

Tree diversity promotes functional dissimilarity and maintains functional richness despite species loss in predator assemblages

Andreas Schuldt · Helge Bruelheide · Walter Durka ·
Stefan G. Michalski · Oliver Purschke ·
Thorsten Assmann

Received: 7 March 2013 / Accepted: 17 September 2013 / Published online: 6 October 2013
© Springer-Verlag Berlin Heidelberg 2013

Abstract The effects of species loss on ecosystems depend on the community's functional diversity (FD). However, how FD responds to environmental changes is poorly understood. This applies particularly to higher trophic levels, which regulate many ecosystem processes and are strongly affected by human-induced environmental changes. We analyzed how functional richness (FRic), evenness (FEve), and divergence (FDiv) of important generalist predators—epigeic spiders—are affected by changes in woody plant species richness, plant phylogenetic diversity, and stand age in highly diverse subtropical forests in China. FEve and FDiv of spiders increased with plant richness and stand age. FRic remained on a constant level despite decreasing spider species richness with increasing

plant species richness. Plant phylogenetic diversity had no consistent effect on spider FD. The results contrast with the negative effect of diversity on spider species richness and suggest that functional redundancy among spiders decreased with increasing plant richness through non-random species loss. Moreover, increasing functional dissimilarity within spider assemblages with increasing plant richness indicates that the abundance distribution of predators in functional trait space affects ecological functions independent of predator species richness or the available trait space. While plant diversity is generally hypothesized to positively affect predators, our results only support this hypothesis for FD—and here particularly for trait distributions within the overall functional trait space—and not for patterns in species richness. Understanding the way predator assemblages affect ecosystem functions in such highly diverse, natural ecosystems thus requires explicit consideration of FD and its relationship with species richness.

Communicated by Sven Bacher.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-013-2790-9) contains supplementary material, which is available to authorized users.

A. Schuldt (✉) · T. Assmann
Institute of Ecology, Leuphana University Lüneburg,
Scharnhorststrasse 1, 21335 Lüneburg, Germany
e-mail: schuldt@uni.leuphana.de

H. Bruelheide · O. Purschke
Institute of Biology/Geobotany and Botanical Garden, Martin
Luther University Halle-Wittenberg, Am Kirchtor 1, 06108 Halle,
Germany

H. Bruelheide · W. Durka · O. Purschke
German Centre for Integrative Biodiversity Research (iDiv)
Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany

W. Durka · S. G. Michalski
Department of Community Ecology, Helmholtz Centre
for Environmental Research, UFZ, Theodor-Lieser-Strasse 4,
06120 Halle, Germany

Keywords BEF China · Biodiversity · Ecosystem function · Invertebrate · Trophic interaction

Introduction

Increasing awareness that major human activities negatively affect species and ecosystems has focused much attention on disentangling the relationship between biodiversity and the functioning of ecosystems (Hooper et al. 2005; Naeem et al. 2012). While many studies have demonstrated positive effects of species richness on ecosystem functioning and stability (Cardinale et al. 2012; Hooper et al. 2012), much of our current knowledge is based on relatively species-poor plant communities and experiments from grassland ecosystems (Schmid et al.

2009). However, species-rich ecosystems such as tropical and subtropical forests are particularly affected by habitat degeneration and alteration, and the consequences of species loss for ecological processes and the resulting ecosystem services are of high ecological and economic importance (Kremen et al. 2000; Lopez-Pujol et al. 2006).

Most importantly, however, it has become clear that in many cases the effects of species richness depend on the diversity of the respective species' functional traits (Hooper et al. 2005). Yet, this functional trait diversity is not necessarily a linear function of species richness (e.g., Mason et al. 2008), and contrasting patterns of species and functional diversity (FD) indicate that species diversity may not always be a consistent predictor of the diversity and strength of functional effects of species assemblages (Böhnke et al. 2013; Devictor et al. 2010; Villéger et al. 2010). Recent studies have shown that FD might better explain biodiversity effects on ecosystem functions than species richness measures (e.g., Cadotte et al. 2009). Yet, our knowledge of how FD, and consequently the functional effects, of species assemblages are affected by environmental changes—whether of an anthropogenic or natural cause—still lags behind our understanding of general patterns in species richness (Feld et al. 2009). This applies particularly to higher trophic levels such as predators, which affect ecosystem functions through their interactions with primary consumers and producers (Haddad et al. 2009; Schmitz 2006). Trophic interactions play a crucial role in species-rich subtropical and tropical forests (Terborgh 2012), but little attention has been paid to how tree diversity or forest age affect predator FD. Knowledge of such relations is also particularly relevant for conservation strategies concerned with the question of whether secondary (and potentially less species-rich) forests can preserve the FD of higher trophic levels in the face of increasing loss of natural forests (Bihn et al. 2010).

Here, we analyze key features of the FD of epigeic spiders across gradients in woody plant species richness and stand age in a highly diverse forest ecosystem in subtropical China. The forest floor compartment contributes a substantial part of the overall arthropod diversity of species-rich forests (Stork and Grimbacher 2006), and epigeic spiders can have an important impact on ecosystem functions in these forests by affecting decomposers (e.g., Wise 2004) and herbivores [which often spend part of their life cycle on the forest floor or are affected by epigeic predators when feeding on tree seedlings; e.g., Riihimäki et al. (2005); Visser et al. (2011)]. A previous study in these forests indicated that the functional effects of these predators might be opposed to species richness effects (Schuldt et al. 2011). However, these indications were based on a coarse assignment of spiders to functional groups that

excluded variation in functional traits within groups and did not account for abundance patterns or body size distributions. Here, we incorporate a variety of traits related to the resource use of spiders into complementary measures of FD which allow for a thorough assessment of the richness, evenness and divergence of functional traits within species assemblages (Mouchet et al. 2010; Villéger et al. 2008). In short, functional richness (FRic) measures the volume of trait space occupied by an assemblage, whereas functional evenness (FEve) and divergence (FDiv) characterize how regular and dissimilar, respectively, the species are distributed in this functional trait space (Pavoine and Bonsall 2011; Villéger et al. 2008). Higher FRic, but also higher evenness or divergence, would indicate a broader resource use within the spider assemblages and might, in consequence, lead to stronger prey control.

Besides testing for the effects of woody plant species richness (as the most general and widely used measure of diversity) and forest age, we included phylogenetic diversity of the forest stands as a predictor of the FD of spiders. Phylogenetic diversity of plant communities might be used as a proxy for unmeasured functional plant traits (see Cadotte et al. 2009; Purschke et al. 2013) and has recently been shown to affect the abundance of predators in a grassland experiment (Dinnage et al. 2012). However, comparative data from other ecosystems are lacking so far. We hypothesize that (1) depending on how strongly FRic is related to spider species richness, it either decreases [strong relationship with the likewise decreasing spider richness observed in the studied forests; Schuldt et al. (2011)] or increases [weak relationship due to functional redundancy; stronger effects of potentially available niches or resources; (Root 1973; Haddad et al. 2009)] with woody plant species richness, phylogenetic diversity and plot age. Moreover, we expect (2) the evenness and divergence of abundances of spiders within the available trait space to increase with plant diversity and plot age, independent of patterns in FRic. Older and more plant species-rich plots might promote resource diversity and allow abundant and more specialized species to effectively separate within the available niche space (Mason et al. 2008).

Materials and methods

Study site and sampling design

The study was conducted in the Gutianshan National Nature Reserve (9°14'N, 118°07'E), Zhejiang Province, southeast China. The reserve covers 81 km² of mountainous, semi-evergreen broad-leaved forest (at 300–1,260 m a.s.l.) and is characterized by a subtropical monsoon climate (mean annual temperature ca. 15 °C, mean annual

precipitation ca. 2,000 mm) (Legendre et al. 2009). Dominant tree species are *Castanopsis eyrei* (Champ. ex Benth.) Tutch. and *Schima superba* Gardn. et Champ. A total of 27 study plots (30 × 30 m) were established in 2008. The plots were selected based on stand age (ranging between <20 and >80 years) and species richness of woody plants (25–69 species) [see Bruelheide et al. (2011) for details].

Four pitfall traps were installed in the corners of the central 10 × 10-m square of each plot in 2009. Traps (550-ml plastic cups with an upper diameter of 8.5 cm) were filled with an ethanol-glycerol-acetic acid solution as a trapping fluid and emptied fortnightly during the main growing season from 30 March to 2 September 2009 (Schuldt et al. 2011).

Functional traits

Adult spiders, which accounted for almost 80 % of the total catch, were determined to species or morphospecies (within families or genera) on the basis of their genitalia. For our analyses of FD, we selected five traits that are considered to have a major effect on the foraging characteristics of spiders (Cardoso et al. 2011) and thus strongly determine the functional impact of spider assemblages on their prey. Specifically, these were body size, phenology, hunting type, vegetational stratification and prey range. Body size was measured as the total length from the front of the carapace to the end of the abdomen. Body size influences a wide range of ecological and physiological characteristics of a species (e.g., locomotion, space use, life history) and, in particular, strongly affects resource use (Brose et al. 2006). Up to six individuals per species were measured, and mean body size (averaged across male and female data) was used as a continuous variable. Phenology was based on the main activity periods of each species over the trapping season. The three categories (early, late, or whole season) were reclassified as two binary variables (early and late, where whole-season species have positive values in both cases) for the analyses, and each of the two variables was assigned a weight = 0.5 in the calculation of the FD indices to ensure overall equal weights for each trait (Laliberté and Legendre 2010). Differences in species phenology determine temporal patterns of predator pressure within species assemblages and can promote the coexistence of otherwise ecologically similar species (Uetz 1977). Spiders can further be separated in terms of their hunting type into web-building and cursorial species, and this classification can be refined by the vegetation stratum that is primarily used and the range of prey organisms consumed. These characteristics contribute to resource partitioning among species and thus to defining the functional effects of predators on prey communities. Hunting type, vegetation stratum and prey range were coded as binary variables depending

on whether species were web builders or cursorial hunters, preferred forest floor habitats or higher vegetational strata, and whether they were generalists or prey specialists [e.g., many Mimetidae and Zodariidae are specialized spider and ant hunters, respectively; Jocqué and Dippenaar-Schoeman (2007)]. Data on hunting type, stratum and prey range are mostly available at a family or genus level only. However, these traits have been shown to be largely conserved within families and are sufficient to enable adequate classification of species in most cases (Cardoso et al. 2011). We used data from Jocqué and Dippenaar-Schoeman (2007), Cardoso et al. (2011), and our own observations to assign species to the respective hunting type, preferred stratum and prey range.

Environmental variables

Woody plant species richness was based on all tree and shrub individuals >1 m height. Plot age was estimated from stem cores and diameter at breast height measurements (Bruelheide et al. 2011). We also calculated Shannon diversity and evenness of the woody plant communities based on the total basal area of each species in the plots. Shannon diversity was highly correlated with woody plant species richness ($r = 0.81$; $P < 0.001$), and we only included evenness (less strongly correlated, $r = 0.57$; $P < 0.001$) as an additional measure of woody plant diversity in our analyses. We also included the species richness of the herb layer, measured as the species richness of all plant individuals <1 m in the central 10 × 10 m of each plot (Both et al. 2011). To assess the potential impacts of the phylogenetic composition of the woody plant communities on spiders, we calculated several measures of phylogenetic diversity (see “Statistical analysis”). As functional measures of plant diversity based on traits that can be meaningfully related to spider diversity were difficult to obtain for our study, phylogenetic diversity might help to quantify functional differences among woody plant species in the studied forests stands (e.g., Cadotte et al. 2009).

Observational studies in natural ecosystems have the advantage of testing ecological hypotheses under real world conditions with established plant and animal communities; however, plot characteristics that might potentially confound the results need to be taken into account. We therefore included altitude (m), soil pH, canopy cover (%) and cover of the herb layer (%) at the plot level, and litter cover (%), litter depth (cm) and vegetation cover (%) at the trap level as covariables in our analyses. These variables can influence spiders via effects on microclimate or habitat structure (Southwood and Henderson 2000). Altitude, canopy and herb layer cover were assessed during plot establishment in 2008. Soil pH (0–5 cm) was measured from dried and sieved samples in the summer of

2009 (Bruehlheide et al. 2011). At the same time, trap-level data were measured in a 1×1 -m square around each pit-fall trap. Measures of tree density and basal area were not included in the analyses due to strong collinearity with plot age (see Schuldt et al. 2011). While none of these variables were strongly correlated with, and their effects thus independent of, woody plant species richness (maximum correlation was $r = 0.24$), not accounting for this environmental variability might obscure potential effects of woody plant species richness on spider FD.

Statistical analysis

FD, like all measures of diversity, can be split into independent components that characterize distinct aspects of this diversity, namely richness, regularity or evenness, and divergence of FD within species assemblages (Mouchet et al. 2010; Pavoine and Bonsall 2011; Schleuter et al. 2010). For our study, we used the multidimensional FRic, FEve and FDiv indices proposed by Villéger et al. (2008). These indices have been shown to be adequate and complementary measures of FD, which allow for incorporation of different data types and (in the case of FEve and FDiv) species abundances (Laliberté and Legendre 2010; Mouchet et al. 2010; Schleuter et al. 2010). FRic usually increases with the number of species in an assemblage, whereas FEve and FDiv are less affected by species richness (Pavoine and Bonsall 2011; Schleuter et al. 2010). FRic estimates the amount of functional space occupied by a given species assemblage by calculating the convex hull volume that comprises the entire trait space filled by all species of this assemblage (Villéger et al. 2008). It can thus be used as a proxy of the range of functional traits represented in an assemblage, but does not take into account (in contrast to FEve and FDiv) differences in species abundance. Whereas FRic can increase with the overall range of trait values in an assemblage, FEve and FDiv are relative measures of the evenness and divergence, respectively, of trait distributions within the convex hull of FRic and are thus independent of the overall range of functional traits. FEve increases with increasing regularity of species' abundances within the trait space. FEve is highest when the spacing among species with different trait values is identical and all species are equally abundant. FDiv complements this measure by quantifying how species abundances are distributed in trait space. It is low when species with high abundances have trait values that are close to the center of functional trait space of an assemblage, and high when abundant species strongly deviate from these central trait values (Villéger et al. 2008).

The FD indices were calculated on the basis of the above spider traits (log-transformed body size, phenology, hunting type, vegetational stratification and prey range) with

the R package FD (Laliberté and Legendre 2010). We used dimensionality reduction (using both binary and continuous variables increased the number of dimensions) in the principal coordinates analysis required for the calculation of FRic (Laliberté and Legendre 2010), and the five axes retained accounted for 89 % of the overall trait information. The principal coordinates analysis was calculated from a Gower dissimilarity matrix and based on standardized trait values as implemented in the FD package. It is difficult to know whether species recorded with very few individuals are biologically associated with a habitat, as in many cases they only represent accidental occurrences of vagrant species. For a meaningful analysis we thus focused on species that were recorded with more than four individuals in the total catch. On average, the species excluded made up 3.6 % (± 1.4 SD) of spider individuals recorded per plot and were smaller than the species analyzed, indicating that their functional impact is low (see also Bihn et al. 2010). Species richness patterns were not affected by this procedure (cf. Schuldt et al. 2011). We also tested the extent to which each of the five traits contributed to the effects of the multivariate diversity indices. For this, we recalculated the indices for each combination of only four of the five traits by downweighting each trait in turn (by a factor of 10,000) and reanalyzed effects on plant diversity measures with these modified FD indices. This approach produces five different versions of the indices, where each version basically excludes the impact of one of the five traits, but it avoids numerical problems in the calculation of the indices that can arise from complete exclusion of a trait. To assess whether observed values of FD were simply a reflection of the species richness at a particular site, observed values of FRic, FEve and FDiv were compared to those obtained from 999 random communities. The latter were generated using null model 1s in Hardy (2008), shuffling the species' abundances in the species \times plot matrix across species and sites. This null model keeps constant (1) species richness within a plot, (2) species abundance distributions among plots, and (3) levels of spatial clustering (e.g., caused by dispersal limitation). For each plot and each of the three FD indices, standardized effect sizes (ses) [FRic.ses, FEve.ses, FDiv.ses; according to Gotelli and Rohde (2002)] were calculated as the observed FD relative to expected values from the random communities: $\text{ses} = (\text{observed FD index score} - \text{mean expected index score}) / \text{SD of the index across the 999 randomizations}$.

As a measure of phylogenetic diversity of the woody plant communities that is independent of species richness [in our study: $r = -0.24$; $P = 0.221$; Fig. S2a, Electronic supplementary material (ESM 1)], we calculated the mean pairwise phylogenetic distance (MPD). In comparison to woody species, herb species contributed relatively little to overall plant diversity (Both et al. 2011) and were

not considered. Plant diversity effects on epigeic spiders (via litter structure, prey availability) are probably driven primarily by the tree and shrub layers (see Schuldt et al. 2011), which contribute most to overall plant biomass. MPD quantifies the mean divergence between species (non-abundance-weighted MPD) or individuals (abundance-weighted MPD) within a community (Webb et al. 2002). Phylogenetic diversity measures were calculated based on an ultrametric phylogenetic tree of all woody species of the 27 study plots (Fig. S1, ESM 1; O. Purschke, S. G. Michalski, H. Bruelheide and W. Durka, unpublished data). Of the two measures of phylogenetic diversity, only the unweighted MPD index showed a significant relationship with the FD of spiders. Thus, we only included this index in the analysis.

Patterns in FD were analyzed with linear mixed effects models and FRic, FEve, and FDiv, and their corresponding standardized effect sizes (FRic.ses, FEve.ses, FDiv.ses) as response variables. As fixed effects, we included plot characteristics (canopy cover, herb layer cover, altitude, soil pH) and characteristics of the trap surroundings (litter depth, litter cover, vegetation cover) as covariables in addition to woody plant species richness, evenness of woody plant diversity, herb layer species richness, MPD, and plot age. We also included the interactions between plot age and woody plant species richness or MPD, respectively, in the full models. Woody plant species richness, MPD, and vegetation cover were log transformed to increase normality and homoscedasticity of the models. For the minimal model on FRic.ses, we included an exponential variance structure of the predictors as a weighting factor to achieve homogeneous variances of the model residuals (Zuur et al. 2009). We also checked for non-linear relationships between the FD indices and the predictor variables by analyzing second-order polynomials of the variables. Predictors were checked

for multicollinearity ($r > 0.7$) before being included in the full models. Due to the hierarchical structure of our data, we included plot identity as a random effect. We used model simplification by excluding predictor variables in an automated stepwise procedure based on the corrected Akaike information criterion (AICc) (Burnham and Anderson 2004). The models with the smallest number of predictors and the lowest global AICc were chosen as the most parsimonious, best-fit models for each FD index. Model residuals were checked for normality and homogeneity of variances. All analyses were conducted in R 2.15.1 (<http://www.R-project.org>).

Results

The analysis comprised 5,967 individuals of 80 spider species, with five species [*Pardosa laura* Karsch, *Pirata morphospecies 1*, *Liocranidae morphospecies 2*, *Pardosa wuyiensis* Yu & Song, *Itatsina praticola* (Bösenberg & Strand)] accounting for 55 % of all individuals. Mean species richness of spiders per trap strongly declined with increasing species richness of woody plants across the 27 study plots (Fig. 1a), but was not significantly related to plot age ($t = -0.59$; $P = 0.561$; Fig. S2b, ESM 1).

As expected, mean FRic of the spider assemblages increased with spider species richness across the plots (Fig. 1b). All other measures of FD were not related to spider species richness or FRic ($P > 0.2$ in all cases), indicating that FRic, FDiv and FEve indeed represented distinct and independent aspects of spider FD.

Despite the correlation with spider richness, FRic was not significantly related to woody plant species richness or plot age ($t = -0.23$; $P = 0.822$, and $t = -0.65$; $P = 0.521$, respectively, Fig. S2c, d in ESM 1). None of the explanatory variables were retained in the minimal

Fig. 1 Relationships between mean spider species richness per trap and **a** woody plant species richness and **b** functional richness (FRic) of the spider assemblages across a diversity gradient of 27 study plots in subtropical China

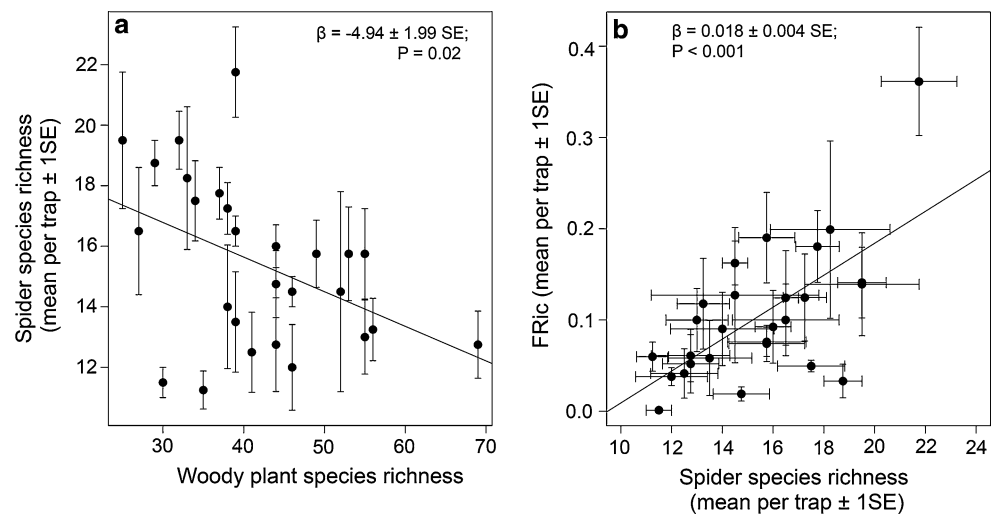


Table 1 Fixed factors retained in the minimal mixed-effects models for functional richness (FRic), evenness (FEve), and divergence (FDiv) (Observed values), and for their standardized effect sizes (ses) from null model comparisons (FRic.ses, FEve.ses, FDiv.ses)

Response	Fixed effects	Standardized estimate (±SE)	df	t	P
<i>Observed values</i>					
FRic	–	–	–	–	–
	AICc full/minimal model: –168.8/–194.4				
FEve	Mean phylogenetic distance ^a	–0.249 (±0.109)	25	–2.29	0.031
	AICc full/minimal model: –251.1/–265.7				
FDiv	Elevation (plot)	–0.322 (±0.089)	22	–3.59	0.002
	Woody plant species richness (plot) ^a	0.258 (±0.092)	22	2.28	0.011
	Plot age	0.211 (±0.095)	22	2.22	0.037
	Mean phylogenetic distance ^a	–0.392 (±0.094)	22	–4.16	<0.001
	AICc full/minimal model: –266.2/–279.4				
<i>Standardized effect sizes</i>					
FRic.ses	Vegetation cover (trap) ^a	0.182 (±0.071)	80	2.55	0.012
	Woody plant species richness (plot) ^a	0.275 (±0.128)	25	2.15	0.041
	AICc full/minimal model: 252.6/232.3				
FEve.ses	Litter cover (trap)	0.228 (±0.093)	80	2.45	0.017
	Herb layer plant species richness	0.224 (±0.094)	25	2.38	0.025
	AICc full/minimal model: 315.4/294.0				
FDiv.ses	Canopy cover (plot)	0.357 (±0.097)	21	3.68	0.001
	Elevation (plot)	–0.238 (±0.091)	21	–2.61	0.016
	Herb layer plant species richness (plot)	–0.296 (±0.097)	21	–3.05	0.006
	Woody plant species richness (plot) ^a	0.436 (±0.093)	21	4.70	<0.001
	Plot age	0.207 (±0.098)	21	2.13	0.460
	AICc full/minimal model: 309.6/291.5				

AICc Corrected Akaike's information criterion

^a Log transformed

model of FRic (Table 1). In contrast to FRic, however, FDiv significantly increased with woody plant species richness (Table 1; Fig. 2a), indicating that in particular the spread of abundances within the convex hull of the assemblages' functional traits increased with plant species richness. At the same time, FDiv and also FEve decreased with increasing MPD of the woody plant communities (Table 1; Fig. 2c, d). However, this was primarily an effect of the presence or absence of conifers (Fig. 2c). Excluding conifers and basing MPD calculations only on angiosperms removed any effect of MPD on FDiv and FEve, and instead revealed a positive effect of woody plant species richness also on FEve (Table S1 in ESM 1). Plot age was only included in the minimal model of FDiv, where it had a positive effect (Table 1; Fig. 2b). There were no significant effects of quadratic plant species richness or plot age terms on the relationships between woody plant species richness and FD in any of the models. The evenness of woody plant diversity was not included in the minimal models of any of the FD measures. Downweighting the impact of each of the five traits in turn showed that while the relationship between spider FDiv and woody plant species richness (and similarly MPD) was particularly strongly affected by spider phenology, the other traits as

well contributed to the strength of this relationship (i.e., standardized slopes became weaker when the impact of any of the traits, except for vegetational stratum, was downweighted; Table S2 in ESM 1). Variability in FEve was particularly strongly affected by the spider assemblages' phenological, hunting type (for the relationship with woody plant species richness), and body size characteristics (for the relationship with MPD; Table S2 in ESM 1).

Spider FRic.ses, FDiv.ses and FEve.ses, generated from the null model randomizations, were independent of spider species richness ($P > 0.75$ in all cases). The minimal model for FRic.ses showed a marginally significant, positive effect of woody plant species richness (Table 1), i.e., spider FRic tended to be on a higher level than expected, given the levels of spider species richness, in the more plant species-rich plots (Fig. 3a). In contrast, the minimal adequate model for FDiv.ses was qualitatively similar to the results for FDiv (Table 1; Fig. 3b). Likewise, results for FEve.ses showed a significant positive effect of plant species richness (Table 1; in this case an effect of herb layer plant species richness) that was similar to the effects observed for FEve when MPD was based on angiosperm community structure (see above).

Fig. 2 Independent effects on functional diversity indices of **a** woody plant species richness, **b** plot age, and **c, d** mean phylogenetic distance of woody plant species across the 27 study plots (partial residuals and 95 % confidence bands). *FEve* Functional evenness, *FDiv* functional divergence. All relationships are significant at $P < 0.05$ (see Table 1)

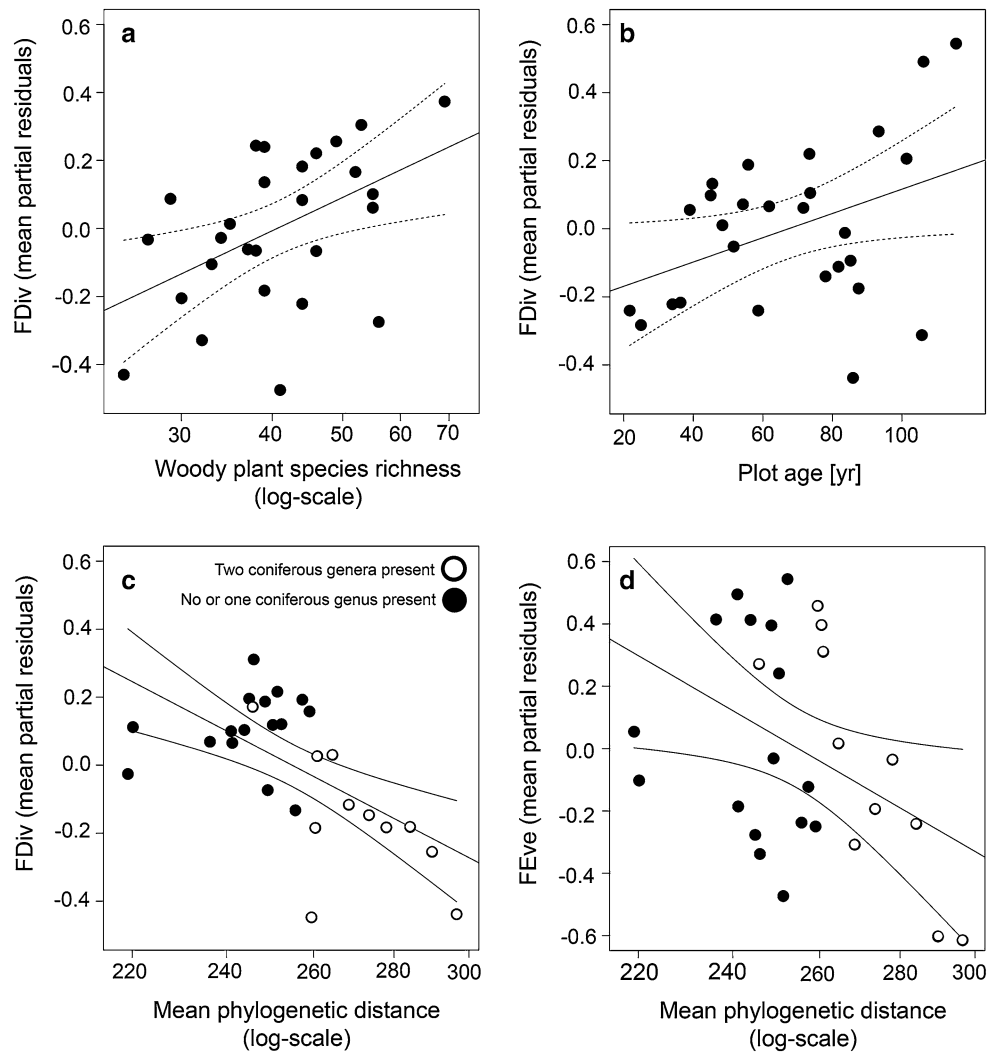
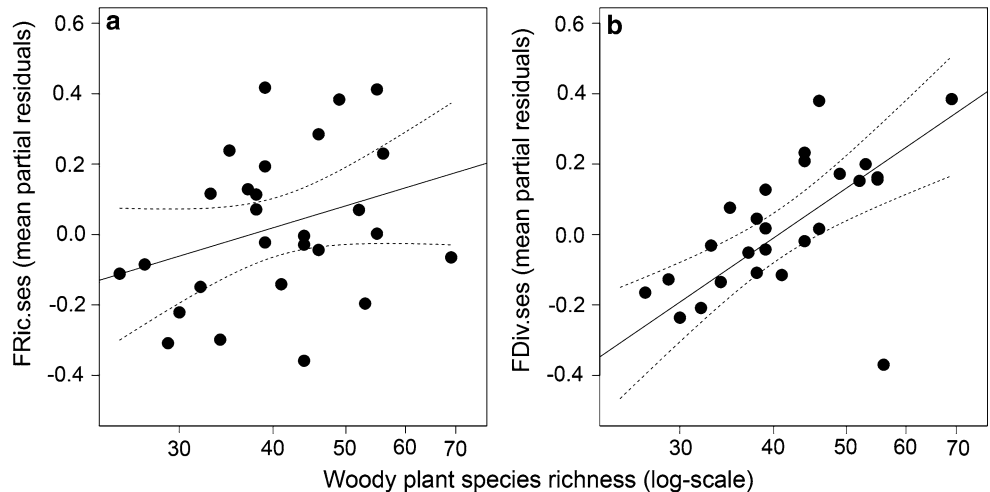


Fig. 3 Independent effects of woody plant species richness on **a** standardized effect sizes of *FRic*, and **b** standardized effect sizes of *FDiv* (partial residuals and 95 % confidence bands). Both relationships are significant at $P < 0.05$ (see Table 1)



Discussion

Our study shows that patterns in the FD of predators can deviate from those based solely on species richness.

Accounting for differences in the functional characteristics of species can thus help to better understand the potential effects, and the change in effects along environmental gradients, of predator assemblages on ecosystem functions.

FRic: decreasing redundancy of spiders with increasing tree diversity

Despite a strong decline in the species richness of spiders with increasing woody plant species richness, their FRic did not change. Similarly, plot age had no effect on spider FRic. The latter finding may be due to the high dispersal power of many spiders, which promotes relatively rapid immigration from surrounding forest sites (Niemelä et al. 1996; Oxbrough et al. 2010). This could also explain deviating results for taxa such as ants, which were shown to continuously increase in FRic with stand age in tropical forests (Bihn et al. 2010). Regarding the gradient in woody plant species richness, contrasting patterns in the functional and species richness of spiders indicate that functional redundancy within spider assemblages decreased with increasing plant richness. Similar levels of FRic were based on far fewer spider species in the more plant species-rich stands than in the less plant species-rich ones. Likewise, the weakly increasing spider FRic.ses with woody plant species richness, together with the fact that FRic.ses was independent of spider species richness, indicate that the maintenance of constant FRic observed across the woody plant diversity gradient was due to the non-random assembly and non-random loss of spider species in the more plant species-rich plots. This means that woody plant species richness tended to keep spider FRic on a higher level than expected by chance, despite decreasing spider species richness.

Possible explanations for these patterns could be higher resource quality or decreased intraguild interactions in the more plant species-rich plots, and we discuss these in more detail below (patterns in FDiv). In any case, the results suggest that despite a higher than expected FRic in the more plant species-rich plots, the effect of woody plant species richness at our study site is apparently not strong enough to increase overall niche space to a level that might reflect the positive predator-plant diversity effects reported from less species-rich or less complex ecosystems (e.g., Haddad et al. 2009). Previous studies have suggested that the impact of plant diversity on higher trophic levels is attenuated at high levels of plant diversity (e.g., Scherber et al. 2010), such that effects observed at low diversity levels might be less relevant for our study system with medium to high plant diversity. At high levels of plant diversity, even negative diversity effects might be conceivable via increased spatial heterogeneity leading to tradeoffs with the area available to individual species (Allouche et al. 2012)—and we in fact observed a negative relationship between the species richness of spiders and woody plants in our study. However, such an effect would only be likely for highly specialized taxa and should have led to functionally less rich and less divergent spider communities in the more plant species-rich plots [as only more generalized species would be able to

cope with such high environmental heterogeneity; Allouche et al. (2012)], a pattern that does not match our findings for FRic and particularly for FDiv [see Schuldt et al. (2011) for a discussion on species richness patterns].

However, decreasing redundancy of spider species with increasing plant species richness and a non-random spider assemblage structure could indicate that the functional impact of these assemblages is sensitive to the loss of individual spider species and thus to disturbances caused, for instance, by human activities—at least on a larger, landscape scale where species loss will not be as easily compensated for by immigration of new species. Previous results for these assemblages suggest that woody plant species richness does not affect the stability of patterns in the species richness of spiders (Schuldt et al. 2012); however, it might still affect the stability of their functional effects if FRic is only moderately related to species richness (see also Finke and Snyder 2010). These relationships have not as yet been tested rigorously in natural systems, and more research is needed to address their functional consequences.

FDiv and FEve: plant species richness promotes complementary resource use

While the FRic of spiders and thus the overall niche space used remained on a constant level along the woody plant richness gradient, FDiv—and to a lesser extent FEve—within the available niche space increased with plant species richness (and FDiv also with plot age). Low FDiv and FEve values in the less plant species-rich (and younger) plots indicate that the dominant spider species were functionally similar and characterized by trait values close to the center of the assemblages' overall functional trait space. In the more plant species-rich (and older) plots, in contrast, trait values showed a more regular and diverging pattern, meaning that abundance distributions in these plots were functionally more differentiated, with a higher dominance of functionally dissimilar species. In fact, the relative abundance of *Pardosa laura*, the species with the highest overall number of individuals, strongly decreased from 32 % in the least diverse to 3 % in the most diverse forest stand. Several other of the most abundant species showed similar trends (not shown), indicating that a decrease in these highly abundant species caused a more even and less centered distribution of spider abundances within the functional trait space. Böhnke et al. (2013) described a similar pattern for FEve of the community of woody species along the same succession series. While FRic decreased with age, the trait values became more evenly distributed among the resident species.

These shifts might cause differences in the functional effects of the spider assemblages along the woody plant

richness and plot age gradients, despite similar FRic. These effects would be in a direction opposite to those expected from mere spider richness patterns (see also Schuldt et al. 2011). Despite lower spider species richness, spider assemblages in the more plant species-rich (and in older) forest plots could have a strong impact on prey because the most abundant spider species display more dissimilar and complementary resource use (high FDiv) than the assemblages in the less plant species-rich (and younger) plots. The latter might have more spider species, but a more centered resource use (low FDiv) by abundant species (see also Mouillot et al. 2011; Villéger et al. 2010). Even among largely generalist predators such as spiders, differences in body size, phenology and microhabitat use may lead to differences in resource use and the partitioning of prey (Schmitz 2007; Uetz 1977).

FDiv and FEve were unaffected by both spider species richness and FRic, and the observed effects were supported by the models for the standardized effect sizes FDiv.ses and FEve.ses. The fact that the standardized effect sizes increased with plant species richness (in the case of FEve.ses with a stronger impact of herb layer rather than tree and shrub layer species richness) indicates that, similar to FRic, the increase with plant species richness in the abundance-based spread and regularity of trait values of the spider assemblages were higher than expected from the number of spider species; i.e., non-random assembly processes became more evident with increasing niche differentiation of the spider assemblages. Again, these patterns point to lower redundancy among dominant species in the more plant species-rich plots, as already discussed above. Contrasting patterns between species richness and FRic on the one hand and FDiv and FEve on the other were also shown in other studies (Gerisch et al. 2012; Mouillot et al. 2011; Villéger et al. 2010). These findings indicate that the relative distribution of abundant species in functional trait space strongly affects ecological functions, independent of potentially contrasting patterns in species richness or the overall available functional trait space (Mouillot et al. 2011).

The mechanisms responsible for causing the observed trait divergence are difficult to elucidate in an observational study. Increasing productivity and higher resource availability, as often occur with increasing plant diversity (e.g., Haddad et al. 2009), are unlikely explanations, as we would have expected a simultaneous increase in the number of spider species. Rather than the amount of available resources, however, the quality of these resources may be part of the explanation. Higher plant species richness is likely to increase the diversity of herbivores (Lewinsohn and Roslin 2008). This, in turn, results in higher prey diversity and alternative prey resources for predators, which may allow for, and promote adaptations in, resource use and thus increase FDiv among the dominant predator species (and it

might also promote higher than expected FRic). Intraguild predation and competition might also have an effect (Finke and Snyder 2010). Lycosids are well known for their strong impact on other spiders, and the dominance of *Pardosa* species in the low-diversity and young forest plots [which might be due to particularly suitable conditions and a competitive advantage of these relatively large cursorial species in these environments; Hurd and Fagan (1992); Mallis and Hurd (2005)] could negatively affect the relative abundances of many other species (Schmidt-Entling and Siegenthaler 2009). Moreover, competitive pressure due to the generally high spider species richness in the less plant species-rich forest plots could lead to further trait convergence if dissimilar species are systematically excluded as weaker competitors (de Bello et al. 2012). Research into the mechanisms of community assembly patterns may yield further insight in this respect, but is beyond the focus of our study.

MPD: phylogenetic diversity does not consistently explain predator FD

Dinnage et al. (2012) recently showed that the phylogenetic diversity of grassland plant communities can have effects on higher trophic level diversity that are in part complementary to the effects of plant species richness. For predators, they explained these patterns by positive effects of increasing productivity with potentially decreasing niche overlap in more distantly related plant species. In our study, effects of plant phylogenetic diversity were basically due to the absence or presence of conifers in the study plots. The negative influence of conifers on FDiv and FEve might have been caused by increased shading or a homogenization of the litter layer that promoted the abundances of spiders with very general resource use characteristics (again, Lycosids were particularly abundant in these plots). When the three coniferous species occurring at the study site were excluded from the calculation of MPD, the phylogenetic distance among woody plant species was no longer included in any of the minimal models. This might underline our assumption that FD patterns of spiders in the forests we studied are not primarily affected by plant productivity (but more research is needed to directly test for productivity relationships). Our study comprised forest stands from medium to high woody plant species richness, and the effects of productivity might not be as limiting as in comparisons including monocultures (see also Scherber et al. 2010).

Conclusions

Our study shows that FD patterns provide insights into the assemblage structure of predatory arthropods that go beyond, and in part contrast with, the information provided

by mere species richness patterns. In contrast to other studies (e.g., Haddad et al. 2009), our results for epigeic spiders are supportive of the promoting effects that plant diversity is generally hypothesized to have on predators, only in the context of FD [and here particularly in terms of the divergence of trait distributions within the overall functional space, and less evident in terms of the size of this functional space (see also Villéger et al. 2010) and not for patterns of species richness (see also Zhang and Adams 2011)]. As for the strength of predator functional effects, carefully designed experiments are required to test whether a higher total abundance of very generalist predators (as in the less plant species-rich forest stands of our study) or a broader divergence in resource use (but lower total abundances, as in our plant species-rich plots) can achieve, for instance, a more effective top-down control. Several studies have demonstrated that abundance distributions of predators strongly mediate the impact of species richness on predator functional effects (Finke and Snyder 2010; Griffiths et al. 2008). While these studies were limited to small-scale manipulations of just a small number of predator species, they highlight that hypotheses of the relationship between plant diversity and predators need to incorporate functional aspects more explicitly. The contrasting findings of our study regarding the species richness and FD of spiders show the need for a more rigorous assessment of these aspects in complex, highly diverse natural systems.

Acknowledgments We thank the administration of the Gutianshan National Nature Reserve and the BEF China team for their support. Data on basal area of trees were provided by Martin Baruffol and Martin Böhnke. We are grateful to Sabine Both and Alexandra Erfmeier for providing data on herb layer plant diversity. The comments of two anonymous reviewers helped to improve the manuscript. Funding by the German Research Foundation (DFG FOR 891) and the National Science Foundation of China (NSFC 30710103907 and 30930005) is gratefully acknowledged. O. P. acknowledges the support of the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, funded by the German Research Foundation (FZT 118).

References

- Allouche O, Kalyuzhny M, Moreno-Rueda G, Pizarro M, Kadmon R (2012) Area: heterogeneity tradeoff and the diversity of ecological communities. *Proc Natl Acad Sci* 109:17495–17500
- Bihn JH, Gebauer G, Brandl R (2010) Loss of functional diversity of ant assemblages in secondary tropical forests. *Ecology* 91:782–792
- Böhnke M, Kröber W, Welk E, Wirth C, Bruehlheide H (2013) Maintenance of constant functional diversity during secondary succession of a subtropical forest in China. *J Veg Sci*. doi:10.1111/jvs.12114
- Both S et al (2011) Lack of tree layer control on herb layer characteristics in a subtropical forest, China. *J Veg Sci* 22:1120–1131
- Brose U et al (2006) Consumer-resource body-size relationships in natural food webs. *Ecology* 87:2411–2417
- Bruehlheide H et al (2011) Community assembly during secondary forest succession in a Chinese subtropical forest. *Ecol Monogr* 81:25–41
- Burnham KP, Anderson DR (2004) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York
- Cadotte MW, Cavender-Bares J, Tilman D, TH O (2009) Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *PLoS One* 4:e5695
- Cardinale BJ et al (2012) Biodiversity loss and its impact on humanity. *Nature* 486:59–67
- Cardoso P, Pekar S, Jocque R, Coddington JA (2011) Global patterns of guild composition and functional diversity of spiders. *PLoS One* 6:e21710
- de Bello F et al (2012) Functional species pool framework to test for biotic effects on community assembly. *Ecology* 93:2263–2273
- Devictor V, Mouillot D, Meynard C, Jiguet F, Thuiller W, Mouquet N (2010) Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. *Ecol Lett* 13:1030–1040
- Dinnage R, Cadotte MW, Haddad NM, Crutsinger GM, Tilman D (2012) Diversity of plant evolutionary lineages promotes arthropod diversity. *Ecol Lett* 15:1308–1317
- Feld CK et al (2009) Indicators of biodiversity and ecosystem services: a synthesis across ecosystems and spatial scales. *Oikos* 118:1862–1871
- Finke DL, Snyder WE (2010) Conserving the benefits of predator biodiversity. *Biol Conserv* 143:2260–2269
- Gerisch M, Agostinelli V, Henle K, Dziock F (2012) More species, but all do the same: contrasting effects of flood disturbance on ground beetle functional and species diversity. *Oikos* 121:508–515
- Gotelli NJ, Rohde K (2002) Co-occurrence of ectoparasites of marine fishes: a null model analysis. *Ecol Lett* 5:86–94
- Griffiths GJK, Wilby A, Crawley MJ, Thomas MB (2008) Density-dependent effects of predator species-richness in diversity-function studies. *Ecology* 89:2986–2993
- Haddad NM, Crutsinger GM, Gross K, Haarstad J, Knops JMH, Tilman D (2009) Plant species loss decreases arthropod diversity and shifts trophic structure. *Ecol Lett* 12:1029–1039
- Hardy OJ (2008) Testing the spatial phylogenetic structure of local communities: statistical performances of different null models and test statistics on a locally neutral community. *J Ecol* 96:914–926
- Hooper DU et al (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol Monogr* 75:3–35
- Hooper DU et al (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486:105–108
- Hurd LE, Fagan WF (1992) Cursorial spiders and succession: age or habitat structure? *Oecologia* 92:215–221
- Jocqué R, Dippenaar-Schoeman AS (2007) Spider families of the world. Royal Museum for Central Africa, Tervuren
- Kremen C et al (2000) Economic incentives for rain forest conservation across scales. *Science* 288:1828–1832
- Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91:299–305
- Legendre P et al (2009) Partitioning beta diversity in a subtropical broad-leaved forest of China. *Ecology* 90:663–674
- Lewinsohn TM, Roslin T (2008) Four ways towards tropical herbivore megadiversity. *Ecol Lett* 11:398–416
- Lopez-Pujol J, Zhang F-M, Ge S (2006) Plant biodiversity in China: richly varied, endangered, and in need of conservation. *Biodivers Conserv* 15:3983–4026
- Mallis RE, Hurd LE (2005) Diversity among ground-dwelling spider assemblages: habitat generalists and specialists. *J Arachnol* 33:101–109

- Mason NWH, Irz P, Lanoiselee C, Mouillot D, Argillier C (2008) Evidence that niche specialization explains species-energy relationships in lake fish communities. *J Anim Ecol* 77:285–296
- Mouchet MA, Villéger S, Mason NWH, Mouillot D (2010) Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Funct Ecol* 24:867–876
- Mouillot D, Villéger S, Scherer-Lorenzen M, Mason NWH (2011) Functional structure of biological communities predicts ecosystem multifunctionality. *PLoS One* 6
- Naeem S, Duffy JE, Zavaleta E (2012) The functions of biological diversity in an age of extinction. *Science* 336:1401–1406
- Niemelä J, Haila Y, Punttila P (1996) The importance of small-scale heterogeneity in boreal forests: variation in diversity in forest-floor invertebrates across the succession gradient. *Ecography* 19:352–368
- Oxbrough A, Irwin S, Kelly TC, O'Halloran J (2010) Ground-dwelling invertebrates in reforested conifer plantations. *For Ecol Manage* 259:2111–2121
- Pavoine S, Bonsall MB (2011) Measuring biodiversity to explain community assembly: a unified approach. *Biol Rev* 86:792–812
- Purschke O et al (2013) Contrasting changes in taxonomic, phylogenetic and functional diversity during a long-term succession: insights into assembly processes. *J Ecol* 101:857–866
- Riihimäki J, Kaitaniemi P, Koricheva J, Vehviläinen H (2005) Testing the enemies hypothesis in forest stands: the important role of tree species composition. *Oecologia* 142:90–97
- Root RB (1973) Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecol Monogr* 43:95–124
- Scherber C et al (2010) Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature* 468:553–556
- Schleuter D, Daufresne M, Massol F, Argillier C (2010) A user's guide to functional diversity indices. *Ecol Monogr* 80:469–484
- Schmid B et al (2009) Consequences of species loss for ecosystem functioning: meta-analyses of data from biodiversity experiments. In: Naeem S, Bunker DE, Hector A, Loreau M, Perrings C (eds) *Biodiversity, ecosystem functioning, and human wellbeing. An ecological and economic perspective*. Oxford Univ Press, Oxford, pp 14–29
- Schmidt-Entling MH, Siegenthaler E (2009) Herbivore release through cascading risk effects. *Biol Lett* 5:773–776
- Schmitz OJ (2006) Predators have large effects on ecosystem properties by changing plant diversity, not plant biomass. *Ecology* 87:1432–1437
- Schmitz OJ (2007) Predator diversity and trophic interactions. *Ecology* 88:2415–2426
- Schuldt A et al (2011) Predator diversity and abundance provide little support for the enemies hypothesis in forests of high tree diversity. *PLoS One* 6:e22905
- Schuldt A, Bruelheide H, Härdtle W, Assmann T (2012) Predator assemblage structure and temporal variability of species richness and abundance in forests of high tree diversity. *Biotropica* 44:793–800
- Southwood TRE, Henderson PA (2000) *Ecological methods*, 3rd edn. Blackwell Science, Oxford
- Stork NE, Grimbacher PS (2006) Beetle assemblages from an Australian tropical rainforest show that the canopy and the ground strata contribute equally to biodiversity. *Proc R Soc B* 273:1969–1975
- Terborgh J (2012) Enemies maintain hyperdiverse tropical forests. *Am Nat* 179:303–314
- Uetz GW (1977) Coexistence in a guild of wandering spiders. *J Anim Ecol* 46:531–541
- Villéger S, Mason NWH, Mouillot D (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89:2290–2301
- Villéger S, Ramos Miranda J, Flores Hernandez D, Mouillot D (2010) Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecol Appl* 20:1512–1522
- Visser MD, Muller-Landau HC, Wright SJ, Rutten G, Jansen PA (2011) Tri-trophic interactions affect density dependence of seed fate in a tropical forest palm. *Ecol Lett* 14:1093–1100
- Webb CO, Ackerly DD, McPeck MA, Donoghue MJ (2002) Phylogenies and community ecology. *Annu Rev Ecol Syst* 33:475–505
- Wise DH (2004) Wandering spiders limit densities of a major microbe-detrivore in the forest-floor food web. *Pedobiologia* 48:181–188
- Zhang YA, Adams J (2011) Top-down control of herbivores varies with ecosystem types. *J Ecol* 99:370–372
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) *Mixed effects models and extensions in ecology with R*. Springer, New York