Biodiversity and ecosystem functioning relations in European forests depend on environmental context

Sophia Ratcliffe1*, Christian Wirth1,2,3, Tommaso Jucker4,5, Fons van der Plas6,7, Michael Scherer-Lorenzen8, Kris Verheyen9, Eric Allan6, Raquel Benavides10, Helge Brueelheide2,11, Bettina Ohse1, Alain Paquette12, Evy Ampoorter9, Cristina C. Bastias10, Jürgen Bauhus13, Damien Bonal14, Olivier Bouriaud15, Filippo Bussotti16, Monique Carnol17, Bastien Castagneroll18,19, Ewa Chećko20, Seid Muhie Dawud21, Hans De Wandeler22, Timo Domisch23, Leena Finé23, Markus Fischer6, Mariangela Fotelli24, Arthur Gessler25, André Granier14, Charlotte Grossiord26, Virginie Guyot18,19, Josephine Haase8,27,28, Stephan Hättenschwiler29, Hervé Jactel18,19, Bogdan Jaroszewicz20, François-Xavier Joly29, Stephan Kambach2,10,30, Simon Kolb31, Julia Koricheva32, Mario Liebersgesell1,2, Harriet Milligan32, Sandra Müller1, Bart Muys22, Diem Nguyen33,34, Charles Nock8,13, Martina Pollastrini16, Oliver Purschke2, Kalliopi Radoglou35, Karsten Raulund-Rasmussen36, Fabian Roger37, Paloma Ruiz-Benito38, Rupert Seidl39, Federico Selvi16, Ian Seiferling40,41, Jan Stenlid33, Fernando Valladares10, Lars Vesterdal36, Lander Baeten9

Author Affiliations

1Department of Systematic Botany and Functional Biodiversity, University of Leipzig, Johannisallee 21-23, 04103 Leipzig, Germany.
2German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5E, 04103 Leipzig, Germany.

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/ele.12849

This article is protected by copyright. All rights reserved
Author Contributions
SR, LB, CW, TJ, FvdP, RB, HB, BO, MSL, EA, PRB and AP developed the ideas of the study. SR and LB analysed the data. All authors, except SR, CW, FvdP, EA, BO, AP, MF, JH, SK, FR, CN, PRB and RS contributed data. SR and LB wrote the first draft of the manuscript, which was revised by all co-authors.

Data accessibility
The data supporting the results will be made publicly available, including a DOI.

Abstract
The importance of biodiversity in supporting ecosystem functioning is generally well accepted. However, most evidence comes from small-scale studies, and scaling up patterns of biodiversity-ecosystem functioning (B-EF) remains challenging, in part because the importance of environmental factors in shaping B-EF relations is poorly understood. Using a forest research platform in which 26 ecosystem functions were measured along gradients of tree species richness in six regions across Europe, we investigated the extent and the potential drivers of context dependency of B-EF relations. Despite considerable variation in species richness effects across the continent, we found a tendency for stronger B-EF relations in drier climates as well as in areas with longer growing seasons and more functionally diverse tree species. The importance of water availability in driving context dependency suggests that as water limitation increases under climate change, biodiversity may become even more important to support high levels of functioning in European forests.

Running title
Context dependency of diversity effects

Keywords
Functional diversity, FunDivEUROPE, growing season length, multifunctionality, resource heterogeneity, species richness, water availability

Type of article: Letter

Number of words
Abstract: 150
Main text: 5000

Number of references: 63
Number of figures: 4
Number of tables: 2
Number of text boxes: 0

Introduction
Forests have helped sustain humans for millennia; from the water we drink to the houses we live in, forests provide us with a wealth of goods and services. Tree species diversity is
known to promote key forest ecosystem functions, including primary production (Paquette & Messier 2011; Liang et al. 2016), stability of wood production (Jucker et al. 2014), resistance to biotic and abiotic disturbances (Pretzsch et al. 2013b; Jactel et al. 2017) and nutrient cycling (Richards et al. 2010; Handa et al. 2014), amongst others. Despite evidence that diverse forests are able to support higher levels of ecosystem functioning than species-poor ones (Gamfeldt et al. 2013), the importance of tree diversity as a driver of ecosystem functioning is also known to vary considerably amongst forest types, geographic regions, and in relation to climatic conditions (Paquette & Messier 2011; Pretzsch et al. 2013a; Forrester 2014; Grossiord et al. 2014; Jucker et al. 2016; Liang et al. 2016; Ratcliffe et al. 2016). This context dependency of diversity effects is seen as an obstacle to scaling up and generalising biodiversity experiments, because the importance of environmental conditions in shaping biodiversity-ecosystem functioning (B-EF) relationships is poorly understood, particularly for ecosystem functions other than biomass production (Cardinale et al. 2000; Srivastava & Vellend 2005; Allan et al. 2015).

A number of mechanisms have been put forward to explain why B-EF might be context-dependent. Here we focus on four factors that have received the most attention in the literature: (i) **Resource availability**: the number of resource-related niche dimensions, and thus the potential for niche partitioning, is predicted to be greater in resource-limited environments (Harpole et al. 2016). Following this reasoning, a greater potential for niche partitioning should promote higher levels of ecosystem functioning in conditions less favourable for growth. Forest stands with poor soil quality have been found to exhibit stronger positive diversity effects than stands on highly fertile soils (Pretzsch et al. 2013a; Toïgo et al. 2015). In addition, along broad climatic gradients B-EF relationships have been reported to be strongest in conditions less favourable for growth (e.g. Paquette & Messier 2011; Ratcliffe et al. 2016); (ii) **Resource heterogeneity**: niche partitioning between species can be promoted by spatial heterogeneity of resources (Pacala & Tilman 1994; Cardinale et al. 2000) and diversity may be more important to guarantee functioning in heterogeneous environments, due to spatial insurance effects (Loreau et al. 2003). Heterogeneity of soil nutrients has been found to promote aboveground biomass production in experimental grassland communities through increased resource partitioning (Wacker et al. 2008); (iii) **Biotope space**: an increase in biotope space (i.e. the physical space associated with a species’ niche) could also lead to more pronounced diversity effects, as demonstrated in experimental grasslands where greater soil depth and rooting space increased biodiversity effects on
biomass production, due to greater differentiation of rooting architectures through the soil profile (Dimitrakopoulos & Schmid 2004); and (iv) **Species functional dissimilarity**: niche partitioning requires coexisting species to have different attributes that enable them to utilise available resources in different ways (Díaz & Cabido 2001). B-EF relations are therefore predicted to be stronger where coexisting species are more functionally dissimilar (Chesson 2000), for example via phenological differences (Sapijanskas et al. 2014) or heterogeneity in rooting or canopy architectures and shade tolerance (Brassard et al. 2013; Jucker et al. 2015).

How multiple functions co-vary in their response to diversity across complex environmental gradients is rarely investigated (Cardinale et al. 2013; Dooley et al. 2015; Ruiz-Benito et al. 2017). However, identifying patterns in these responses is a key step towards understanding the mechanisms that give rise to general patterns of B-EF. Using a continent-wide forest research platform (FunDivEUROPE; Baeten et al., 2013) in six European regions with differing climatic, edaphic and biotic conditions, we tested the extent and potential drivers of context dependency of species richness effects on 26 ecosystem functions (EFs). In a first step, we quantified the proportion of total variation in functioning attributable to interregional differences in species richness effects. We did this to determine the importance of species richness relative to other potential drivers, and to evaluate the extent of context dependency in B-EF. Subsequently, we explored the environmental modulators of species richness effects for each EF. For this we designed a hierarchical approach, which first tested the strength and direction of EF responses to species richness, and then identified key drivers of variation in any response (hereafter ‘context variables’). This allowed us to identify the functions that were most strongly promoted by tree species richness and the environmental conditions in which the effect was strongest. We expected B-EF relations to vary between the six regions and hypothesised that species richness effects on individual functions will increase along one or more of the following gradients:

- (H1) decreasing resource availability, such as low water availability and poor soil fertility;
- (H2) increasing soil resource heterogeneity;
- (H3) increasing biotope space, such as increasing soil volume; and
- (H4) increasing functional dissimilarity of the regional tree species pool.

**Methods**

This article is protected by copyright. All rights reserved
We used data collected from mature forest plots in six regions across Europe as part of the FunDivEUROPE project (http://www.fundiveurope.eu). Baeten et al. (2013) provides full details of the ‘Exploratory Platform’ plot selection procedure. In short, 209 30 x 30 m plots were set up in mature forests in six regions across Europe: boreal forest (Finland); hemiboreal (Poland); temperate deciduous (Germany); mountainous deciduous (Romania); thermophilous deciduous (Italy); and Mediterranean mixed (Spain). In each region between three and five tree species were selected for the species pool, representing regionally common species with a clear importance for forestry. Forest stands were selected to differ in tree species composition and richness; plots consisted of target species sampled from the species pool, along richness gradients of one to up to five target species (see Supplementary Material S1 for the location and species pool of each region). Co-variation between environmental conditions (soil texture, depth, slope) and tree species richness and composition within each region was avoided as much as possible (Baeten et al. 2013). In each plot the diameter at breast height (DBH) of all trees \( \geq 7.5 \) cm DBH was measured and each tree mapped.

**Ecosystem functions**

We used 26 ecosystem properties and functions (EFs) measured in the plots and classified them into groups reflecting basic ecological processes, such as nutrient and carbon cycling, primary production, regeneration and resistance to perturbation and disturbance (Table 1). A major strength of the FunDivEUROPE project was that all EFs were measured following the same protocol in each region (see Supplementary Material S1.1). This led to a consistent and extensive coverage of EFs, with 21 of the functions measured in at least 207 of the 209 plots (Table 1). EFs were generally weakly correlated (Fig. S1.2).

EF data was used to calculate two multifunctionality measures for each plot: i) the *threshold approach*, following Gamfeldt et al. (2008) and van der Plas et al. (2016), estimates the number of EFs whose value exceeded 30, 50 and 70% of the 95 percentile for that EF observed across all plots. The 95 percentile was used to avoid any large outliers unduly influencing the estimation; and ii) the *averaging approach*, estimates the average standardised value of all EFs in each plot (Hooper & Vitousek 1998). See Supplementary Material S1.2 and Byrnes et al. (2014) for the calculation of both approaches.
**Plot-level predictors**

To explain plot-level variation in EFs and multifunctionality, we used target species richness as a continuous variable. Non-target species made up 5% of the basal area across all the plots and given that their contribution to ecosystem functioning is likely to be low, they were not included in the species richness measure. Plot species composition (a categorical variable with 92 levels, where each level reflects a unique combination of target species), total tree basal area (the sum of the basal area of all trees per plot, m$^2$) and the proportion of conifers were included as covariates. Species composition was included to account for the identity of the species, which can greatly influence ecosystem functioning (Hooper et al. 2005). Basal area was included to account for within-region variability due to historical management effects and natural disturbances and the proportion of conifers was included to account for within-region functional effects of the two highly dissimilar clades (Stahl et al. 2013), which are known to be important for several of the EFs (e.g. Guyot et al. 2016; Dawud et al. 2017).

**Regional context variables**

To test our four hypotheses, we chose context variables that describe the climatic, edaphic and biotic conditions of each region. All context variables were measured on site except for the climate variables. (H1): Differences in the abiotic conditions between the regions were described using a water availability index (WAI = (precipitation–potential evapotranspiration)/potential evapotranspiration), actual evapotranspiration (AET, mm), annual growing season length (GSL, number of days above 10 °C, following Pretzsch et al. (2014)), soil sand content (SAND, %) and soil pH (pH). WAI and GSL were both calculated from AGRI4CAST (https://ec.europa.eu/jrc/en/mars) using daily data from 1997 to 2011. AET was derived from the water balance model BILJOU (Granier et al., 1999; https://appgeodb.nancy.inra.fr/biljou/). WAI reflects the potential drought stress experienced by plants, whilst AET reflects the magnitude and length of conditions favourable to plant growth (Stephenson 1998). Both GSL and AET are measures of potential climate influence on the productivity of the region, however they were weakly correlated (Pearson correlation: $r = 0.13; p=0.80$) and we used both in the analyses. SAND was used to describe soil nutrient and water retention potential, which declines as the percentage of sand increases (Brady 1984), and the pH of the top 10 cm mineral soil layer was used as an indicator of the soil nutrient status.
(H2): Soil resource heterogeneity was quantified as the coefficient of variation of soil moisture in each plot (M_VAR). (H3): The volumetric stone content (STONES) in the upper 30 cm of mineral soil was used as an indicator of the available belowground growing space or biotope space (see Appendix S1.3). We did not use soil depth because of the lack of a precise measurement in each plot; however, soils with high rock content are typically also shallower.

(H4): The functional diversity of the species pool (FD_pool) in each region was used to describe the dissimilarity in traits of the tree species and thus their potential for niche partitioning. The use of FD_pool assumes that the propensity for complementarity between species has more to do with their functional traits than with their biogeographic origin, for instance, if complementarity between native and non-native species is reduced due to the lack of mutualists (Tobner et al. 2014). FD_pool was calculated using the mean dissimilarity index of Pavoine & Bonsall (2011) based on seed mass (mg), maximum height (m), maximum life span (yrs), leaf nitrogen content (mg g⁻¹), litter lignin/nitrogen ratio, litter SLA and wood density (g cm⁻³). These are key functional traits that are indicative of species’ ecological strategies of resource acquisition, growth and litter quality (Westoby et al. 2002; Appendix S1.3). ANOVA indicated significant (p < 0.05) differences in all the context variables between the regions (Figure S1.3).

Statistical methods

Variance partitioning was used to quantify the proportion of total variation in functioning attributable to species richness, interregional differences in the effect of species richness and other potential drivers of ecosystem functioning. Using the same base model, we then explored how species richness effects varied between the regions and what factors could explain this variation. The analyses were run in a Bayesian framework using the Stan probabilistic modelling language, called from R (version 3.2.4) using the rstan package (Stan Development Team 2016). All models were run for 5000 iterations of both warm up and sampling. We tested for model convergence by running three MCMC chains with different starting values and checked the trace plots and Rhat statistics (Gelman & Hill 2007).

Variance partitioning
For each EF and multifunctionality measure, we partitioned the total variance into several components using a multilevel analysis of variance (Gelman & Hill 2007; Hector et al. 2011). Between-plot variation was attributed to: i) region effects; ii) species richness effects; iii) region × species richness interaction effects; iv) species composition effects; v) other plot-level effects (basal area and proportion of conifers); and vi) residual variation, in the following model:

\[
EF_i = \beta^0 + \beta^{region}_{j(i)} + \beta^{sr}_{j(i)} \cdot SR_i + \beta^{mix}_{k(i)} + \beta^{ba}_i \cdot BA_i + \beta^{cp}_i \cdot CP_i + \varepsilon_i \tag{1}
\]

where \(EF_i\) is the predicted ecosystem function in plot \(i\), \(\beta^0\) is the grand mean for the EF, \(\beta^{region}_{j(i)}\) is the effect of region (\(j = 1, \ldots, 6\)), \(\beta^{sr}_{j(i)}\) is the region-specific slope of the species richness effect, i.e. the interaction between region and species richness, \(\beta^{mix}_{k(i)}\) is the effect of species composition (\(k = 1, \ldots, 92\)), and \(\beta^{ba}_i\) and \(\beta^{cp}_i\) are the slopes for the effects of basal area (BA) and proportion of conifers (CP), respectively. Plot-level residual error was modelled from a normal distribution (\(\varepsilon_i \sim N(0, \sigma^2)\)) and the region, region × species richness interaction and composition effects were modelled from separate zero-mean normal distributions (e.g., \(\beta^{region}_{j(i)} \sim N(0, \sigma^2_{region})\), with \(\sigma^2_{region}\) a super-population variance). EF values were transformed where necessary to meet assumptions of normality and were centred on 0 and scaled by their standard deviation. Following Gelman & Hill (2007) and Hector et al. (2011), the variance components were estimated as the standard deviation of the \(\beta_s\) (e.g., \(s_{region}\), the finite population standard deviation of the region-level effects) and are independent of the order of terms in the model. Plot-level basal area and proportion of conifers were centred on their regional mean to reduce their influence on any context variable effect (see the following section for more details) especially in the case where the covariates and context variables were correlated (Bell & Jones, 2015). This form of scaling allows for the within-region effects of the covariates to be accounted for in the model but excludes any between-region effects. The variance partitioning analysis was repeated with the dataset restricted to mixtures of up to three species, to check that the patterns were not influenced by the different lengths of the species richness gradients in the different regions.

*Estimation of species richness effects and drivers of context dependency*
In order to test the drivers of context dependency, for each EF and multifunctionality measure we estimated the sensitivity of the EF–species richness relationship to each context variable in a hierarchical model. Plot-level EF or multifunctionality was modelled as in equation 1 of the variance partitioning analysis. In addition, the region-specific effect of species richness ($\beta_j^{\text{SR}}$) was modelled as a function of each region-level context variable separately, such that:

$$\beta_j^{\text{SR}} = \alpha_{\text{sens}} + \beta_{\text{sens}} \cdot \text{CONTEXT}_j + \epsilon_j$$  \hspace{1cm} (2)

where $\alpha_{\text{sens}}$ is the estimated intercept, $\beta_{\text{sens}}$ is the sensitivity coefficient, $\text{CONTEXT}_j$ is the context variable in region $j$ and $\epsilon_j$ is the residual error (again modelled from a normal distribution). The context variables were centred on 0 and scaled by the standard deviation.

The hierarchical model (i.e. equations 1 and 2) was run on each EF (and multifunctionality measure) and context variable separately, thus we obtained a sensitivity estimate ($\beta_{\text{sens}}$) for each EF and context variable combination. We then used PCA analysis on the sensitivity estimates ($\beta_{\text{sens}}$) to identify the dominant patterns of co-variation between the EFs in terms of how the effects of species richness on each EF responded to the context variables. We used PCA because some of the context variables were highly correlated (notably water availability and soil pH; Pearson correlation: $r = -0.90; p < 0.05$; Table S1.1) and PCA is a powerful tool for multivariate analysis of correlated variables. The PCA reflects how the context variables relate to one another in terms of explaining variation in B-EF, i.e. whether certain types of EFs show similar context-dependent responses to species richness. We used ANOVA and Tukey’s HSD post-hoc tests to determine how EF groups differed in each of the main principal components from the PCA. We also estimated: 1) the overall mean species richness effect for each EF (and multifunctionality measure), using equation 1 without the region $\times$ SR interaction term; and ii) the species richness effect in each region without the influence of the context variable (i.e. only equation 1).

**Results**

*Species richness effects and the degree of context dependency*

Species richness (SR) explained only 4% of the total variation across all the ecosystem functions (EFs, Fig. 1). However, SR was more important for multifunctionality (assuming a
50% threshold) than for any of the individual EFs (explaining 11% of the total variation, Fig. 1). For most of the EFs the importance of SR varied between regions and the interaction between region and SR explained more variance on average (10%) than the main effect of SR (Fig. 1). For the individual variance components estimates see Fig. S2.1 and Table S2.1. The interaction between region and SR explained the greatest variation in the resistance EFs (13%) and the least in the production EFs (8%, Fig. S2.2); however, the differences were not significant (ANOVA: F=1.622, p=0.206). At the highest threshold of multifunctionality tested (70%) the interaction of region with SR variance component was larger than for any of the individual EFs (25% of the total variation, Fig. S2.2). The magnitude of the interaction of region with SR variance components, across the EFs, was generally supported when the SR gradient was restricted to three species (Fig. S2.3). Species composition effects, on average, explained only slightly more variation than the interaction of region with SR (14% and 10% of the total variation, respectively, Fig. 1). For multifunctionality, species composition was of comparable importance to SR and the interaction of region with SR (11%, 11% and 8%, respectively, Fig. 1).

Across the EFs, the mean effect of SR was positive (mean effect size 0.06 ± 0.03 95% CIs; Fig. 2) and there were no significant differences between the EF groups (F=2.01; p = 0.129; Fig. S2.4). In addition, the mean effect of SR on multifunctionality (50% threshold and average-based) was positive with 95% credible intervals that did not include zero. The boreal forest (Finland) had the largest number of negative SR effects (46%) and the temperate deciduous forest (Germany) the least (19%); consistent with this, SR effects on multifunctionality (50% threshold) varied across the regions, from strongly positive in Germany to neutral in Finland.

Drivers of context dependency in species richness effects

There was considerable variability in the extent of context dependency in the B-EF relationships (Fig. S2.5). However, there was a tendency for stronger and more positive species richness (SR) effects with decreasing water availability (WAI) and soil sand content and with increasing growing season length (GSL), soil pH, and species pool functional diversity (FD$_{pool}$) (Fig. 3). On average, the absolute sensitivity estimates (degree of context dependency) were greatest for WAI and evapotranspiration (AET; mean $|\beta_{sen}|$: 0.075 ± 0.02 and 0.069 ± 0.02 [95% CIs], respectively; Fig. S2.5) and the coefficient of variation in soil moisture (M$_{VAR}$) was the least important (mean $|\beta_{sen}|$: 0.048 ± 0.01). Variation in SR effects

This article is protected by copyright. All rights reserved
was more strongly related to the context variables in the resistance EFs (mean $|\beta_{\text{ens}}| = 0.081 \pm 0.02$) than in the production and regeneration EFs (0.044 ± 0.01 and 0.047 ± 0.01, respectively; ANOVA: $F = 5.363$; $p < 0.001$; Fig. S2.6). See Supplementary Material S3 and Table S2.2 for the individual $\beta_{\text{ens}}$ figures and estimates, and Fig. S2.7 for the variance explained by each model. Species richness effects on multifunctionality (50% threshold) were more positive in regions with high AET (Figs. S2.5 & S3.28). However, at higher levels of functioning (70% threshold), and for average-based multifunctionality, SR effects on multifunctionality were highly sensitive to WAI, GSL and sand content, becoming negative in regions with shorter growing seasons, high sand content and high water availability (i.e. Finland, Figs. S2.5 & S3.29 & S3.30).

Co-variation in context dependency between ecosystem functions

The largest amount of variation in the B-EF sensitivities was explained by water availability and soil pH (PC1; 53.7%, Table 2 & Fig. S2.8); followed by actual evapotranspiration (PC2; 23.3%); and finally growing season length (PC3; 19.4%). The sensitivity of SR effects to the main drivers of context dependency differed between the EFs (Fig. 4); however, there were no significant differences between the EF groups (Fig. S2.9). With increasing water availability, SR had increasingly positive effects on nutrient cycling processes but increasingly negative effects on nutrient and carbon cycling drivers. Species richness effects in both groups tended to decrease, and turn weakly negative, with increasing growing season length, whilst the reverse was the case in the EFs related to regeneration and resistance (Figs. 4, S2.9 & S2.10).

Discussion

Against a background of pronounced context dependency we found a significant positive effect of tree species richness on a wide range of ecosystem functions in Europe’s forests. In addition, our results indicate a tendency for species richness effects to become more beneficial for multiple ecosystem functions with decreasing climatic water availability as well as increasing growing season length and functional diversity of the tree species.

Regional importance of species richness for forest ecosystem functioning

Regional differences in species richness effects accounted for 10% of the variation in EFs (ranging from 4% to 20%, Fig. 1), which is an important contribution across such broad gradients in forest types, climates and soils. Thus, our study is in accordance with growing
evidence that biodiversity effects on ecosystem functioning can be substantially modified by environmental conditions (Cardinale et al. 2000; Hättenschwiler et al. 2005; Paquette & Messier 2011; Pretzsch et al. 2013a; Forrester 2014; Liang et al. 2016; Ratcliffe et al. 2016).

We also found that at a continental scale, across multiple functions, species richness was comparable in importance to species composition for ecosystem functioning. We found a clear tendency for more positive than negative species richness effects (Fig. 2). As a consequence, our indices of multifunctionality were also positively related to tree species richness in all regions (low or medium threshold), or were positive in most regions (high threshold and average-based). Interestingly, no ecosystem function responded negatively to increasing tree species richness in all regions. From a forest management perspective this means that conversion of mono-specific stands to multi-species forests should generally result in a higher delivery of ecosystem goods and services, thus supporting current policies of forest conversion in several countries (Knoke et al. 2008).

Our results indicate that species richness effects are more beneficial for the resistance-related EFs than for the production and nutrient cycling processes. This is consistent with a qualitative review of biodiversity effects across a broad range of ecosystems and functions (Srivastava & Vellend 2005). We also found that species richness effects on the resistance-related EFs were much more sensitive to the environmental context than the other EF groups. This is in agreement with two recent reviews in which the effect of tree species richness on forest resistance to stress and disturbance was found to strongly depend on the type of disturbance and the tree species involved (Bauhus et al. 2017; Jactel et al. 2017). It also suggests that resistance and regulatory functions may be especially susceptible to changes in biodiversity, as recently reported in grasslands (Soliveres et al. 2016).

Water availability is the most important driver of context-dependent species richness effects

From the set of context variables that we tested, water availability was the most important in changing the relationship between species richness and forest functioning (Fig. 3 & Table 2). We therefore found the greatest support for our first hypothesis (H1) that the positive effects of species richness should increase with resource limitation, consistent with earlier studies demonstrating the importance of abiotic gradients in modulating diversity effects (Pretzsch et al. 2013a; Forrester & Pretzsch 2015; Ratcliffe et al. 2016). We acknowledge that water availability and soil pH were highly correlated and that we cannot rule out that soil pH contributed to context dependency. However, water availability loaded more strongly on
PC1 than soil pH and, in general, B-EF relations were more sensitive to water availability than soil pH, especially for functions related to resistance and nutrient cycling. Water availability explained the variability in species richness effects better than evapotranspiration rates or growing season length, which suggests that species richness effects may be more influenced by the length and severity of drought conditions than they are by the magnitude and length of conditions favourable to plant growth (Seddon et al. 2016). In general, B-EF relations tended to be more positive in water-limited regions (e.g. Spain) and to turn neutral or negative in regions with high water availability (e.g. Finland). This is consistent with a pan-European study of diversity effects on tree growth (Ratcliffe et al. 2016) and provides further evidence, across multiple EFs, that niche partitioning may be particularly important in water-limited forests (Grossiord et al. 2014).

Species richness effects, in some functions, were highly sensitive to evapotranspiration rate (AET), especially in the regeneration and resistance functions. However, across the EFs there was no general pattern in the direction of the sensitivity to AET. The only exception was for the regeneration functions, in which species richness effects became more strongly positive in regions with high AET (central Europe), in contrast to our expectations from H1. Although growing season length was a weaker modulator of B-EF relations than water availability, our synthesis revealed a tendency for B-EF relations to become more strongly positive with increasing growing season length, especially in the resistance EFs. This also contradicts our expectations from H1, and suggests that seasonal complementarity between co-existing species may be an important underlying mechanism of positive species richness effects where growing seasons are long enough (Hooper & Vitousek 1998; Sapijanskas et al. 2014).

Soil sand content, moisture variability and stone content were less important in modulating species richness effects than climatic variables. One general pattern, which was in contrast to our predictions from H1, was that tree species richness had stronger effects on functioning in forests with soils that had higher nutrient and water-holding capacities (low sand content; e.g. Germany and Romania), especially for the nutrient and carbon cycling processes, than in soils with poor nutrient and water-holding capacities (e.g. Poland and Finland). It is likely that the sensitivity of B-EF to soil sand content was an artefact of its correlation with several other context variables. We found limited evidence that an increase in soil moisture variability (H2), or biotope space (H3), promoted stronger positive species richness effects.
However, the ephemeral nature of soil moisture variability makes it challenging to generalise from single point estimates. Our results provide some support for the hypothesis that a greater tree species functional diversity promotes stronger B-EF relations (H4). Functional diversity appeared particularly important for driving positive species richness effects in the resistance EFs, consistent with studies on tree growth resilience to wildfires (Spasojevic et al. 2016) and associational resistance to herbivores (Castagnevrol et al. 2014).

We found that diversity effects were stronger, and more important, when multiple ecosystem functions were considered simultaneously (van der Plas et al. 2016). However, our study emphasises that there may be trade-offs between different facets of forest functioning in their response to species richness along environmental gradients (Bauhus & Schmerbeck 2010; Cardinale et al. 2013), highlighting the need for context-specific management approaches. Nevertheless, we found that species-rich forests in central and southern Europe support higher levels of multiple ecosystem functions than species-poor ones. In southern Europe water stress appeared to be the dominant driver of B-EF relations. In central Europe, characterised by more moderate water stress, factors relating to increased niche partitioning, such as longer growing season lengths and greater interspecific functional differences also appeared to be important, resulting in stronger overall B-EF relations.

Although we found clear patterns in B-EF relationships, there are several limitations to our study. Firstly, we excluded non-target species from the species richness measure. Whilst the basal area of non-target species was very low, rare species may disproportionately contribute to biodiversity effects if they benefit more from reduced intraspecific competition in diverse assemblages than common species (Comita et al. 2010). However, including non-target species would have made the assessment of the species composition effect impossible, due to the many different combinations. Differences in the diversity gradient between the regions may also explain some of the regional variation in the magnitude of species richness effects (e.g. in Finland, with only three target species, there may be fewer opportunities for complementarity compared to regions with five species). However, a reanalysis of the data with a reduced diversity gradient suggests that our results were robust in this regard (Fig. S2.3). Whilst a major strength of the study was the high level of data coverage, this degree of sampling intensity comes at a cost in terms of replication. Similar inventory-based observational studies often include thousands of plots but six or less ecosystem functions (e.g. Gamfeldt et al. 2013; Ruiz-Benito et al. 2017). Finally, the magnitude of the patterns
that we detected only reflects environmental conditions in Europe. Larger scale studies are needed to determine whether these same patterns hold true across wider climatic gradients.

Conclusions

Our study detected strong context dependency of biodiversity-ecosystem functioning relationships in forests across a broad range of functions. The importance of water availability and growing season length in modulating species richness effects is critical in the context of climate change. Temperature-driven increases in evapotranspiration are predicted to aggravate regional drought stress in the future (Jacob et al. 2014) and plant phenology has already started shifting in response to global change (Cleland et al. 2007). Taken together these changes may have profound effects on the potential of mixed forests to support multiple functions in the future. Our findings suggest that as water limitation increases under climate change, biodiversity may become even more important to support high levels of functioning in European forests. However, evidence that mixed forests which are already under water stress will have a greater resistance to higher levels of water stress is equivocal (Forrester et al. 2016). The insights presented here, across a broad range of ecosystem functions and environmental contexts, are of fundamental relevance in providing the basis for unravelling the mechanisms behind the environmental controls of biodiversity-ecosystem functioning relationships and their application to the management of mixed forests.

Acknowledgements

This paper is a joint effort of the working group ‘Scaling biodiversity-ecosystem functioning relations: a synthesis based on the FunDivEUROPE research platforms’ on the 24th-26th November 2014 in Leipzig, Germany, kindly supported by sDiv, the Synthesis Centre of the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, funded by the German Research Foundation (FZT 118). We are grateful to three anonymous reviewers for their insightful suggestions and comments that have helped to improve the quality of the manuscript. The FunDivEUROPE project received funding from the European Union’s Seventh Programme (FP7/2007–2013) under grant agreement No. 265171. Additional support was received from the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig for SR. CW acknowledges the support of the Max-Planck-Society.

Supplementary Materials

This article is protected by copyright. All rights reserved
References


This article is protected by copyright. All rights reserved
diversity reduces pest damage in mature forests across Europe. *Biol. Lett.*, 12, 20151037


This article is protected by copyright. All rights reserved


This article is protected by copyright. All rights reserved


This article is protected by copyright. All rights reserved


This article is protected by copyright. All rights reserved
**Table 1.** Overview of the 26 ecosystem functions (EFs) and their classification. For full details on their measurement see Supplementary Material S1. Number of measurements indicates the number of plots in which each function was measured (maximum of 209 plots). Twelve functions were measured in all plots and 21 of the functions were measured in at least 207 plots. Pairwise Pearson correlation coefficients between the EFs are given in Fig. S1.2 of the Supplementary Material.

<table>
<thead>
<tr>
<th>Ecosystem function</th>
<th>Description</th>
<th>Number of measurements</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Nutrient and carbon cycling drivers</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Earthworm biomass</td>
<td>Biomass of all earthworms (g m$^{-2}$)</td>
<td>209</td>
</tr>
<tr>
<td>Fine woody debris</td>
<td>Snags and standing dead trees shorter than 1.3 m and thinner than 5 cm DBH, and all stumps and other dead wood pieces lying on the forest floor.</td>
<td>208</td>
</tr>
<tr>
<td>Microbial biomass</td>
<td>Mineral soil (0-5 cm layer) microbial biomass carbon</td>
<td>206</td>
</tr>
<tr>
<td>Soil carbon stock</td>
<td>Total soil carbon stock (Mg ha$^{-1}$) in forest floor and 0-10 cm mineral soil layer combined</td>
<td>209</td>
</tr>
<tr>
<td><strong>Nutrient cycling processes</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Litter decomposition</td>
<td>Decomposition of leaf litter using the litterbag methodology (% daily rate)</td>
<td>204</td>
</tr>
<tr>
<td>Nitrogen resorption efficiency</td>
<td>Difference in N content between green and senescent leaves divided by N content of green leaves (%)</td>
<td>202</td>
</tr>
<tr>
<td>Soil C/N ratio</td>
<td>Soil C/N ration in forest floor and 0-10 cm mineral soil layer combined</td>
<td>209</td>
</tr>
<tr>
<td>Wood decomposition</td>
<td>Decomposition of flat wooden sticks placed on forest floor (% daily rate)</td>
<td>209</td>
</tr>
<tr>
<td><strong>Production</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fine root biomass</td>
<td>Total biomass of living fine roots in forest floor and 0-10 mineral soil layer combined (g m$^{-2}$)</td>
<td>208</td>
</tr>
<tr>
<td>Photosynthetic efficiency</td>
<td>Chlorophyll fluorescence methodology (ChlF)</td>
<td>201</td>
</tr>
<tr>
<td>Leaf mass</td>
<td>Leaf Area Index (LAI)</td>
<td>208</td>
</tr>
<tr>
<td>Litter production</td>
<td>Annual production of foliar litter dry mass (g)</td>
<td>209</td>
</tr>
<tr>
<td>Tree biomass</td>
<td>Aboveground biomass of all trees (Mg C ha$^{-1}$)</td>
<td>209</td>
</tr>
<tr>
<td>Tree productivity</td>
<td>Annual aboveground wood production (Mg C)</td>
<td>209</td>
</tr>
</tbody>
</table>
Understorey biomass

Dry weight of all understorey vegetation in a quadrant (g)

Regeneration

Sapling growth

Growth of saplings up to 1.60 m tall (cm)

Tree juvenile regeneration

Number of saplings up to 1.60 m tall

Tree seedling regeneration

Number of tree seedlings less than a year old

Resistance

Resistance to drought

Difference in carbon isotope composition in wood cores between dry and wet years

Resistance to insect damage

Foliage not damaged by insects (%)  

Resistance to mammal browsing

Twigs not damaged by browsers (%)  

Resistance to pathogen damage

Foliage not damaged by pathogens (%)  

Tree growth recovery

Ratio between post-drought growth and growth during the respective drought period  

Tree growth resilience

Ratio between growth after and before the drought period  

Tree growth resistance

Ratio of tree growth during a drought period and growth during the previous five year high-growth period  

Tree growth stability

Mean annual tree growth divided by standard deviation in annual tree growth between 1992 and 2011

Table 2. Percentage contributions of the context variables to the first three axes of the PCA of the sensitivity estimates ($\beta_{sen}$) from all 26 ecosystem functions. The variance explained by the first three principal components is given in the footer. The values in bold face indicate the strongest loadings on each axis. AET: actual evapotranspiration; WAI: water availability index; GSL: growing season length; Sand: percentage sand in soil; pH: pH of mineral soil layer; Stones: volume of stones in 0-30 cm mineral soil layer; M$\text{VAR}$: mean coefficient of variation in soil moisture; and FD$\text{pool}$: functional diversity of the species pool.

<table>
<thead>
<tr>
<th></th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
</tr>
</thead>
<tbody>
<tr>
<td>AET</td>
<td>12.5</td>
<td>36.89</td>
<td>7.23</td>
</tr>
<tr>
<td>WAI</td>
<td>27.26</td>
<td>13.69</td>
<td>2.61</td>
</tr>
<tr>
<td>GSL</td>
<td>4.44</td>
<td>2.68</td>
<td>35.67</td>
</tr>
<tr>
<td>Sand</td>
<td>2.86</td>
<td>24.46</td>
<td>0.83</td>
</tr>
</tbody>
</table>
**FIGURES**

**Figure 1.** Variance components showing the proportion of total variation in each EF explained by each predictor variable. Estimates of the variance components (means of the posterior distributions of standard deviation parameters) for each predictor variable were standardised by the sum of all the variance components for each ecosystem function (EF). The mean variance component for each predictor variable across all EFs (mean) and the variance components of the multifunctionality measures (50% threshold-based multifunctionality and average-based multifunctionality) are also presented. See Table 1 for the description of each ecosystem function.

**Figure 2.** The predicted effect of species richness across all regions (left panel) and in each region (right panel) for each ecosystem function and for multifunctionality (50% threshold-based multifunctionality and average-based multifunctionality). The horizontal lines are 95% credible intervals. Dark blue: Finland; light blue: Poland; dark green: Germany; light green: Romania; orange: Italy; and red: Spain. The predictions are from the base model (i.e. equation 1), where species richness effect is the slope of the relationship between the EF and the tree species richness. The mean species richness effect across all regions was estimated from a model without a region x species richness interaction term.

**Figure 3.** Mean sensitivity estimates ($\beta_{sens}$) across all the ecosystem functions (EFs) for each context variable. The thick and thin vertical lines indicate 75% and 95% confidence intervals, respectively. Actual evapotranspiration; Water availability index; Growing season length; Soil sand content: percentage of sand in soil; Soil pH: pH of mineral soil layer; Soil stone content: volume of stones in 0 – 30 cm soil layer; Soil moisture variability: coefficient of variation in soil moisture; and Functional diversity: functional diversity of the regional species pool. Positive $\beta_{sens}$ values indicate an increasingly positive species richness effect.
with increasing values of the context variable, whilst negative values indicate the opposite. ANOVA test indicated no significant differences in the sensitivity of species richness effects to the difference contexts across all 26 EFs (F=1.063; p = 0.389).

**Figure 4.** The scores of each ecosystem function (EF) on the first three principal components to illustrate sensitivity of species richness effects to the main drivers of context dependency tested in the study. The arrows and associated text indicate an increasingly positive species richness - EF relationship with increasing values of the context variable. pH: pH of the mineral soil layer; WAI: water availability index; AET: actual evapotranspiration; Sand: percentage of sand in soil; and GSL: growing season length.

**Figure 1.**
Figure 2.
Figure 4.

Sensitivity of species richness effects ($\beta_{\text{senS}}$)
Sensitivity of species richness effects ($\beta_{\text{sens}}$)

- Evapotranspiration
- Water availability
- Growing season length
- Soil sand content
- Soil pH
- Soil stone content
- Soil moisture variability
- Functional diversity

Context variable

This article is protected by copyright. All rights reserved