

Research article

Functional diversity changes during tropical forest succession

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ARTICLE INFO

Article history:

Received 7 January 2011

Received in revised form 19 July 2011

Accepted 15 October 2011

Keywords:

Chiapas

Chronosequence

Mexico

Functional redundancy

Secondary forests

Species diversity

Specific leaf area

Wood density

ABSTRACT

Functional diversity (FD) 'those components of biodiversity that influence how an ecosystem operates or functions' is a promising tool to assess the effect of biodiversity loss on ecosystem functioning. FD has received ample theoretical attention, but empirical studies are limited. We evaluate changes in species richness and FD during tropical secondary forest succession after shifting cultivation in Mexico. We also test whether species richness is a good predictor of FD. FD was calculated based on a combination of nine functional traits, and based on two individual traits important for primary production (specific leaf area) and carbon sequestration (wood density). Stand basal area was a good predictor of successional changes in diversity and FD, in contrast to fallow age. Incidence-based FD indices increased logarithmically with stand basal area, but FD weighted by species' importance values lacked pattern with succession. Species richness and diversity are strong predictors of FD when all traits were considered; linear relationships indicate that all species are equally functionally complementary, suggesting there is little functional redundancy. In contrast, when FD was calculated for individual traits and weighted for abundances, species richness may underestimate FD.

Selection of functional trait(s) critically determines FD, with large consequences for studies relating biodiversity to ecosystem functioning. Careful consideration of the traits required to capture the ecosystem process of interest is thus essential.

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Introduction

Functional traits are important for the response of species to their environment, and for the effects that species have on ecosystem processes (e.g. Lavorel and Garnier, 2002; McGill et al., 2006; Cornwell et al., 2008; Lavorel et al., 2010). Functional diversity has been defined as the value, range, and distribution of functional traits in a given ecosystem (Díaz et al., 2007a) or as those components of biodiversity that influence how an ecosystem operates or functions (Tilman, 2001b). Many researchers recognize that functional diversity is more important to local scale ecosystem functioning than taxonomic diversity (Grime, 1998; Tilman, 2001b; Micheli and Halpern, 2005), because functional diversity may be a good indicator of ecosystem resource dynamics, stability and productivity (Tilman, 2000; Díaz and Cabido, 2001; Cardinale et al., 2006; Díaz et al., 2007b).

Two main index types have been proposed for measuring functional diversity, those based on species incidence (presence/absence) and those based on species abundance. Incidence-based indices, which are comparable to functional richness measures (e.g. Walker et al., 1999; Petchey and Gaston, 2002), emphasize the full range of functional strategies present in the community, proposing that both dominant and rare species contribute equally to functional diversity. The rationale underlying this idea is that each species may strongly influence ecosystem functioning and that rare species are especially important contributors to long-term ecosystem resilience (Walker et al., 1999; Hooper et al., 2005). In contrast, indices based on species abundance emphasize the role of dominant species (e.g. Mason et al., 2003; Mouillot et al., 2005) in a similar way as the biomass-ratio hypothesis (Grime, 1998), which also states that dominant species have a greater effect on ecosystem functioning than rare species. Processes that are mostly influenced by the trait values of dominant species are, for example, specific primary productivity and decomposition (Garnier et al., 2004; Cornwell et al., 2008). Thus, the type of index useful in a particular

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study depends on the ecosystem process of interest (Díaz et al., 2007b).

Functional diversity has received ample theoretical attention (e.g. Díaz and Cabido, 2001; Tilman, 2001b; Ackerly and Cornwell, 2007; Díaz et al., 2007a,b; Hillebrand and Matthiessen, 2009; Petchey et al., 2010), and has become the central paradigm of the Millennium Ecosystem Assessment (MEA, 2005). Still there is surprisingly little empirical data showing how functional diversity varies across environmental and successional gradients in forests, despite their importance for maintaining ecosystem functioning (Scherer-Lorenzen et al., 2005, but see; Scherer-Lorenzen et al., 2007; Baraloto et al., 2010a; Paquette and Messier, 2011). Here we apply the concept of functional diversity to secondary tropical forest succession.

The changes in forest structure and species composition along succession strongly imply concurrent changes in both functional diversity and ecosystem functioning. Tree communities of tropical agricultural lands are poorer than those of old-growth forests in both species and functional diversity (Mayfield et al., 2005), and species richness increases asymptotically during secondary succession (e.g. van Breugel et al., 2006; Norden et al., 2009; Lebrija-Trejos et al., 2010a), but how functional diversity changes with secondary succession is largely unknown. Understanding this phenomenon is of paramount importance for managing ecosystem processes in secondary forests, especially tropical landscapes subjected to shifting cultivation and abandoned land practices (MEA, 2005).

The relation between functional diversity and species diversity (FD–SD) can be used to explore to what extent functional trait values are complementary among species (Petchey and Gaston, 2002; Laliberté et al., 2010), i.e. to what extent does functional redundancy among species exist. Overall, functional diversity is expected to scale positively to species diversity because each new species added to the ecosystem will not only contribute to species diversity but will also contribute to functional diversity, assuming that the suite of functional trait values possessed by each new species is not present yet in the community. In case of a linear FD–SD relationship, species richness is a good proxy for functional diversity. Detailed and time consuming measurements of functional traits then are unnecessary. Such linear relations are not commonly found in nature (Díaz and Cabido, 2001), however, rather partial complementarity (logarithmic) or non-complementarity (no relation) is predominant (Schmid et al., 2002). A logarithmic FD–SD relationship indicates functional redundancy since new species added to the community sometimes have functional attributes that are already represented by other species. Species diversity and functional diversity may also be uncoupled, as species diversity is hypothesized to be limited by the regional species pool whereas functional diversity is hypothesized to be limited by the local availability of niches (Schmid et al., 2002).

The FD–SD relationship is influenced by the ‘effective dimensionality of trait space’ (Petchey and Gaston, 2002). ‘Effective’ dimensionality equals the number of functional traits that are orthogonal, or the number of ways in which species can be complementary. A higher dimensionality allows more species to be functionally equally similar (or dissimilar) resulting in a linear FD–SD relationship. The addition of any one species thus increases functional diversity in the same way as adding any other species to the community. The effective dimensionality of trait space increases with the number of independent traits and decreases when species abundances are included because weighting species focuses on the dominant species (Petchey and Gaston, 2002).

This study provides the first assessment of the FD–SD relationship for tree communities in a tropical forest successional system (see Bihn et al., 2010 for similar work on ant communities). We use 11 forest plots that vary in fallow age from 3.3 to 24.6 years

of regeneration after shifting cultivation in Southeast Mexico, this early successional stage is where most of the changes in diversity are expected to take place (van Breugel et al., 2006). For the most important species in each plot (making up 92% of the importance value on average) we have analysed nine functional traits that are important for plant performance and ecosystem processes (Appendix A). Functional diversity is calculated for all nine traits combined as an indicator of the overall plant strategy, as well as for specific leaf area (SLA) and wood density (WD) separately. SLA and WD have been chosen because they are among the most important and commonly studied traits and are of paramount importance for different ecosystem processes (Lavorel and Garnier, 2002; Chave et al., 2009). SLA affects primary production, carbon and nutrient cycling and litter decomposition (Poorter et al., 2009) whereas WD is a key trait for biogeochemical ecosystem processes such as carbon sequestration, forest stratification and turnover rates (Chave et al., 2009).

We address the questions (1) how do functional and species diversity change during secondary tropical forest succession? and (2) is species diversity a good proxy for functional diversity in successional tree communities? Because evidence exists that species diversity increases asymptotically during secondary succession, we hypothesized that functional diversity will show a similar trend. We further hypothesized that functional diversity based on individual traits (e.g. SLA or WD) will have a saturating relationship with species richness, as the trait values of additional species are likely to be present in the community. Functional diversity based on all nine traits combined, however, will be linearly related to species diversity because the effective dimensionality of trait space increases with the number of traits included (cf. Petchey and Gaston, 2002).

Methods

Research site and species selection

Research plots were located in the Marqués de Comillas region in southeast Mexico (16°01'N, 90°55'W). The climate is warm-humid with an average annual temperature of 24°C and an annual rainfall of 3000 mm, with a dry period (less than 100 mm per month) from February through April (van Breugel et al., 2006). The 11 permanent study plots are located around the village of Loma Bonita, and upon site selection great care was taken to obtain as much environmental homogeneity as possible with regard to soil, topography and management history (van Breugel et al., 2006). Sites are established on abandoned cornfields, having experienced mostly one cycle of cultivation (Chazdon et al., 2007). They are located within the rather uniform low hill geomorphological unit, characterized by small hills and valleys with sandy or limestone soils of low pH (<5.5), which is one out of the four geomorphological units identified in the area (Siebe et al., 1996). The landscape matrix is dynamic and under high anthropogenic pressure, currently 65% of the land area around Loma Bonita is used for agricultural practices (mostly livestock pasture), 14% is mature forest and 21% consist of secondary forests of different ages (I. Zermeño-Hernández, unpublished results). The secondary forest plots (10 m × 50 m) had fallow ages between 3.3 and 24.6 years, all trees with a diameter at breast height (DBH) ≥ 1 cm were identified and their diameter was measured. For each plot those species were selected that made up at least 80% of the importance value (mean 92 ± 5.7%) (see below for calculation of the importance value index) in that plot, as these determine most of the key ecosystem processes (Garnier et al., 2004; Pakeman and Quested, 2007). On average 32 species per plot were selected (range 9–47), being 79 species in total.

Functional traits

For each species, nine functional traits that are important for the carbon-, water- and nutrient-balance of plants were measured (Appendix A). Leaf traits were measured on two sun-lit leaves per individual, on small adult trees of ca. 5 m high, having 10 replicate individuals per species. The specific force to punch and wood density were measured for 5 individuals per species. Traits were measured following standardized protocols given by Cornelissen et al. (2003). For analyses mean trait values were used per species, although we acknowledge that species per plot trait values could have improved the accuracy (Baraloto et al., 2010b).

Leaves were dark-adapted for 1 h after which the Instantaneous Chlorophyll Fluorescence (F_0) was measured with a fluorpen (Photon Systems Instruments, FP100) on exposure to 445 nm light at a saturating intensity of 3000 μ E. The quantum yield (F_v/F_m) was measured as the ratio between variable fluorescence and maximum fluorescence. This ratio reflects the proportion of light used in photochemistry or emitted as heat.

After collection the leaves were placed in water to rehydrate for at least 5 h and fresh weight was determined. Leaf petiole length (cm) was measured with a digital caliper or a tape-measure and leaf thickness (mm) was determined with a digital caliper in the middle of the leaf avoiding the main and secondary veins (0.01 mm accurate). Leaves (excluding petiole) were photographed on a light box and leaf area (cm^2) was calculated using pixel counting software ImageJ (Rasband, 2008). Leaves were subsequently oven-dried for 48 h at 70 °C and weighed. Specific Leaf Area (SLA , $\text{m}^2 \text{kg}^{-1}$) was calculated as the fresh leaf area divided by the oven-dried mass (excluding petiole). Leaf Dry Matter Content (g g^{-1}) was calculated as the oven-dry weight divided by the fresh weight. In case of compound leaves the smallest photosynthetic unit was taken.

Fresh leaf laminae were punched with a penetrometer built with a flat-end nail attached to the inner part of a syringe and a waterbasin on top. Water was added to the basin until the leaf ruptured. The total weight added was converted into Mega Newton. The specific force to Punch (MN m^{-2}) was calculated as the force divided over the breaking surface of the hole (circumference of the nail \times thickness of the leaf). This alternative punching method is comparable to cutting and tearing tests and is a good indicator of leaf mechanical resistance (Onoda et al., 2011).

Species specific wood density was based on wood cores or stem slices. With an increment borer (12 mm, Suunto, Finland) a core of wood was extracted from the outer bark up to at least the heart of the tree (firmly attached bark or phloem tissue was considered part of the stem). For some species the stems did not reach sufficient size for this method and for these a slice of the stem was extracted. The wood cores were divided in three parts (across the pith, heartwood and sapwood) and the wood density was measured for these parts separately by dividing the dry weight (70 °C, 48 h) over the fresh volume. The fresh volume was determined with the water displacement method. Wood densities of these three parts were averaged, to obtain the species' specific wood density (WD , g cm^{-3}). This measurement was taken for 32 of the 79 species studied: data on WD for remaining species were taken from comparable studies by the authors (unpub. data) in Mexican wet forests in the same location around Loma Bonita (Chiapas), Las Margaritas (Puebla) and Los Tuxlas (Veracruz).

Calculating species diversity and functional diversity

Species diversity and functional diversity indices were calculated based on incidence and weighted by species dominance (Table 1). An importance value index was used as an indicator of species dominance, and was calculated as:

Table 1

The diversity indices used to describe the secondary forest communities.

Diversity index; abbreviation	Method of calculation	References
Species number; SD	Total number of species sampled in the site, making up at least 80% of the importance value	
Shannon Weaver diversity, weighted by species importance values; wSD	$wSD = -\sum_{i=1}^S p_i \ln p_i$ p_i = importance value of species i ; S = total number of species; calculated in fDiversity	Shannon and Weaver (1949), Casanoves et al. (2008)
Functional diversity based on incidence (presence/absence); FD	Distance matrix among species based on trait values. $FD = \text{total branch length of the functional dendrogram} \times S^2$; S = total number of species; calculated in fDiversity	Petchey and Gaston (2006), Casanoves et al. (2008), Casanoves et al. (2011)
Functional diversity weighted by species importance values; wFD	Distance matrix among species based on trait values, matrix loaded by importance values. $wFD = \text{total branch length of the functional dendrogram} \times S^2$; S = total number of species; calculated in fDiversity	Petchey and Gaston (2006), Casanoves et al. (2008), Casanoves et al. (2011)

$(BA_i/BA_{\text{total}} + D_i/D_{\text{total}})/2$, where BA_i is the basal area of the i th species and D_i is the stem density of the i th species and total reflects the total basal area or stem density in the plot. Weighting with the importance value was chosen because we assume that if ecosystem processes are mainly determined by dominant species, this may be expressed by species with large numbers of individuals, just as by species with few individuals but large biomasses.

All diversity indices were based on the cumulative number of species in a site that account for at least 80% (mean $92\% \pm 5.7$) of the importance value in the plot ($\text{DBH} > 1 \text{ cm}$). Species richness was used as incidence-based species diversity measure, whereas Shannon Weaver index includes species' importance values (Table 1). Species richness and Shannon Weaver were based on the same selection as the functional diversity indices, rather than on the total number of species in a plot. This makes species and functional diversity best comparable, as these are limited to including those species for which functional trait data was available. This species richness however tightly correlates to the total plot species richness (Pearson correlation 0.98).

Two measures of functional diversity were calculated, one based on the functional traits of species present in the plots (incidence-based functional diversity) and the other based on the traits weighted by the importance value of the species (Table 1). Functional diversity was calculated using the fDiversity software program based on Euclidean distance and average linkage (Casanoves et al., 2008, 2011) after the traits have been standardized to ensure equal contribution of each trait. Standardization was calculated as: $Z_i = (x_i - x_{\text{mean}})/sd$, where Z_i is the standardized trait value for a species, x_i is the trait value for species, x_{mean} is the mean value of a trait across all species and sd is the standard deviation of the variation in trait values across all 79 species studied.

We used the 'multiplicative extended functional diversity' (Casanoves et al., 2008, 2011) based on a dendrogram-based measure proposed by Petchey and Gaston (2006) and modified by Pla et al. (2008) to be able to include species relative abundances.

Weighting by abundances is done by loading the species dissimilarity matrix with the species importance values and subsequently the multiplicative extended weighted functional diversity is computed as the total branch length of the functional dendrogram of the community multiplied by the squared species number. This dendrogram based functional diversity calculation is suggested to have a great power to explain variation in ecosystem functioning (Petchey and Gaston, 2007). We used weighted functional diversity (wFD), including species relative importance values in every site and incidence based functional diversity (FD) where the importance values in the input file are set to 1, ensuring equal contribution of every species. In the literature three primary functional diversity components have been proposed; functional richness, evenness and divergence (Mason et al., 2005). Incidence-based functional diversity (FD) is best comparable to functional richness (Mouchet et al., 2010; Schleuter et al., 2010). When weighted for the importance value, more emphasis is placed on dominant species and wFD becomes higher when abundant species are functionally far apart on the dendrogram, thereby we argue that wFD is best comparable to functional divergence (Villéger et al., 2008). Functional diversity (weighted and incidence-based) was calculated for all 9 traits together and for two key traits (SLA and WD) separately.

Statistical analysis

Regression analysis and Pearson correlations were used to evaluate how species diversity and functional diversity change during secondary succession. Diversity was not only related to time since abandonment, but also to stand basal area. Stand basal area increases asymptotically with fallow age in the chronosequence used and is a good structural variable of succession (van Breugel et al., 2006). To evaluate how species and functional diversity change during succession, linear and logarithmic models were used; to evaluate relationships between functional diversity and species diversity (FD–SD relationship), linear, logarithmic and exponential regression models were used.

The best fitting model was selected based on the highest R^2 . We considered 5% the minimum difference needed for being significant, and in case of insignificant difference we chose the linear (most parsimonious) model. All statistical analyses were carried out using IBM SPSS statistics 19.0 (SPSS Inc., Chicago).

Results

None of the taxonomic or functional diversity measures were significantly related to the fallow age (Table 2). In contrast, three of the incidence-based diversity measures increased logarithmically

Table 2

Diversity changes along a successional gradient (time after abandonment and stand basal area). Diversity indices include: incidence-based species diversity or species richness (SD), species diversity weighted by species importance (wSD), incidence-based functional diversity (FD), and functional diversity weighted by importance (wFD). Functional diversity is based on all nine traits (FD_{ALL}) or based on a single trait (FD_{SLA}, FD_{WD}). Pearson correlation (R) coefficient and the significance levels (p) are shown. Significant correlations in bold ($N=11$).

Diversity	Time after abandonment		Basal area	
	R	p	R	p
SD	0.36	0.279	0.66	0.028
wSD	−0.00	0.990	0.19	0.570
FD _{ALL}	0.40	0.219	0.68	0.022
FD _{SLA}	−0.12	0.720	−0.24	0.473
FD _{WD}	0.34	0.302	0.67	0.023
wFD _{ALL}	0.10	0.770	0.57	0.066
wFD _{SLA}	0.39	0.238	0.39	0.238
wFD _{WD}	0.04	0.914	0.49	0.130

with stand basal area (Fig. 1), species richness, incidence-based functional diversity of all traits, and incidence-based functional diversity of wood density. The weighted diversity measures (Shannon Weaver, weighted functional diversity of all traits, SLA and WD) did not vary significantly with stand basal area, although weighted functional diversity of all traits was close ($p=0.066$) (Table 2).

We examined the ability to use species diversity as a proxy for functional diversity by analyzing the shape of the relation of functional diversity plotted against species diversity. Most combinations showed significant relations indicating that functional diversity indeed is predictable. Incidence-based functional diversity of all traits combined (FD_{ALL}) was linearly related to species richness (Fig. 2a), as was incidence-based functional diversity in WD (FD_{WD}) (Fig. 2c), but FD_{SLA} was unrelated to species richness (Fig. 2b).

Weighted functional diversity of all traits combined (wFD_{ALL}) was linearly related to species richness (Fig. 2d), while SLA (wFD_{SLA}) and WD (wFD_{WD}) were exponentially related to species richness (Fig. 2e and f). Weighted functional diversity was also well predicted by weighted species diversity (Shannon Weaver index): linear relationships are found for all traits combined (wFD_{ALL}), for SLA (wFD_{SLA}) and for WD (wFD_{WD}) (Fig. 2g–i).

Discussion

In this study we asked how functional and species diversity change during secondary tropical forest succession, and if functional diversity was predictable by species diversity, basal area or forest age. We found incidence-based species and functional

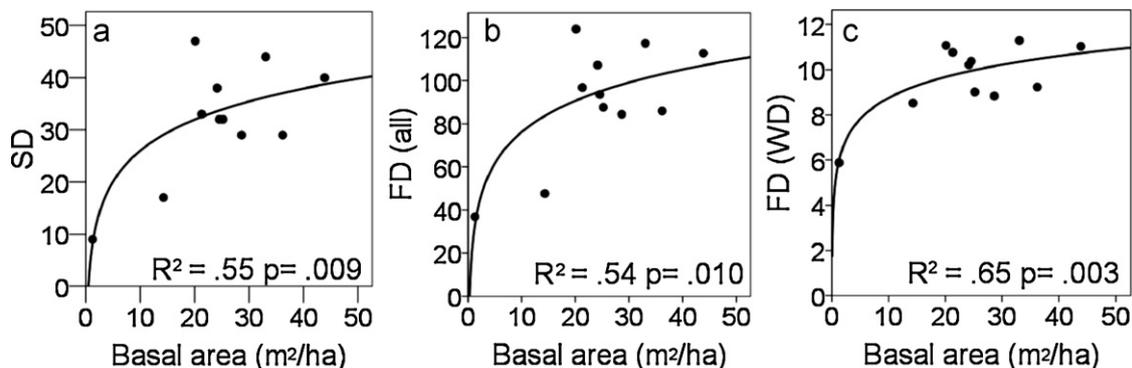


Fig. 1. Species and functional diversity changes during secondary forest succession at Marqués de Comillas, Southeastern Mexico. Stand basal area is used to reflect vegetation changes along a successional gradient. (a) Species richness (SD) as a logarithmic function of stand basal area; (b) incidence-based functional diversity (FD) including all 9 traits as a logarithmic function of stand basal area; (c) incidence-based functional diversity in wood density (FD_{WD}) as a logarithmic function of stand basal area.

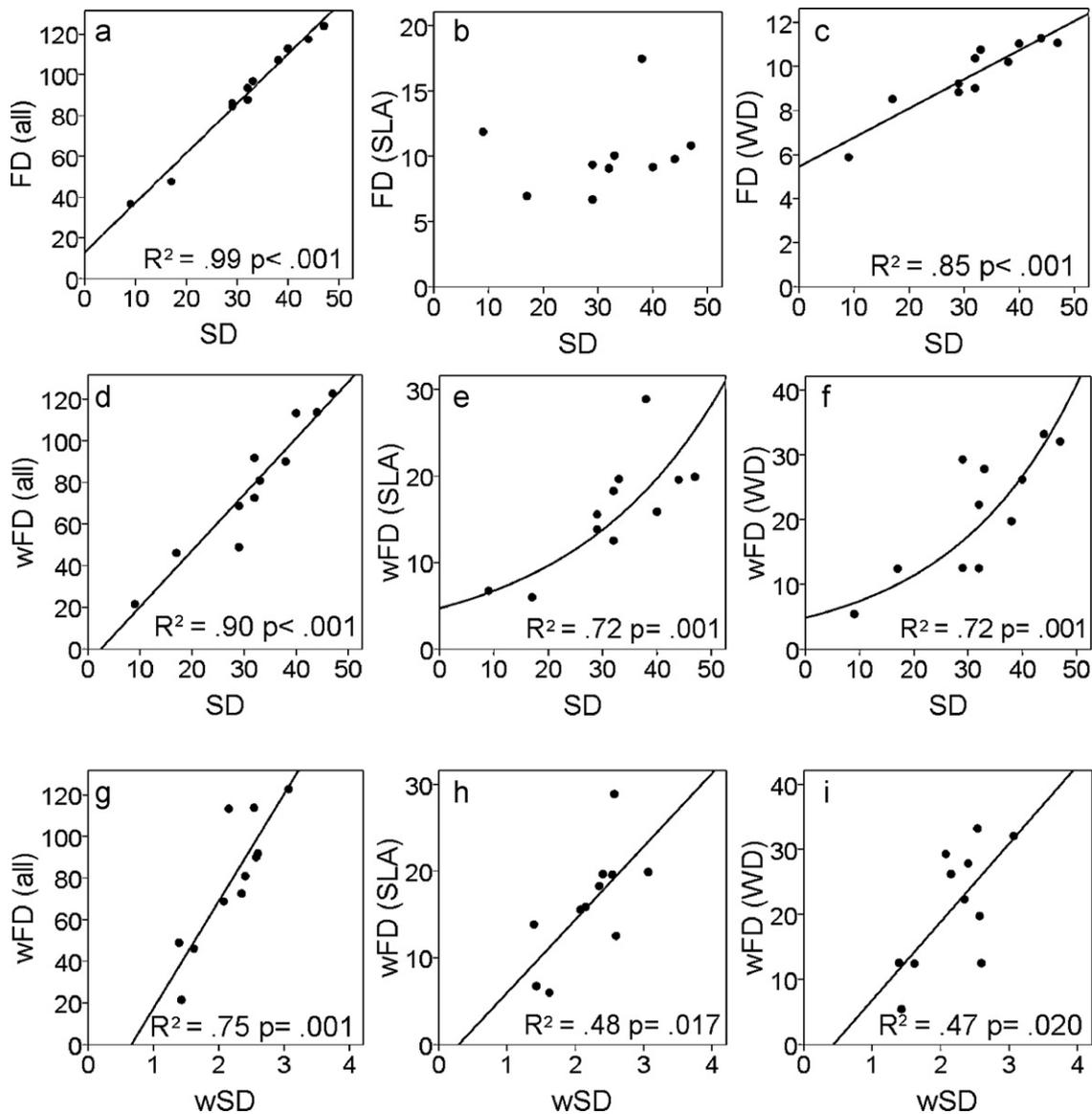


Fig. 2. Functional diversity as a function of species diversity indices in secondary forests in Southeastern Mexico. Left, middle and right columns illustrate functional diversity measures based on all traits, SLA and wood density respectively. Upper row illustrates the relations between species richness (SD) and incidence-based functional diversity (FD), middle row shows the relations between species richness (SD) and weighted functional diversity (wFD) and the lower row illustrates weighted functional diversity (wFD) as a function of weighted species diversity (wSD). The best fitting curves (tested for linear, logarithmic and exponential) are depicted in the figures with the R^2 and significance levels.

diversity to increase with stand basal area, but not with successional age. We showed that species richness and species diversity are good predictors of functional diversity (weighted by abundance or based on species incidence) when all traits are included. When only a single trait is considered in the measurement of functional diversity, however, species richness underestimated the weighted functional diversity in a site. Here we discuss these results in the light of functional diversity theory.

Do species and functional diversity increase predictably during succession?

We predicted that functional and species diversity would increase during early secondary succession. Despite the sharp successional gradient considered, we found no relation with time after abandonment, but basal area clearly predicted some diversity measures (Table 2). Basal area reflects not only time since

abandonment, but also land use history and within-plot environmental heterogeneity and may therefore be a better descriptor of diversity changes during succession than fallow age per se (van Breugel et al., 2006; Chazdon et al., 2007). Stand basal area is considered to be an important indicator of succession because it modifies the local environment (Lebrija-Trejos et al., 2011) and acts as an important filter for functional traits well adapted to local conditions (Lebrija-Trejos et al., 2010b).

The incidence-based diversity measures increased logarithmically (Fig. 1a–c) with basal area, but the pattern is largely determined by few sites only. Inclusion of more young sites is needed to solve this question. The asymptotic increase suggests that in early structural development of the forest recruiting individuals are species not yet present in the plot, with functional strategies complementary to the ones already present. With increasing basal area, the increases in species and functional richness slow down. This suggests that plot-level increases in basal

area are either caused by growth of present individuals, or result from newly recruited individuals functionally similar to the ones already present in the community. The first alternative is supported by data from our sites showing that biomass accumulated in fewer, bigger individuals (van Breugel et al., 2006). The second alternative reflects the fact that with a higher number of species already present in the community the chance that ‘new’ species or functional types disperse to a site decreases (Schmid et al., 2002). Since functional redundancy is not found in our sites (see below) the first alternative is most plausible.

None of the importance-weighted diversity measures significantly changed with stand basal area, probably as a result of rapid, variable changes in some of the plots. For example, massive mortality of the pioneer *Ochroma pyramidale* (Bombacaceae), or a strong dominance of *Vochysia guatemalensis* (Vochysiaceae, 63% of total importance) in our older secondary forest has been reported (van Breugel et al., 2007). Such site-specific demography will swamp any subtle successional patterns in functional diversity when weighed by importance.

As most of the changes in diversity take place in early successional development (van Breugel et al., 2006, 2007), our 11 sites, covering the first 25 years of succession, provide us with a high resolution picture of early successional development. Moreover, this shifting cultivation land-use system is characterized by high pressure for land and older secondary forests are again brought into cultivation resulting in a high abundance of young secondary forests (van Breugel, 2007; I. Zermeño-Hernández, unpublished results). These are therefore specifically relevant to study for biodiversity-effects of land-use change and its consequences for ecosystem functioning. This puts changes in species and functional diversity during long term succession beyond the scope of this work. The asymptotic increase of species richness and functional richness with stand basal area suggests that diversity remains constant. An alternative possibility is a peak in functional diversity occurring at intermediate successional time, in line with the Intermediate Disturbance Hypothesis predicting a peak in species richness after disturbance (e.g. Sheil, 1999; Sheil and Burslem, 2003; Bongers et al., 2009). Whether species and functional diversity remain tightly correlated (see next section) is also important for discussing long term successional changes in diversity. Possibly functional redundancy starts to play an important role at later stages of succession (Laliberté et al., 2010; Paquette and Messier, 2011), or on the contrary limiting similarity causes functional diversity to increase disproportionately to allow species to co-exist (Holdaway and Sparrow, 2006; Cardinale et al., 2007). More research needs to be conducted to clarify such long term successional dynamics in species and functional diversity.

Our analysis testing for diversity as a response of stand basal area suggests that increased productivity during succession is a driver of increases in diversity. The opposite causal direction, increased productivity as a response of increases in diversity, is also frequently studied (e.g. Tilman, 2001a; van Ruijven and Berendse, 2005). The use of one or the other, of course, depends on the research interests. The present study focuses on the effect of land-use change on (functional) diversity in tropical forests, making diversity as a response to changes in stand basal area (structural variable of succession) most appropriate. Such effect of succession on functional diversity is likely to have major implications for ecosystem functioning (e.g. Díaz and Cabido, 2001; Nadrowski et al., 2010). It must be noted however that the present study does not explicitly link functional diversity to ecosystem functioning, and that changes in functional diversity may not proportionally translate into changes in particular ecosystem functions (cf. Bihn et al., 2010).

Does species diversity predict functional diversity?

We found that functional diversity generally increased with species diversity (e.g. Biswas and Mallik, 2011). The shape of this relationship, however, depends on the number and nature of functional traits included. Incidence-based and weighted functional diversity (9 traits) were strongly linearly related to species richness and to species diversity (Fig. 2a, d and g). These linear relationships suggest that species are functionally complementary; each species added to the system represents therefore a functional profile that was not present before (cf. Díaz and Cabido, 2001). Thus, our results suggest a lack of functional redundancy during early secondary forest succession, although we recognize that implying redundancy from the SD–FD relationship depends on the FD index as well as on the functional traits selected and methods of classification (continuous or in functional groups) (Rosenfeld, 2002). Lack of functional redundancy may indicate that ecological resilience is lacking since functional redundancy rather than functional diversity is what maintains or restores ecosystem functioning under changing environmental conditions or disturbance events (Walker et al., 1999; Díaz and Cabido, 2001; Micheli and Halpern, 2005). However linking redundancy with resilience of ecosystem functioning requires knowledge on whether ‘redundant’ species also respond differently to disturbance (‘response diversity’), so that the functions can be maintained with species loss due to disturbance (Elmqvist et al., 2003; Laliberté et al., 2010). Considering this we can only conclude that the linear relation between species and functional diversity offers no reason to believe that ecological functions are safeguarded against species loss through functional redundancy (c.f. Bihn et al., 2010). Further research should clarify how ‘response diversity’ develops with succession in the study sites.

Incidence-based functional diversity of single traits was either not related to species richness (FD_{SLA} , Fig. 2b) or linearly related to species richness (FD_{WD} , Fig. 2c). In single-trait functional diversity the effective dimensionality is reduced, and as such an increase in FD depends strongly on species identity and the particular trait values of the species added (Petchev and Gaston, 2002), which causes different traits to respond differently. We hypothesized a logarithmic relationship when functional richness of single traits is plotted against species richness, which would indicate partial complementarity. The linear pattern in the case of FD_{WD} indicates that additional species are complementary in their wood density values to the ones already present. The logarithmic model showed a slightly higher fit (R^2 of 0.88) but because of the minimal difference (<0.05) we chose the most parsimonious model (linear: R^2 of 0.85) to describe the data. This suggests that a saturating relationship may be underlying these data but a longer chronosequence is needed to detect it.

The biomass ratio hypothesis (Grime, 1998) predicts that the functional traits of the most abundant species largely determine ecosystem processes and is supported by several studies (e.g. Garnier et al., 2004; Mokany et al., 2008). Abundance-weighted measures of functional diversity are thus needed when ecosystem processes are the point of concern. Since collection of functional trait data for a large suite of species is time, money and labour intensive (Baraloto et al., 2010b), the use of species number as an easy to obtain proxy for weighted functional diversity is much desired. Indeed, species richness strongly predicted weighted functional diversity for all traits, and could serve therefore as an adequate proxy. However, the usefulness of species richness as an indicator of wFD depends on the functional trait included, and hence, on the ecosystem process under concern. Indeed, we found that species richness underestimated weighted functional diversity in SLA (wFD_{SLA}) as well as wFD in wood density (wFD_{WD}). The

reduction of effective dimensionality of trait space that results from weightings and from using single traits, increases the importance of community composition and highlights the functional identity of the dominant species. This allows functional diversity to further differentiate between communities beyond differentiation based on species richness only. The exponential increase in weighted functional diversity of single traits with species richness results from either more evenly distributed species importance values, or from co-occurring species becoming more functionally distant due to niche differentiation. Since single trait functional diversity indices (wFD_{SLA} and wFD_{WD}) are linearly related to weighted species diversity (wSD) (next section), the exponential relation is mainly determined by more evenly distributed importance values.

Both functional diversity and species diversity indices have a reduced effective dimensionality when weighted for abundances because weighting species brings the focus towards fewer, dominant species (cf. Petchey and Gaston, 2002). Linear relationships are found when weighted functional diversity (wFD_{ALL} , wFD_{SLA} and wFD_{WD}) is plotted against weighted species diversity (wSD) (Fig. 2g–i). This indicates that species diversity is a better proxy for weighted functional diversity (wFD) than species richness (SD) in our early successional sites, specifically when a single trait is included. It also reflects that there is no indication of increased functional distance between species (niche differentiation) since differentiation of communities based on weighted species diversity is proportional to that of weighted functional diversity. Whether indeed this is a general pattern legitimating the use of species diversity as a proxy for weighted functional diversity should be confirmed by additional studies across different ecosystems.

Our results of functional diversity patterns with forest structural development and of functional diversity against species diversity demonstrate that trait choice is crucial when comparing functional diversity among sites, just as the choice of functional diversity index, which has been discussed previously (e.g. Scherer-Lorenzen et al., 2007; Bihn et al., 2010).

Our study has a limited sampling size and chronosequence length which reduces extrapolative power across regions. The significant trends are in line with our expectations based on theory, suggesting that our results are a conservative estimate of real patterns found in nature.

Conclusions

Species and functional richness increase logarithmically with structural development during forest succession (less than 25 years of abandonment). Stand basal area predicts functional richness well, but time after abandonment does not. Species richness and diversity are good predictors of functional diversity (based on incidence or weighted by species importance) when a range of traits is considered; the linear relationship between species and functional richness suggests that functional redundancy is limited in secondary forest. When a single trait is included in the functional diversity measure, species richness may underestimate weighted functional diversity. Careful consideration of the traits required to capture the ecosystem process of interest is thus essential: number and nature of traits significantly determine the outcome.

Acknowledgements

We thank Gilberto Jamangapee for fieldwork assistance and species identification. Jorge Rodríguez-Velázquez has been of great technical support. We are grateful for the statistical advice of P. Jansen, F. van Langevelde and K. Tomlinson. ML was supported by a research grant from Wageningen University and Research

center. MvB and FB were supported by NWO-WOTRO (Netherlands Organisation for Scientific Research - Science for Global Development) grant W85-326. MMR was supported by MABOTRO projects SEMARNAT-CONACYT 2002-C01-0597 and SEP-CONACYT CB-2005-01-51043. Fieldwork was partly supported by US National Science Foundation grant DEB-0639393. LP and LP were partly funded by the DiverSus project through Inter-American Institute for Global Change Research (IAI) CRN 2015, which is supported by the US National Science Foundation (Grant GEO-0452325). B. Williamson, C. Baraloto and three anonymous reviewers constructively commented on an earlier version of this manuscript.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ppees.2011.10.002.

References

- Ackerly, D.D., Cornwell, W.K., 2007. A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. *Ecology Letters* 10, 135–145.
- Baraloto, C., Marcon, E., Morneau, F., Pavoine, S., Roggy, J.-C., 2010a. Integrating functional diversity into tropical forest plantation designs to study ecosystem processes. *Annals of Forest Science* 67, 303.
- Baraloto, C., Timothy Paine, C.E., Patiño, S., Bonal, D., Hérault, B., Chave, J., 2010b. Functional trait variation and sampling strategies in species-rich plant communities. *Functional Ecology* 24, 208–216.
- Bihn, J.H., Gebauer, G., Brandl, R., 2010. Loss of functional diversity of ant assemblages in secondary tropical forests. *Ecology* 91, 782–792.
- Biswas, S.R., Mallik, A.U., 2011. Species diversity and functional diversity relationship varies with disturbance intensity. *Ecosphere* 2, 1–10.
- Bongers, F., Poorter, L., Hawthorne, W.D., Sheil, D., 2009. The intermediate disturbance hypothesis applies to tropical forests, but disturbance contributes little to tree diversity. *Ecology Letters* 12, 798–805.
- Cardinale, B.J., Srivastava, D.S., Emmett Duffy, J., Wright, J.P., Downing, A.L., Sankaran, M., Jouseau, C., 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* 443, 989–992.
- Cardinale, B.J., Wright, J.P., Cadotte, M.W., Carroll, I.T., Hector, A., Srivastava, D.S., Loreau, M., Weis, J.J., 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences of the United States of America* 104, 18123–18128.
- Casanoves, F., Di Rienzo, J.A., Pla, L., 2008. User Manual f-Diversity: Statistical Software for the Analysis of Functional Diversity, 1st ed., Argentina, (ISBN 978-987-05-5238-3). <http://docs.google.com/viewer?a=v&pid=sites&srcid=ZGVmYXVsdGRvbWpbnxmdW5jdGlubmFsZGI2ZjZjaXR5fGd40jNkYThjMDIhNmE0MDI5NDg>.
- Casanoves, F., Pla, L., Di Rienzo, J.A., Díaz, S., 2011. FDiversity: a software package for the integrated analysis of functional diversity. *Methods in Ecology and Evolution* 2, 233–237.
- Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., Zanne, A.E., 2009. Towards a worldwide wood economics spectrum. *Ecology Letters* 12, 351–366.
- Chazdon, R.L., Letcher, S.G., van Breugel, M., Martínez-Ramos, M., Bongers, F., Finegan, B., 2007. Rates of change in tree communities of secondary neotropical forests following major disturbances. *Philosophical Transactions of the Royal Society B: Biological Sciences* 362, 273–289.
- Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., Steege, H.T., Morgan, H.D., Heijden, M.G.A.v.d., Pausas, J.G., Poorter, H., 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51, 335–380.
- Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O., Hobbie, S.E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Quested, H.M., Santiago, L.S., Wardle, D.A., Wright, I.J., Aerts, R., Allison, S.D., van Bodegom, P., Brovkin, V., Chatain, A., Callaghan, T.V., Díaz, S., Garnier, E., Gurvich, D.E., Kazakou, E., Klein, J.A., Read, J., Reich, P.B., Soudzilovskaia, N.A., Vaieretti, M.V., Westoby, M., 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters* 11, 1065–1071.
- Díaz, S., Cabido, M., 2001. Vive la difference: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution* 16, 646–655.
- Díaz, S., Lavorel, S., Chapin III, F.S., Tecco, P.A., Gurvich, D.E., Grigulis, K., 2007a. Functional diversity—at the crossroads between ecosystem functioning and environmental filters. In: Canadell, J.G., Pataki, D.E., Pitelka, L.F., Díaz, S., Lavorel, S., Chapin, F.S., Tecco, P.A., Gurvich, D.E., Grigulis, K. (Eds.), *Terrestrial Ecosystems in a Changing World*. Springer, Berlin, Heidelberg, pp. 81–91.
- Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K., Robson, T.M., 2007b. Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences of the United States of America* 104, 20684–20689.

- Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B., Jon, N., 2003. Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment* 1, 488–494.
- Garnier, E., Cortez, J., Billes, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C., Toussaint, J.-P., 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology* 85, 2630–2637.
- Grime, J.P., 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* 86, 902–910.
- Hillebrand, H., Matthiessen, B., 2009. Biodiversity in a complex world: consolidation and progress in functional biodiversity research. *Ecology Letters* 12, 1405–1419.
- Holdaway, R.J., Sparrow, A.D., 2006. Assembly rules operating along a primary riverbed-grassland successional sequence. *Journal of Ecology* 94, 1092–1102.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75, 3–35.
- Laliberté, E., Wells, J.A., DeClerck, F., Metcalfe, D.J., Catterall, C.P., Queiroz, C., Aubin, I., Bonser, S.P., Ding, Y., Fraterrigo, J.M., McNamara, S., Morgan, J.W., Merlos, D.S., Vesk, P.A., Mayfield, M.M., 2010. Land-use intensification reduces functional redundancy and response diversity in plant communities. *Ecology Letters* 13, 76–86.
- Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* 16, 545–556.
- Lavorel, S., Grigulis, K., Lamarque, P., Colace, M., Garden, D., Girel, J., Pellet, G., Douzet, R., 2010. Using plant functional traits to understand the landscape distribution of multiple ecosystem services. *Journal of Ecology* 99, 135–147.
- Lebrija-Trejos, E., Meave, J.A., Poorter, L., Pérez-García, E.A., Bongers, F., 2010a. Pathways, mechanisms and predictability of vegetation change during tropical dry forest succession. *Perspectives in Plant Ecology, Evolution and Systematics* 12, 267–275.
- Lebrija-Trejos, E., Pérez-García, E.A., Meave, J.A., Bongers, F., Poorter, L., 2010b. Functional traits and environmental filtering drive community assembly in a species-rich tropical system. *Ecology* 91, 386–398.
- Lebrija-Trejos, E., Pérez García, E.A., Meave, J.A., Poorter, L., Bongers, F., 2011. Environmental changes during secondary succession in a tropical dry forest in Mexico. *Journal of Tropical Ecology* 27, 1–13.
- MEA, 2005. Millennium Ecosystems Assessment. World Resources Institute, Washington DC.
- Mason, N.W.H., MacGillivray, K., Steel, J.B., Wilson, J.B., 2003. An index of functional diversity. *Journal of Vegetation Science* 14, 571–578.
- Mason, N.W.H., Mouillot, D., Lee, W.G., Wilson, J.B., 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos* 111, 112–118.
- Mayfield, M.M., Boni, M.F., Daily, G.C., Ackerly, D., 2005. Species and functional diversity of native and human-dominated plant communities. *Ecology* 86, 2365–2372.
- McGill, B., Enquist, B., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution* 21, 178–185.
- Micheli, F., Halpern, B.S., 2005. Low functional redundancy in coastal marine assemblages. *Ecology Letters* 8, 391–400.
- Mokany, K., Ash, J., Roxburgh, S., 2008. Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. *Journal of Ecology* 96, 884–893.
- Mouchet, M.A., Villéger, S., Mason, N.W.H., Mouillot, D., 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology* 24, 867–876.
- Mouillot, D., Mason, W.H.N., Dumay, O., Wilson, J.B., 2005. Functional regularity: a neglected aspect of functional diversity. *Oecologia* 142, 353–359.
- Nadrowski, K., Wirth, C., Scherer-Lorenzen, M., 2010. Is forest diversity driving ecosystem function and service? *Current Opinion in Environmental Sustainability* 2, 75–79.
- Norden, N., Chazdon, R.L., Chao, A., Jiang, Y.-H., Vilchez-Alvarado, B., 2009. Resilience of tropical rain forests: tree community reassembly in secondary forests. *Ecology Letters* 12, 385–394.
- Onoda, Y., Westoby, M., Adler, P.B., Choong, A.M.F., Clissold, F.J., Cornelissen, J.H.C., Díaz, S., Dominy, N.J., Elgart, A., Enrico, L., Fine, P.V.A., Howard, J.J., Jalili, A., Kitajima, K., Kurokawa, H., McArthur, C., Lucas, P.W., Marksteijn, L., Pérez-Harguindeguy, N., Poorter, L., Richards, L., Santiago, L.S., Sosinski, E.E., Van Bael, S.A., Warton, D.I., Wright, I.J., Joseph Wright, S., Yamashita, N., 2011. Global patterns of leaf mechanical properties. *Ecology Letters* 14, 301–312.
- Pakeman, R.J., Quedsted, H.M., 2007. Sampling plant functional traits: what proportion of the species need to be measured? *Applied Vegetation Science* 10, 91–96.
- Paquette, A., Messier, C., 2011. The effect of biodiversity on tree productivity: from temperate to boreal forests. *Global Ecology and Biogeography* 20, 170–180.
- Petchey, O.L., Gaston, K.J., 2002. Functional diversity (FD), species richness and community composition. *Ecology Letters* 5, 402–411.
- Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward. *Ecology Letters* 9, 741–758.
- Petchey, O.L., Gaston, K.J., 2007. Dendrograms and measuring functional diversity. *Oikos* 116, 1422–1426.
- Petchey, O.L., O’Gorman, E.J., Flynn, D.F.B., 2010. A functional guide to functional diversity measures. In: Naeem, S., Bunker, D.E., Hector, A., Loreau, M., Perrings, C. (Eds.), *Biodiversity, Ecosystem Functioning, & Human Wellbeing and Ecological and Economic Perspective*. Oxford University Press, New York, pp. 49–59.
- Pla, L., Casanoves, F., di Rienzo, J.A., Fernandez, F., Finegan, B., 2008. Confidence intervals for functional diversity indices considering species abundance. In: *Proceedings of the XXIV International Biometric Conference*, Dublin.
- Poorter, H., Niinemets, Ü., Poorter, L., Wright, I.J., Villar, R., 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist* 182, 565–588.
- Rasband, W.S., 2008. ImageJ. US National Institutes of Health, Bethesda, MD, USA.
- Rosenfeld, J.S., 2002. Functional redundancy in ecology and conservation. *Oikos* 98, 156–162.
- Scherer-Lorenzen, M., Körner, C., Schulze, E.-D., Scherer-Lorenzen, M., Potvin, C., Koricheva, J., Schmid, B., Hector, A., Bornik, Z., Reynolds, G., Schulze, E.D., 2005. The design of experimental tree plantations for functional biodiversity research. In: *Forest Diversity and Function*. Springer, Berlin, Heidelberg, pp. 347–376.
- Scherer-Lorenzen, M., Schulze, E., Don, A., Schumacher, J., Weller, E., 2007. Exploring the functional significance of forest diversity: a new long-term experiment with temperate tree species (BIOTREE). *Perspectives in Plant Ecology, Evolution and Systematics* 9, 53–70.
- Schleuter, D., Dauffresne, M., Massol, F., Argillier, C., 2010. A user’s guide to functional diversity indices. *Ecological Monographs* 80, 469–484.
- Schmid, B., Joshi, J., Schläpfer, F., 2002. Empirical evidence for biodiversity–ecosystem functioning relationship. In: Kinzig, A.P., Pacala, S.W., Tilman, D. (Eds.), *The Functional Consequences of Biodiversity: Empirical Progress and Theoretical Extensions*. Princeton University Press, Princeton, NJ, pp. 120–150.
- Shannon, C., Weaver, W., 1949. *The Mathematical Theory of Communication*. University of Illinois Press, Urbana, USA.
- Sheil, D., 1999. Tropical forest diversity, environmental change and species augmentation: after the intermediate disturbance hypothesis. *Journal of Vegetation Science* 10, 851–860.
- Sheil, D., Burslem, D.F.R.P., 2003. Disturbing hypotheses in tropical forests. *Trends in Ecology & Evolution* 18, 18–26.
- Siebe, C., Martínez-Ramos, M., Segura-Warnholtz, G., Rodríguez-Valázquez, J., Sánchez-Beltrán, S., 1996. Soil and vegetation patterns in the tropical rainforest at Chajul, Chiapas, southeast Mexico. In: *International Congress on Soils of Tropical Forest Ecosystems*. 3rd Conference on Forest Soils. Mulawarman University Press, Samarinda, Indonesia, pp. 40–58.
- Tilman, D., 2000. Causes, consequences and ethics of biodiversity. *Nature* 405, 208–211.
- Tilman, D., 2001a. Diversity and productivity in a long-term grassland experiment. *Science* 294, 843–845.
- Tilman, D., 2001b. Functional diversity. In: Levin, S.A. (Ed.), *Encyclopedia of Biodiversity*. Academia Press, San Diego, pp. 109–120.
- van Breugel, M., 2007. *Dynamics of Secondary Forests*. Wageningen University, Wageningen.
- van Breugel, M., Bongers, F., Martínez-Ramos, M., 2007. Species dynamics during early secondary forest succession: recruitment, mortality and species turnover. *Biotropica* 39, 610–619.
- van Breugel, M., Martínez-Ramos, M., Bongers, F., 2006. Community dynamics during early secondary succession in Mexican tropical rain forests. *Journal of Tropical Ecology* 22, 663.
- van Ruijven, J., Berendse, F., 2005. Diversity–productivity relationships: initial effects, long-term patterns, and underlying mechanisms. *Proceedings of the National Academy of Sciences of the United States of America* 102, 695–700.
- Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89, 2290–2301.
- Walker, B., Kinzig, A., Langridge, J., 1999. Original articles: plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems* 2, 95–113.