Ecosystem multifunctionality was assessed using an average index based on the mean of the scaled responses for each combination of two, three and the four functions of interest, leading to 11 possible scenarios of EMF index values. We asked the following questions:

(i) How does species richness influence EMF index value?
(ii) Which diversity components (functional diversity vs. functional dominance) and metrics (e.g. functional richness, functional evenness, functional divergence, trait community weight mean) better explain EMF? And what is the relative importance of these components, when accounting for possible local environmental effects? We predicted that functional diversity would promote EMF, as a consequence of functionally different species in the natural ecosystem;
(iii) Do diversity effects (species richness or total diversity effects) generally increase with the level of multifunctionality?; because functional effects of these species may complement or oppose each other, we expected that diversity and EMF relationships will be less sensitive to species richness than functional traits-based diversity.

2. Materials and methods

2.1. Study area and data

The data used in this study was collected in the Northern Mistbelt forest, an Afromontane forest type in South Africa. The specific area was located in the Woodbush De Hoek natural forest (23°50′S and 29°59′E) near Magoebaskloof. Further information about Woodbush De

Hoek natural forest can be found in recent studies by the authors (Mensah et al., 2016b, 2017a; Mensah et al., 2018c).

The data consisted of floristic information (tree species names, density, and diameter at breast height – dbh) from thirty 0.05 ha circular plots. Data on functional traits important to plant growth (specific wood density, specific leaf area, and maximum plant height) were obtained from publicly available sources (Kattge et al., 2011; Zanne et al., 2009). More specifically, data on species wood density were obtained from the Global Wood Density Database (Zanne et al., 2009) while specific leaf area and maximum plant height were extracted from TRY database (https://www.try-db.org/; (Kattge et al., 2011)). Information on honey bee forage resources (nectar value, pollen value and flowering time) for each plant species was obtained from Johannsmeier (2005). The flowering time refers to the period (number of months) within which the forage plants are expected to flower. Both nectar and pollen values were ranked from 0 (no nectar/pollen is available) to 4 (very good and major source), with 1, 2 and 3 being poor, minor to medium, and medium to good source of nectar/pollen, respectively (Johannsmeier, 2005).

2.2. Selected ecosystem functions

Four ecosystem functions were studied: aboveground carbon storage, habitat quality, bee forage provision and rockfall protection. These functions were selected to cover a broad spectrum of different aspects. For example, aboveground carbon storage was selected to account not only for timber (as provisioning ecosystem service, if harvested in natural forests), but also for the natural forests' potential in global climate regulation (as regulating ecosystem service). Habitat quality was identified as a function because it generally refers to the property of goodness of the ecosystem (Schuler et al., 2017), considered to be related to its capacity to supply ecosystem services. The interest in bee forage lies in its vital importance not only for bee colonies survivorship, but also for pollination of crops in agricultural farms, taking into account that most of the crops and fruits farms in the study area rely on beekeepers and honey bee colonies for pollination (Mensah et al., 2017b). Finally, forests play a protection role by preventing rockfall particularly in high elevation areas, through their tree crowns and density; they reduce both occurrence frequency and intensity of falling rocks after collisions with tree stems.

Aboveground carbon storage. We used the multispecies allometric biomass equation developed for Northern Mistbelt Forests (Mensah et al., 2016b) to calculate the aboveground biomass (AGB) for all individual trees present in the plots. The formula for the multispecies allometric biomass equation is:

$$AGB = 1.03 \times \exp(-2.69 + 0.69 \cdot \ln(SWD) + 0.95 \cdot \ln(DBH^2 \cdot H)) \qquad (1)$$

where AGB is the aboveground tree biomass in kilograms, SWD the species-specific wood density (g·cm^{-3}), DBH the diameter at breast height (cm), and H the total height (m). The values of the specific wood density were obtained from the global wood density database (Zanne et al., 2009). Wood density provides an indication whether a tree species favours a fast growth, often pioneer like growth, building conductive area rapidly with wood of lower density or rather a slow growth that typically results in heavier wood and could typically be attributed to climax species with longer life spans. Aboveground tree carbon (AGC) was then determined by calculating the aboveground biomass for each individual tree measured and by applying a carbon fraction of 0.5 (Mensah et al., 2016b). Tree carbon data was afterwards scaled up from tree to plot level.

Habitat quality. A habitat quality index (HbQ) was determined through a proxy of vertical structure at plot level. It has been shown that structural variability as expressed by tree height is correlated to habitat quality (Schuler et al., 2017). We thus estimated the vertical structural diversity by calculating the Shannon diversity index based on the number of individual stems in tree height classes, which were <

10 m, 10–20 m and > 20 m. The height class based Shannon diversity was calculated at plot level, as follows:

$$H_{Height\,j} = -\sum_{i=1}^{n} p_i \cdot \ln(p_i) \qquad (2)$$

where pi is the proportion of trees in the ith height class inside the jth sample plot. The higher the H_{Height}, the better the habitat quality.

Honey bee forage provision. A bee Forage Value Index (FVI) was defined for each plant species in each sample plot, based on the flowering time, nectar and pollen values, as in (Mensah et al., 2017b):

$$FVI_{ij} = RD_{ij} \times (N_i + P_i) \times \frac{FT_i}{12} \qquad (3)$$

where FVI_{ij} is the Forage Value Index of the ith honey bee plant species in the jth sample plot. N_i, P_i and FT_i are respectively the nectar value, pollen value and the flowering time (number of months) of the ith honey bee plant species. The value 12 in the above formula refers to the number of months in a year. RD_{ij} denotes the relative density of the ith honey bee plant species in the jth sample plot, and is calculated as follows (Curtis, 1982):

$$RD_{ij} = \frac{G_{ij}}{\sqrt{Dg_{ij}}} \qquad (4)$$

where G_{ij} and Dg_{ij} are the stem basal area and quadratic mean diameter of the ith honey bee plant species in the jth sample plot, respectively. We next calculated the plot level FVI () for all honey bee plant species by summing up the FVI_{ij} values as follows:

$$FVI_j = \sum_{i=1}^{s} FVI_{ij} \qquad (5)$$

where s is the total number of honey bee plant species and FVI_{ij} is the Forage value index of the ith honey bee plant species in the jth sample plot. The higher the value of FVI, the higher the honey bee forage provision function.

Rockfall protection. Mistbelt forests in South Africa are often referred to as Afromontane forest due to the altitudinal belt and slope gradient covered by their woody floristic vegetation. They are tall moist evergreen forests occurring at altitudes up to 1800 m, and consisting of many small, fragmented and widely distributed patches (Mensah et al., 2018b). Rockfall is a natural event in such mountain areas, but forests, through their crowns, help prevent water from splashing directly and washing the stones, thereby preventing rockfall. Forest trees together with moss, ferns and other ground vegetation, form a dense net of roots that provide physical stability to rocks. Furthermore, forest trees, depending on their size may also break or stop rocks that fall from higher altitude. Therefore, the frequency and intensity of rockfall may be regulated by tree size and density, particularly in stands with high stem density in several diameter classes (Schuler et al., 2017). To assess rockfall protection, we calculated a rockfall protection index (RFPI) using the following equation (Elkin et al., 2013; Schuler et al., 2017):

$$RFPI = 30 \times \theta_{d12} + 30 \times \theta_{d24} + 30 \times \theta_{d36} \qquad (6)$$

where θ_{d12}, θ_{d24} and θ_{d36} are the densities of trees per plot with DBH greater than 12, 24 and 36 cm, respectively. Similar to the three previous ecosystem functions, RFPI was computed at plot level to assess the potential of each plot in contributing to the protective role of the forests against rockfalls. The higher the value of the RFPI, the higher the rockfall protection function.

2.3. Ecosystem multifunctionality

There are several approaches to evaluate EMF: the species turnover approach, the single function approach, the averaging approach, the threshold approach and the multivariate modelling framework (Gamfeldt and Roger, 2017), although each approach has its specific weaknesses and strengths (Byrnes et al., 2014). Here, we used the averaging approach based on standardization of the values of each of

the four functions. This approach was used because it helps test the relative importance of predictors across functions, and accounts for correlations among functions in inference (Dooley et al., 2015). Standardization prior to averaging helps remove the effects of differences in the measurement scale between functions (Fanin et al., 2018), attributing an equal weight to each function for our analysis. Although it has received criticism, the averaging approach index measures the functions of interest on a common scale of standard deviation units. It is well correlated with previously proposed indices for quantifying multifunctionality, has good statistical properties (Maestre et al., 2012), and is being increasingly used when assessing multifunctionality (Gross et al., 2017; Jing et al., 2015; Maestre et al., 2012; Quero et al., 2013; Valencia et al., 2015; Wagg et al., 2014). We transformed each function by dividing by the absolute value of the maximum observed level of that function (Lefcheck et al., 2015), resulting in responses on the scale [0;1]. We then derived an average index of EMF by taking a mean of the scaled responses for each combination of two, three and the four functions of interest, leading to 11 possible scenarios of EMF index values at each plot.

2.4. Diversity metrics

We used plot-level taxonomic diversity, functional diversity and functional dominance metrics. We used species richness to characterize the taxonomic diversity. Species richness at plot level is simply defined as the number of distinct species enumerated inside each plot. Functional diversity was quantified by considering the functional traits that are relevant to the ecosystem function of interest (specific leaf area, beeplant status, specific wood density, and maximum plant height). We estimated functional richness (Fric), functional evenness (Feve), functional divergence (Fdiv), and functional dispersion (Fdis), at plot level (Villéger et al., 2008) using the values of the functional traits with the "FD" package in R (Laliberté et al., 2015). A review of these diversity measures can be found in Magurran (1988) and Mouchet et al. (2010). As functional dominance metrics, we computed the plot-level community weight mean (CWM) for each functional trait. CWM is the mean of each species trait value weighted by the relative abundance (stem number) of that species. The plot level CWM was estimated for specific leaf area, specific wood density, and maximum plant height, again using the "FD" package in R.

2.5. Statistical analyses

We first explored how species richness influenced each EMF index value using Ordinary Least Square (OLS) regressions and bivariate scatter plots. The OLS were performed separately to test for individual effect of species richness on each EMF index, using the "lm" functions in the R statistical software package, version 3.3.2. The possible assumptions of normality and linearity were tested prior to the modelling.

It was also explored which diversity components and metrics (functional diversity and functional dominance metrics) better explained EMF, as well as the relative importance of these diversity components, when accounting for possible local environmental effects. Environmental variables such as temperature and precipitation are expected to influence plant structures, productivity, biomass, and carbon stocks (Jing et al., 2015), but were not studied here due to the smaller scale covered by the study. Instead, we focused on environmental factors that are relevant in the study area, i.e. slope and altitude. We tested for combined effects of environmental factors (slope, altitude), functional diversity and dominance metrics on each EMF index using multi-model inference and subset regression analysis of the package "MuMIn" (Barton, 2018). Optimal models were selected based on the AICc (Akaike Information Criterion, adjusted for small sample sizes). Small difference (< 2) in AICc between two subset models indicates that these models are equally supported. For better interpretation of the results, the relative importance values of the predictors were plotted for each model.

A new species—with different functional traits—in an ecosystem would likely contribute to the ecosystem functioning; therefore, the effect of species richness on ecosystem functionality was assumed to be mediated through effects of functional diversity (accounting for niche complementarity), or/and functional dominance (selection effects). To determine the mediation role of these diversity components and metrics, we performed separate Structural Equation Models (SEMs) and examined the indirect and direct effects of species richness on each EMF index, through functional diversity and dominance metrics. For each possibility of EMF index, we tested the a-priori model that species richness has positive effect on EMF through its positive effects on functional diversity and dominance metrics. Due to the high number of functional diversity and dominance metrics, we only used predictors that were selected from the MuMIn analyses. SEMs were fitted in the R platform using "sem" functions from "lavaan" package version 0.5–19 (Rosseel, 2012). The goodness of fit (to the data) of the model was assessed using χ^2 and the comparative fit index (CFI) statistics. Because the results of a structural equation analysis are sensitive to the nature of the computed coefficients (unstandardized vs. standardized), we only used the standardized coefficients to allow for direct comparisons across paths (Grace and Bollen, 2005).

To test whether species richness effects increase with the level of EMF, the slope estimates of fitted OLS models were plotted against the three types of scenarios of EMF. Outputs from the SEM were also used to test whether overall diversity effects generally increased with the level of EMF.

3. Results

3.1. Species richness effects on ecosystem multifunctionality

Results from Ordinary Least Square regressions revealed that, for all possible scenarios, EMF showed considerable plot level variations, and increased significantly with tree species richness (Fig. 1).

3.2. Functional diversity and dominance effects on EMF

3.2.1. Multi-model inference

Results from the model selection process as summarized in Appendix A and Fig. 2 indicated that relevant functional diversity and dominance metrics varied with specific EMF index, whereas none of the studied environmental variables was retained in the selected optimal models (Fig. 2).

For EMF index values obtained from two functions (FVI-AGC, FVI-HbQ and FVI-RFPI), Fdiv and CWM$_{WD}$ were significant predictors, followed by Feve, CWM$_{SLA}$ and CWM$_{PH}$ (Fig. 2). As for AGC-HbQ, AGC-RFPI and HbQ-RFPI, only Fric was retained in the final selected model. When assessing fitted models for EMF indices based on three functions (FVI-AGC-HbQ; FVI-AGC-RFPI and AGC-HbQ-RFPI) and the four functions, Fric was also the most important predictor, followed by Fdiv, CWM$_{WD}$ and CWM$_{SLA}$ (Fig. 2). Overall, results consistently suggested that in most EMF scenarios (e.g. FVI-AGC, AGC-HbQ, AGC-RFPI, HbQ-RFPI, FVI-AGC-HbQ, FVI-AGC-RFPI, AGC-HbQ-RFPI and AGC-FVI-HbQ-RFPI), the most important diversity metrics were Fdiv and Fric. There were few cases (see FVI-HbQ, FVI-RFPI, and FVI-HbQ-RFPI) where functional dominance metrics especially CWM$_{WD}$ was the most important predictor, but was also followed by Fdiv as the second most important variable (Fig. 2).

3.2.2. Structural equation modelling

Chi square statistics testing the deviations between the data and SEM revealed p values higher than 0.05 (0.105–0.702; Table 1) indicating good fits of the models to the data. The values of cfi (> 0.9), and rsmea (< 0.2) were within the acceptable range, also demonstrating very good fits of the models (Table 1). In general, SEMs with
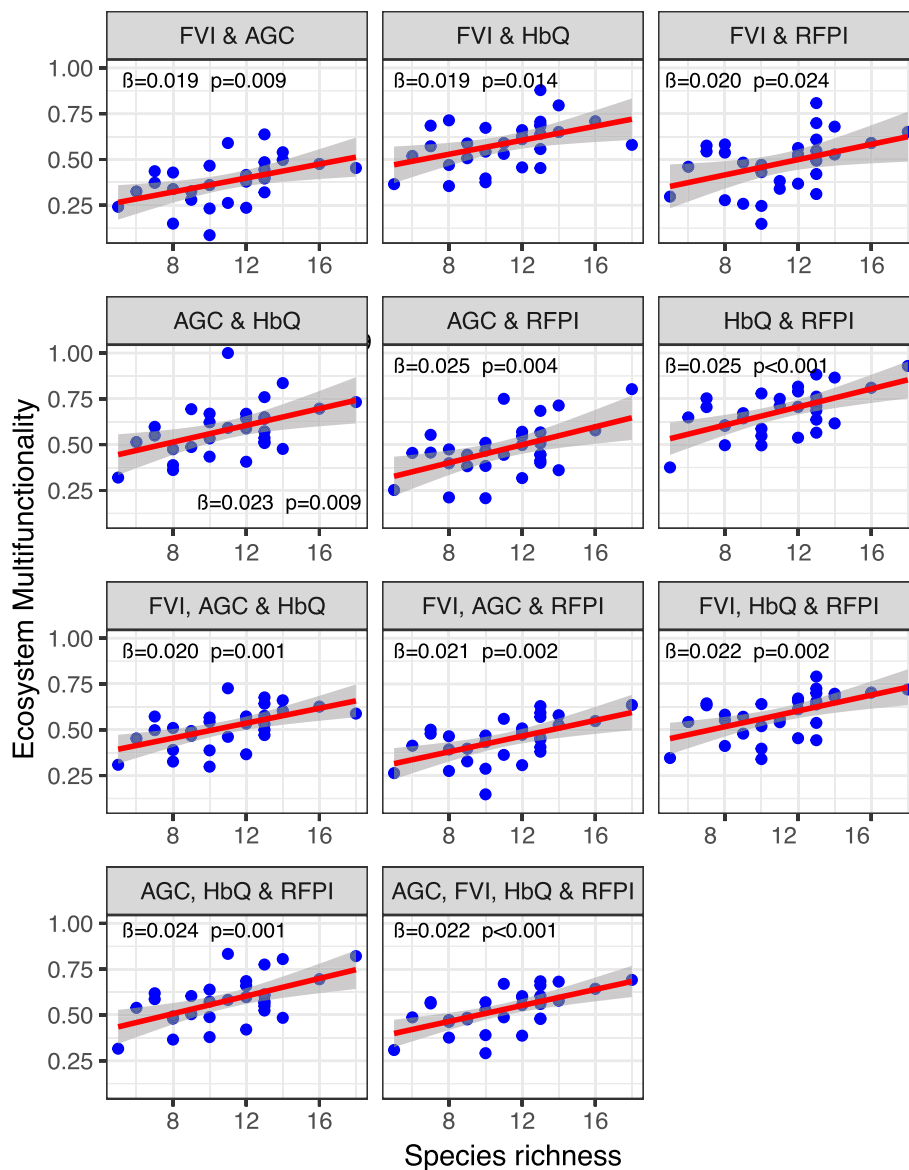
Fig. 1. Bivariate relationship between species richness and ecosystem multifunctionality index. AGC: aboveground carbon; FVI: forage value index; HbQ: habitat quality index; RFPI: rockfall protection index. β is the slope coefficient of the ordinary least square regression testing species richness effect on each EMF index; and p the probability value of the significance of β.

direct path between species richness and EMF showed that species richness effects were fully mediated by functional diversity and dominance metrics (Fig. 3).

For most SEMs, species richness showed significant positive direct effects on Fric (β = 0.88; *p* < 0.001), which also showed positive and significant effects on EMF (β ranging from 0.48 to 0.65; *p* ranging from < 0.001 to 0.044; Fig. 3b, e, f, h, j, k). Therefore, species richness, through Fric had a positive significant effect on EMF. Fdiv also had positive effect on EMF (β ranging from 0.31 to 0.56; *p* ranging from < 0.001 to 0.011), although not significantly influenced by species richness (*p* > 0.05; Fig. 3a, c, d, f, g, i). On the other hand, functional evenness had a negative significant effect (β ranging from −0.30 to −0.23; *p* ranging from 0.001 to 0.036) on EMF, but was not significantly influenced by species richness (*p* > 0.05; Fig. 3c, d).

For functional dominance metrics, CWM of wood density showed significant response to species richness, and also significantly influenced EMF (Fig. 3). On the other hand, CWM$_{PH}$ and CWM$_{SLA}$ showed respectively significant positive and negative effects on EMF, although not significantly influenced by species richness (*p* > 0.05; Fig. 3).

Overall, the SEM results showed that (i) the total effects (i.e. sum of all significant indirect and direct pathways) of species richness on EMF were positive; (ii) species richness effects on EMF were in most cases, mediated by functional diversity; and (iii) diversity effects on EMF were greater for functional diversity metrics (Fdiv and Fric) than for functional dominance.

As we compared the relative influence of species richness and total diversity, we found that species richness – EMF slopes did not increase with the level of multifunctionality (Fig. 4). However, total diversity effects increased with the level of EMF (Table 1; Fig. 4).

4. Discussion

4.1. Positive effects of tree species richness on EMF

Multifunctionality results from the coexistence of multiple trophic groups with functional effects complementing or opposing each other (Jing et al., 2015), thus the need for the analysis of multiple ecosystem functions to decipher existing trade-offs and synergetic patterns and
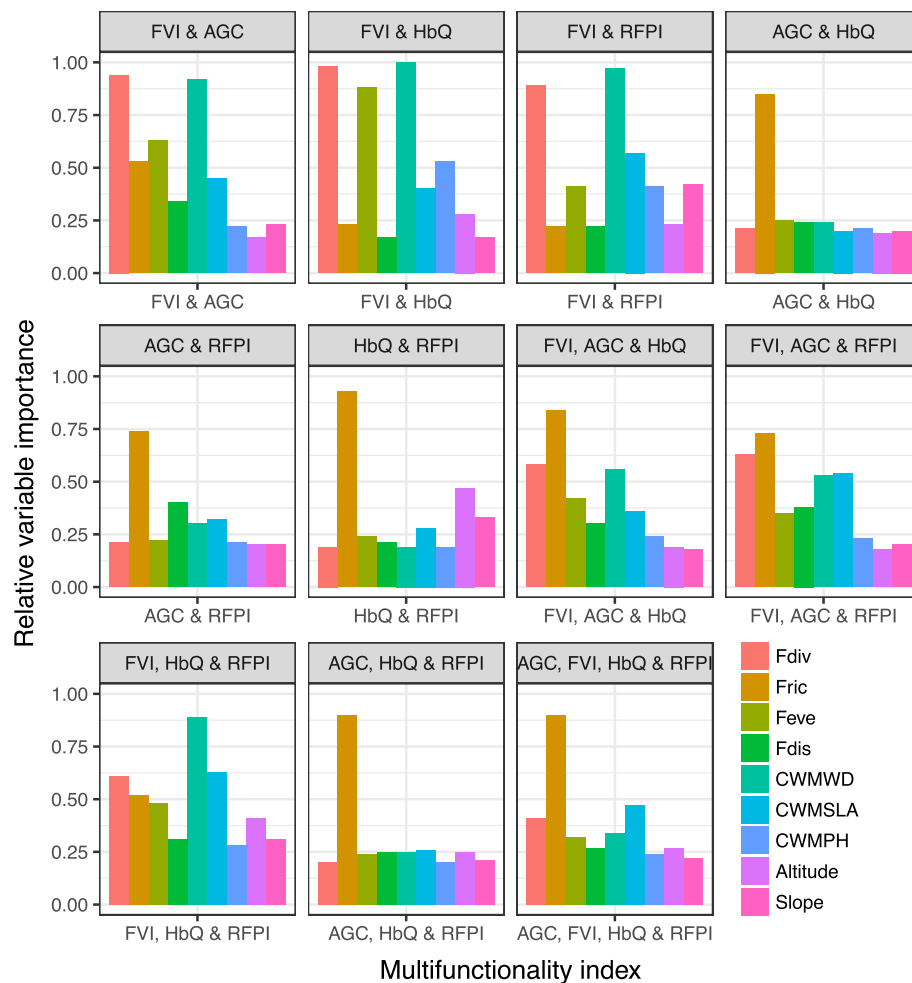
Fig. 2. Relative importance of environmental variables, functional diversity and dominance metrics used as predictors for the eleven possible EMF indices constructed from the combination of two, three and four ecosystem functions. AGC: aboveground carbon; FVI: forage value index; HbQ: habitat quality index; RFPI: rockfall protection index. Fric: functional richness; Feve: functional evenness; Fdiv: functional divergence; Fdis: functional dispersion; CWM: community weight mean; WD: specific wood density; SLA: specific leaf area; PH: maximum plant height. Statistical fit summaries are presented in Appendix A.

support interventions that improve multifunctionality. Similarly to what was observed for single ecosystem functions, our results underscore the evidence that species richness significantly correlates with EMF (Gamfeldt and Roger, 2017; Hector and Bagchi, 2007; Jing et al., 2015; Maestre et al., 2012; Pasari et al., 2013). In particular our findings suggest that improving plant diversity simultaneously improves AGC, habitat quality and protection against rockfall. Higher biodiversity is known to increase ecosystem stability through multiple

functions resulting from the coexistence of multiple trophic groups with diversified but complementary functional effects (Hector and Bagchi, 2007; Isbell et al., 2011). This positive effect of plant diversity on EMF may be mediated by the increased primary production (NPP). Increased NPP has been shown to have cascading effects on multiple organisms and ecosystem processes (Cardinale et al., 2011), which is often used to recommend multi-species plant communities scheme in human made forests.

Table 1

Summary of fit statistics for the SEMs relating species richness, functional diversity and functional dominance metrics to EMF; Chi^2: Chi-square test ($p > 0.05$ indicates absence of significant discrepancy between the data and the model); cfi: comparative fit index; and rmsea: root mean square error of approximation.

EMF index	SEM	cfi	rmsea	Chi^2 (p value)	R Square (%)	Total diversity effects $\pm$ SE
FVI-AGC	Fig. 3a	0.966	0.120	8.597 (0.198)	69.1	0.443** $\pm$ 0.138
AGC-HbQ	Fig. 3b	1.000	0.000	0.328 (0.567)	23.4	0.426*** $\pm$ 0.121
FVI-HbQ	Fig. 3c	0.986	0.071	5.765 (0.330)	76.9	0.396** $\pm$ 0.146
FVI-RFPI	Fig. 3d	0.982	0.071	5.765 (0.330)	64.4	0.379* $\pm$ 0.149
AGC-RFPI	Fig. 3e	0.999	0.041	1.050 (0.305)	24.4	0.435*** $\pm$ 0.119
FVI-AGC-HbQ	Fig. 3f	0.954	0.187	6.150 (0.105)	54.0	0.556*** $\pm$ 0.115
FVI-AGC-RFPI	Fig. 3g	0.961	0.166	7.292 (0.121)	59.5	0.545*** $\pm$ 0.118
HbQ-RFPI	Fig. 3h	0.979	0.197	2.159 (0.142)	29.6	0.479*** $\pm$ 0.111
FVI-HbQ-RFPI	Fig. 3i	0.961	0.166	7.292 (0.121)	60.2	0.530*** $\pm$ 0.121
AGC-HbQ-RFPI	Fig. 3j	0.996	0.081	1.197 (0.274)	29.4	0.477*** $\pm$ 0.111
All functions	Fig. 3k	1.000	0.000	0.146 (0.702)	42.9	0.575*** $\pm$ 0.090

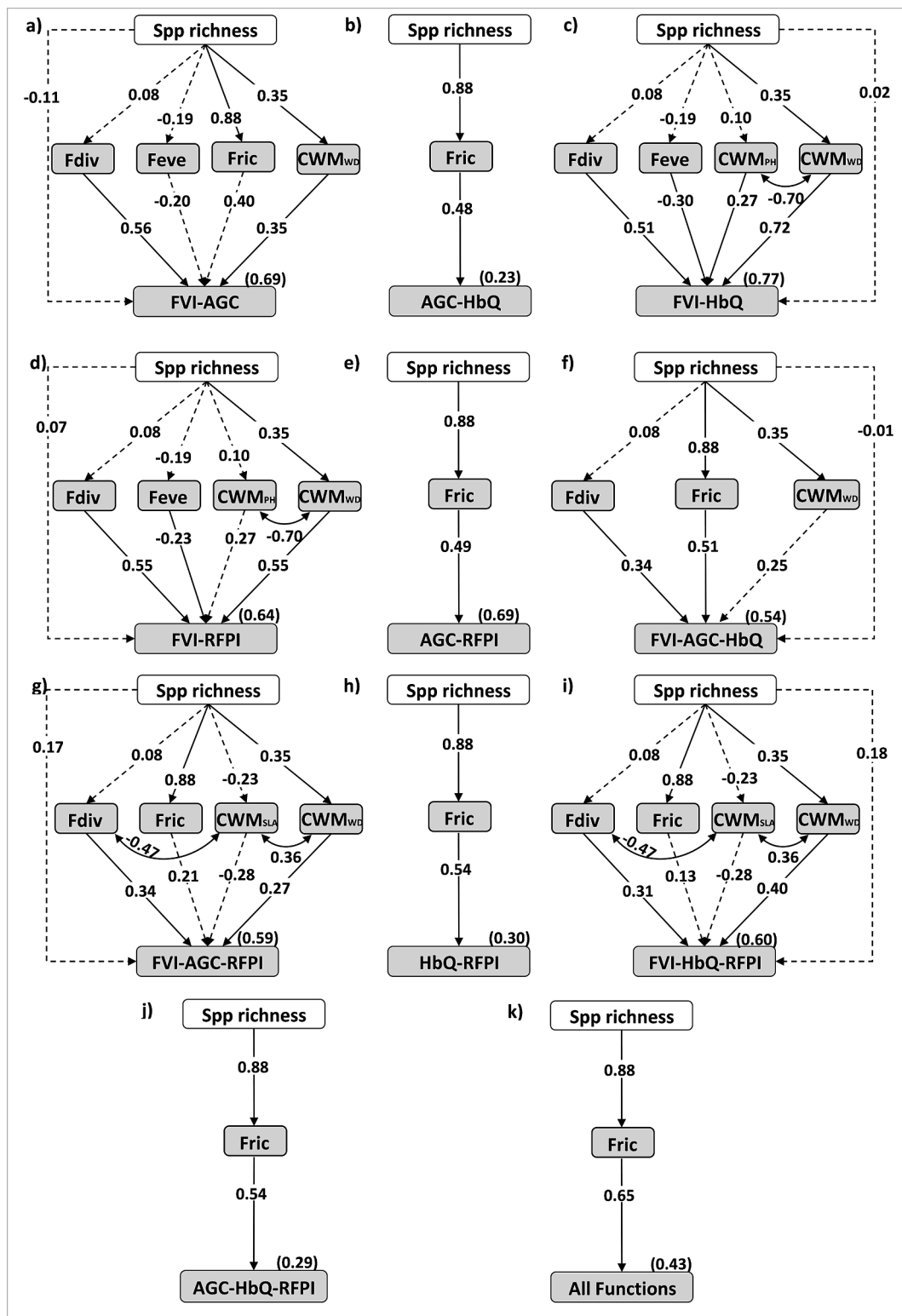*: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

Fig. 3. Summary of the SEM paths linking EMF to diversity metrics. Values with parentheses are the coefficients of determination. Values without parentheses are the standardized path coefficients. Single-pointed arrows and curves stand for causal paths. Double-pointed arrows indicate the correlations. The plain arrows and curves indicate significant effects, while the dotted ones show non-significant effects. See Fig. 2 for the remaining legend. Fit statistics are summarized in Table 1 and Appendix B.

4.2. Functional diversity effects on EMF greater than those of functional dominance

Because no single measure can fully capture all components of biodiversity, recent work on diversity and ecosystem function

relationships has put more focus on taxonomic diversity (e.g. species richness), as well as other biodiversity components such as functional diversity, functional dominance and phylogenetic diversity. Exploring multiple diversity metrics effects also helps to shed light into the mechanisms (selection effects, niche complementarity, etc.) underlying
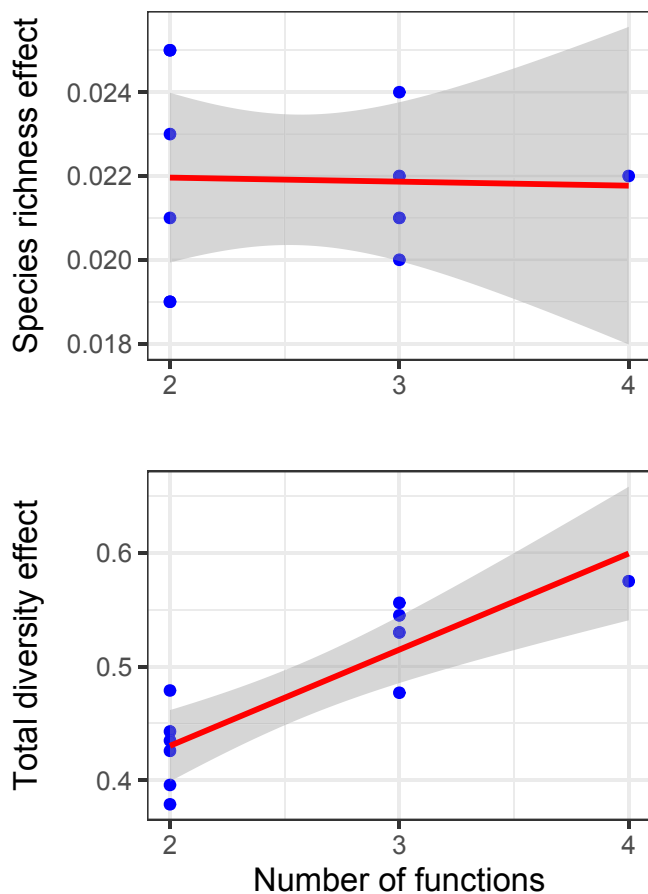
Fig. 4. Change in species richness and total diversity effect (slope values) in relation to the level of EMF. Species richness effect: β = 0.00 ± 0.00 and p = 0.929; total diversity effect: β = 0.08 ± 0.01 and p < 0.001. Additional statistics are presented in Appendix C.

diversity effects on ecosystem function (Laughlin, 2011; Lin et al., 2016; Prado-junior et al., 2016). Since differences in functional traits would drive ecological differences (Cadotte et al., 2009), we expected functional trait diversity to explain higher variation in EMF. Consistently, our results showed that most important diversity metrics were Fdiv and Fric. There were only few cases where functional dominance metrics especially CWM wood density was the most important predictor. We thus concluded that diversity effects on EMF were more strongly mediated by functional diversity metrics (Fdiv and Fric) than by functional dominance. These results are consistent with recent studies on diversity and multifunctionality relationships. For instance, Valencia et al. (2015) showed that functional diversity played important role in enhancing EMF. Gross et al. (2017) also argued that functional trait diversity maximizes EMF. Similarly, Huang et al. (2019) found that functional diversity, especially functional richness was positively related to EMF in *Pinus yunnanensis* natural secondary forest, while Le Bagousse-Pinguet et al. (2019) also showed that functional attributes of species were key drivers of multiple ecosystem functions simultaneously (multifunctionality) across 123 drylands from six continents. Our results however run contrary to Lohbeck et al. (2016), who showed that biodiversity may play a limited role for EMF in tropical human-modified landscapes, as a result of potentially large effect of species dominance on biogeochemical functions. Functional diversity metrics, and in particular, functional richness and functional divergence, as assessed in this study, reflect the range of functional traits. Functional diversity effects were found to be greater on EMF, because (i) these metrics would reflect more the diversity of functionally unique species and the magnitude of ecological niche differences; and (ii) co-

occurring species with considerably different trait values would increase the overall resource utilization. In functionally diversified forest ecosystem, greater ecological differentiation allows species to stably coexist through niche partitioning and efficient utilization of resources by co-occurring species (Mensah et al., 2018a). Unlike functional diversity, functional dominance as assessed here, reflects more the competitive dominance of traits and species within a given community (Mensah et al., 2016a; Ricotta and Moretti, 2011), and therefore is more likely to have greater effects on single functions than on multifunctionality. For instance, in a recent study, Le Bagousse-Pinguet et al. (2019) showed that the importance of dominant species (i.e., community weighted mean of functional traits) increased when considering individual ecosystem function, suggesting that dominance effects would explain more the variation in individual function than in multiple functions simultaneously. By finding that diversity effects on EMF were greater for functional diversity metrics (Fdiv and Fric) than for functional dominance, the present study is supportive of the niche complementarity hypothesis as a key mechanism governing EMF.

4.3. Total diversity effects, not species richness effect, generally increased with the level of EMF

Very few studies assessed the importance of diversity for multiple functions, with the results that the reported patterns were controversial and nonconsistent (Gamfeldt et al., 2008; Gamfeldt and Roger, 2017). Some studies support the claim that increasing biodiversity sustains multiple ecosystem functions (Gamfeldt et al., 2008; Lefcheck et al., 2015; Perkins et al., 2015), while other recent works showed that the relationship between biodiversity and ecosystem functioning does not change with the number of functions considered (Gamfeldt and Roger, 2017). However, most of these studies only focused on species richness as a simple metric to approach the biodiversity-multifunctionality relationship. Here we found that considering more functions does not affect the relationship between species richness and multifunctionality, as also reported in a recent study (Gamfeldt and Roger, 2017). It is possible that using species richness as sole diversity metric may not bring out the contribution of functionally different and unique species. Because species richness, as single biodiversity measure may not fully capture all components of biodiversity, diversity and multifunctionality relationships should be extended to other biodiversity components such as functional diversity, functional dominance and phylogenetic diversity. The results of SEMs opposing functional diversity and dominance metrics effects on EMF further revealed that total diversity effects (i.e. sum of all significant indirect and direct pathways) increased with the level of multifunctionality. Lefcheck et al., (2015) showed that the effects of biodiversity on ecosystem function become more important as more functions are considered. Similarly, a recent study by Gross et al. (2017) revealed that other metrics (skewness and kurtosis) would have a much stronger impact on multifunctionality than species richness. Different functions will likely be maximized by functionally different species, and consequently, diverse mixtures would provide combinations that maximize multiple functions (Zavaleta et al., 2010). The finding that total diversity effects, and not species richness effect, increased with the level of EMF suggests that trait diversity is important to elucidate biodiversity-multifunctionality relationship.

4.4. Limitations of the study

All being considered, it is important to acknowledge that our study presents some limitations. First, we used the averaging approach to quantify EMF; this approach has been criticized in the past (Gamfeldt et al., 2008), as it is often sensitive to single functions with large impact, and does not necessarily distinguish between (i) two functions at similar level and (ii) one function at high level and other function at low level (Byrnes et al., 2014; Dooley et al., 2015). Nevertheless the index is a straightforward and easily interpretable measure of the

ability of ecosystem to sustain multiple functions simultaneously (Byrnes et al., 2014; Jing et al., 2015; Maestre et al., 2012). Other studies have also combined two or three approaches of quantification of EMF, depending on the research questions of interest (Fanin et al., 2018; Gamfeldt and Roger, 2017; Huang et al., 2019; Jing et al., 2015; Lefcheck et al., 2015; Mori et al., 2016). For instance, Fanin et al. (2018) used the averaging approach to evaluate the importance of diversity in explaining EMF, and the multiple threshold approach to determine whether the effect of biodiversity loss on EMF differed across the full range of possible thresholds. Similarly, Le Bagousse-Pinguet et al. (2019) used the multiple threshold approach to evaluate whether multiple functions are simultaneously performing at high levels. Further, when assessing relationships between EMF and biodiversity, Jing et al. (2015) obtained similar results when using the averaging approach and multiple threshold approach. The averaging approach is appropriate for the research questions addressed in this study, in particular for testing the relative importance of predictors across functions (Dooley et al., 2015), and also testing whether the average level of multiple functions increases with the number of species (Byrnes et al., 2014). Second, the range of the functional traits for quantification of functional dominance and diversity is limited to those that are related to the acquisition and utilization of resources in plants, that is, wood density, specific leaf area, plant height; these functional traits might not be sufficient enough to capture the entire functional spectrum needed to explain EMF. Adding other functional traits describing leaf economics (Wright et al., 2004) and wood economics (Chave et al., 2009), such as plant hydraulic conductivity, leaf mass per area, and nitrogen fixing potential could have increased the functional spectrum. Finally, while this study addressed an important aspect of diversity-EMF in a natural forest ecosystem, similar studies should be extended to other natural forests with different structure and physiognomy.

5. Conclusion

In this study, we examined the relationship between species richness and EMF from taxonomic and functional perspectives in natural forests. Species richness and functional diversity (divergence and richness) correlated positively and significantly with EMF, supporting our hypothesis that diversity enhances EMF. On the other hand, functional dominance metrics were also important, but played a limited role in linking species richness to EMF. Of great importance, the study revealed that diversity effects on EMF were greater for functional diversity than for functional dominance. As such, the selection effect may not prevail when considering multiple ecosystem functions. Further analyses exploring importance of species richness versus total diversity effects revealed that the latter, and not species richness effects, increased with the level of EMF. We hence conclude that trait diversity is more important than species richness and trait dominance in explaining multifunctionality. These findings imply that resource-use complementarity, the ability of functionally diverse co-occurring species or individuals within species to more efficiently utilize a pool of available resources, governs EMF. That is to say, in multispecies forests, different species with different traits contribute more to multifunctionality than different but functionally similar species. This has important implications for silviculture and agroforestry systems, as mixture of functionally different species in mixed plantations and agroforestry would allow maximization on multifunctionality.

Declaration of Competing Interest

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

Authors' contributions

SM conceived the idea, and led discussions with TS and VKS. TS acquired the funding. SM collected and analyzed the data, with support from VKS and RGK. SM wrote the manuscript with editorial support and review from BS, AA, TS, VKS and RGK. All authors gave final approval for submission.

Data accessibility

The data used in this study is accessible from the corresponding author upon reasonable request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2020.106415.

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