

LETTER

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

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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.

Keywords

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

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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: (1) *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); (2) *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); (3) *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 (4) *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

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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 covary 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 would 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

FunDivEUROPE exploratory platform

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 $30 \times 30 \text{ m}^2$ 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 five target species (see Supplementary Material S1 for the location and species pool of each region). Covariation

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 $\geq 7.5 \text{ cm}$ 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).

Ecosystem functioning data were used to calculate two multifunctionality measures for each plot: (1) 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 (2) 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

Table 1 Overview of the 26 ecosystem functions (EFs) and their classification

Ecosystem function	Description	Number of measurements
Nutrient and carbon cycling drivers		
Earthworm biomass	Biomass of all earthworms (g m^{-2})	209
Fine woody debris	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	208
Microbial biomass	Mineral soil (0–5 cm layer) microbial biomass carbon	206
Soil carbon stock	Total soil carbon stock (Mg ha^{-1}) in forest floor and 0–10 cm mineral soil layer combined	209
Nutrient cycling processes		
Litter decomposition	Decomposition of leaf litter using the litterbag methodology (% daily rate)	204
Nitrogen resorption efficiency	Difference in N content between green and senescent leaves divided by N content of green leaves (%)	202
Soil C/N ratio	Soil C/N ration in forest floor and 0–10 cm mineral soil layer combined	209
Wood decomposition	Decomposition of flat wooden sticks placed on forest floor (% daily rate)	209
Production		
Fine root biomass	Total biomass of living fine roots in forest floor and 0–10 mineral soil layer combined (g m^{-2})	208
Photosynthetic efficiency	Chlorophyll fluorescence methodology (ChlF)	201
Leaf mass	Leaf area index (LAI)	208
Litter production	Annual production of foliar litter dry mass (g)	209
Tree biomass	Aboveground biomass of all trees (Mg C ha^{-1})	209
Tree productivity	Annual aboveground wood production ($\text{Mg C ha}^{-1} \text{ year}^{-1}$)	209
Understorey biomass	Dry weight of all understorey vegetation in a quadrant (g)	209
Regeneration		
Sapling growth	Growth of saplings up to 1.60 m tall (cm)	209
Tree juvenile regeneration	Number of saplings up to 1.60 m tall	209
Tree seedling regeneration	Number of tree seedlings less than a year old	209
Resistance		
Resistance to drought	Difference in carbon isotope composition in wood cores between dry and wet years	185
Resistance to insect damage	Foliage not damaged by insects (%)	208
Resistance to mammal browsing	Twigs not damaged by browsers (%)	207
Resistance to pathogen damage	Foliage not damaged by pathogens (%)	209
Tree growth recovery	Ratio between post-drought growth and growth during the respective drought period	207
Tree growth resilience	Ratio between growth after and before the drought period	207
Tree growth resistance	Ratio of tree growth during a drought period and growth during the previous 5-year high-growth period	207
Tree growth stability	Mean annual tree growth divided by standard deviation in annual tree growth between 1992 and 2011	207

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.

availability index ($\text{WAI} = (\text{precipitation} - \text{potential evapotranspiration}) / \text{potential evapotranspiration}$), 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's 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 & Weil 2016), and the pH of the top

10 cm of 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 lifespan (years), 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: (1) region effects; (2) species richness effects; (3) region \times species richness interaction effects; (4) species composition effects; (5) other plot-level effects (basal area and proportion of conifers); and (6) residual variation, in the following model:

$$EF_i = \beta^0 + \beta_{j(i)}^{\text{region}} + \beta_{j(i)}^{\text{sr}} \times SR_i + \beta_{k(i)}^{\text{mix}} + \beta_i^{\text{ba}} \times BA_i + \beta_i^{\text{cp}} \times CP_i + \varepsilon_i \quad (1)$$

where EF_i is the predicted ecosystem function in plot i , β^0 is the grand mean for the EF, $\beta_{j(i)}^{\text{region}}$ is the effect of region ($j = 1, \dots, 6$), $\beta_{j(i)}^{\text{sr}}$ is the region-specific slope of the species richness effect, that is the interaction between region and species richness, $\beta_{k(i)}^{\text{mix}}$ is the effect of species composition ($k = 1, \dots, 92$), and β_i^{ba} and β_i^{cp} 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 \times species richness interaction and composition effects were modelled from separate zero-mean normal distributions (e.g. $\beta_{j(i)}^{\text{region}} \sim N(0, \sigma_{\text{region}}^2)$, with σ_{region}^2 a superpopulation 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 β s (e.g. σ_{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 data set 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 eqn 1 of the variance partitioning analysis. In addition, the region-specific effect of species richness (β_j^{sr}) was modelled as a function of each region-level context variable separately, such that:

$$\beta_j^{\text{sr}} = \alpha_{\text{sens}} + \beta_{\text{sens}} \times \text{CONTEXT}_j + \varepsilon_j \quad (2)$$

where α_{sens} is the estimated intercept, β_{sens} is the sensitivity coefficient, CONTEXT_j is the context variable in region j and ε_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. eqns 1 and 2) was run on each EF (and multifunctionality measure) and context variable separately, thus we obtained a sensitivity estimate (β_{sens}) for each EF and context variable combination. We then used PCA analysis on the sensitivity estimates (β_{sens}) to identify the dominant patterns of covariation 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's 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; that is, 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 the following: (1) the overall mean species richness effect for each EF (and multifunctionality measure), using eqn 1 without the region \times SR interaction term; and (2) the species richness effect in each region without the influence of the context variable (i.e. only eqn 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 component 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 that 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 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 $|\beta_{\text{sens}}|$: 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 $|\beta_{\text{sens}}|$: 0.048 ± 0.01). Variation in SR effects was more strongly related to the context variables in the resistance EFs (mean $|\beta_{\text{sens}}|$: 0.081 ± 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 β_{sens} 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 and 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 and S3.30).

Covariation 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 and Fig. S2.8), followed by actual evapotranspiration (PC2; 23.3%) and finally GSL (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 GSL, whilst the reverse was the case in the EFs related to regeneration and resistance (Fig. 4; Fig. S2.9 and 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

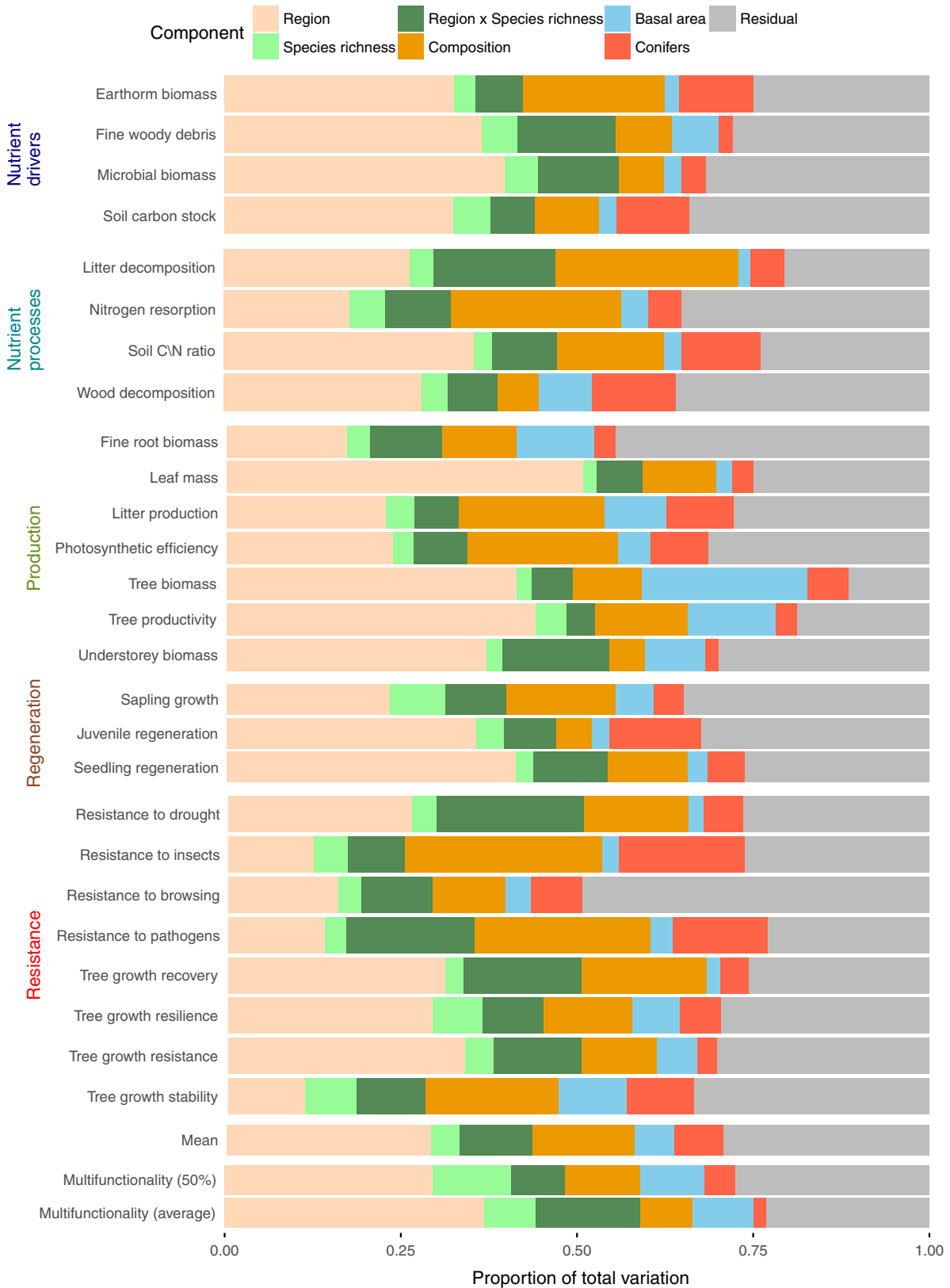


Figure 1 Variance components showing the proportion of total variation in each EF explained by each predictor variable. Estimates of the variance components (means of the posterior distributions of standard deviation parameters) for each predictor variable were standardised by the sum of all the variance 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.

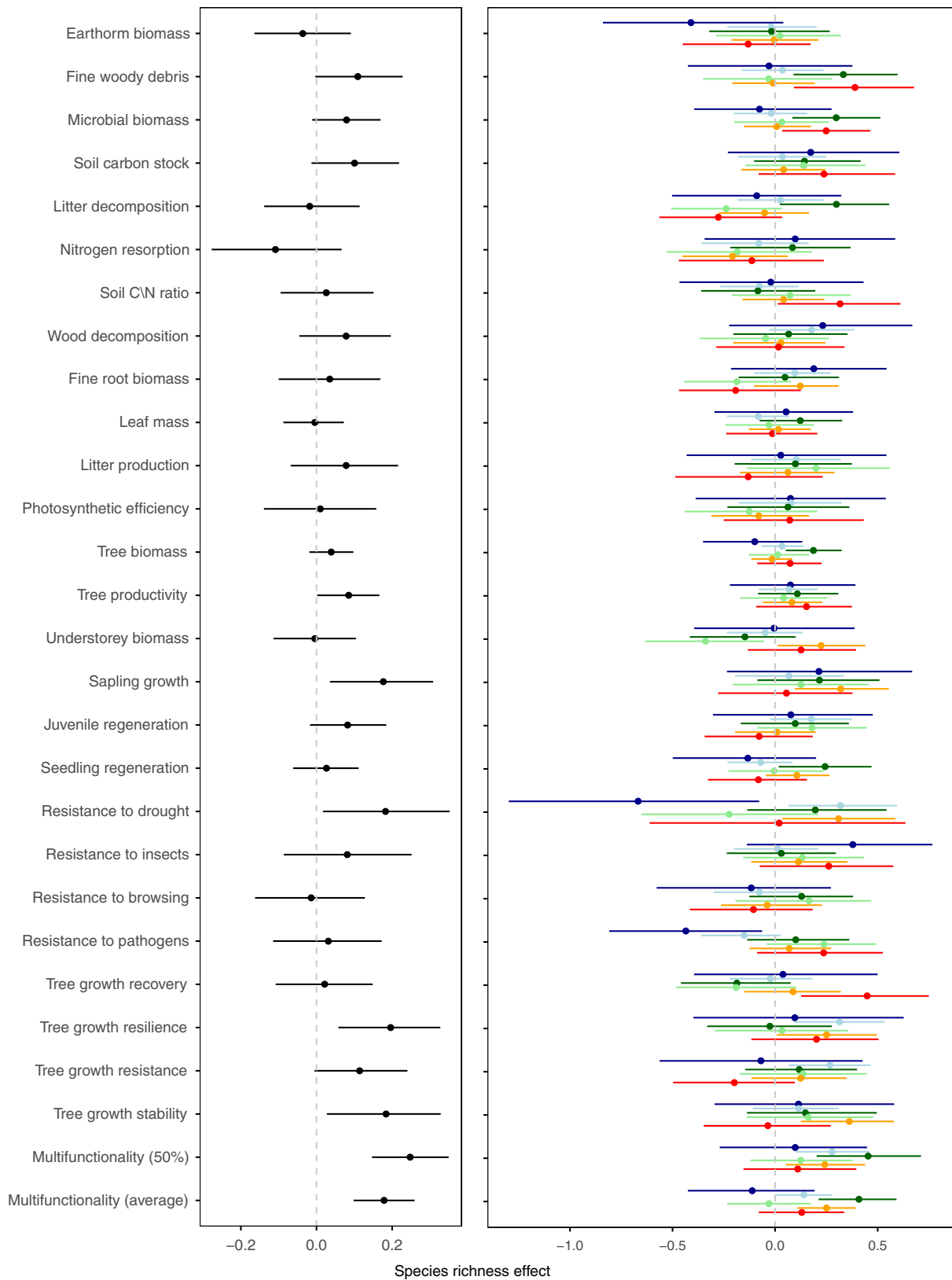


Figure 2 The predicted effect of species richness across all regions (left panel) and in each region (right panel) for each ecosystem function and for multifunctionality (50% threshold-based multifunctionality and average-based multifunctionality). The horizontal lines are 95% credible intervals. Dark 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. eqn 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.

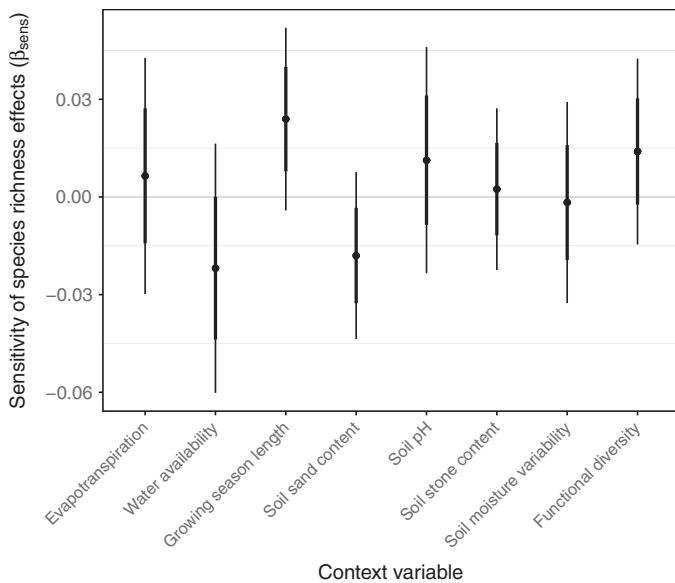


Figure 3 Mean sensitivity estimates (β_{sens}) across all the ecosystem functions (EFs) for each context variable. The thick and thin vertical lines indicate 75 and 95% confidence intervals, respectively. Actual evapotranspiration; water availability index; growing season length; soil sand content: percentage 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 β_{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 ($F = 1.063$; $P = 0.389$).

Table 2 Percentage contributions of the context variables to the first three axes of the PCA of the sensitivity estimates (β_{sens}) from all 26 ecosystem functions

	PC1	PC2	PC3
AET	12.5	36.89	7.23
WAI	27.26	13.69	2.61
GSL	4.44	2.68	35.67
Sand	2.86	24.46	0.83
pH	25.70	0.05	5.84
Stones	16.86	0.16	9.76
M_{VAR}	0.11	16.17	20.02
FD_{pool}	10.27	5.90	18.04

PC1: 53.7%; PC2: 23.3%; PC3 19.4%; total 96.4%.

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_{VAR} , mean coefficient of variation in soil moisture; FD_{pool} , functional diversity of the species pool.

function responded negatively to increasing tree species richness in all regions. From a forest management perspective, this means that conversion of monospecific 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 and 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 GSL, 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 GSL was a weaker modulator of B-EF relations than water availability,

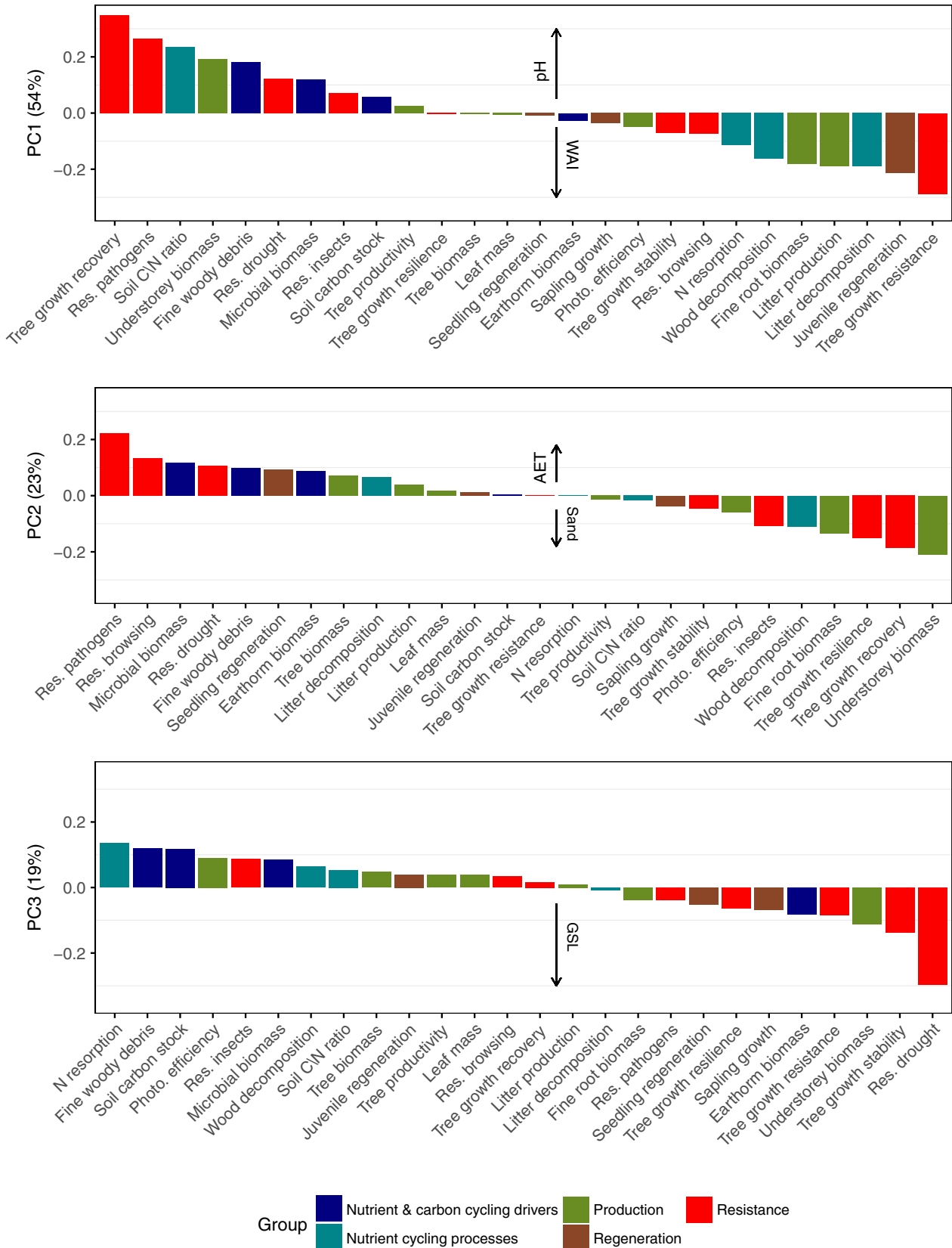


Figure 4 The scores of each ecosystem function (EF) on the first three principal components to illustrate sensitivity of species richness effects to the main drivers of context dependency tested in the study. The arrows and associated text indicate an increasingly positive species richness–EF relationship 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; GSL, growing season length.

our synthesis revealed a tendency for B-EF relations to become more strongly positive with increasing GSL, especially in the resistance EFs. This also contradicts our expectations from H1 and suggests that seasonal complementarity between coexisting 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 (Castagneyrol *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 GSLs 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.

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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.

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