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

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99 **Author Contributions**

100 SR, LB, CW, TJ, FvdP, RB, HB, BO, MSL, EA, PRB and AP developed the ideas of the
101 study. SR and LB analysed the data. All authors, except SR, CW, FvdP, EA, BO, AP, MF,
102 JH, SK, FR, CN, PRB and RS contributed data. SR and LB wrote the first draft of the
103 manuscript, which was revised by all co-authors.

104

105 **Data accessibility**

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

107

108 **Abstract**

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

121

122 **Running title**

123 Context dependency of diversity effects

124

125 **Keywords**

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

128

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139

140 **Introduction**

141 Forests have helped sustain humans for millennia; from the water we drink to the houses we
142 live in, forests provide us with a wealth of goods and services. Tree species diversity is

143 known to promote key forest ecosystem functions, including primary production (Paquette &
144 Messier 2011; Liang *et al.* 2016), stability of wood production (Jucker *et al.* 2014),
145 resistance to biotic and abiotic disturbances (Pretzsch *et al.* 2013b; Jactel *et al.* 2017) and
146 nutrient cycling (Richards *et al.* 2010; Handa *et al.* 2014), amongst others. Despite evidence
147 that diverse forests are able to support higher levels of ecosystem functioning than species-
148 poor ones (Gamfeldt *et al.* 2013), the importance of tree diversity as a driver of ecosystem
149 functioning is also known to vary considerably amongst forest types, geographic regions,
150 and in relation to climatic conditions (Paquette & Messier 2011; Pretzsch *et al.* 2013a;
151 Forrester 2014; Grossiord *et al.* 2014; Jucker *et al.* 2016; Liang *et al.* 2016; Ratcliffe *et al.*
152 2016). This context dependency of diversity effects is seen as an obstacle to scaling up and
153 generalising biodiversity experiments, because the importance of environmental conditions
154 in shaping biodiversity-ecosystem functioning (B-EF) relationships is poorly understood,
155 particularly for ecosystem functions other than biomass production (Cardinale *et al.* 2000;
156 Srivastava & Vellend 2005; Allan *et al.* 2015).

157
158 A number of mechanisms have been put forward to explain why B-EF might be context-
159 dependent. Here we focus on four factors that have received the most attention in the
160 literature: (i) *Resource availability*: the number of resource-related niche dimensions, and
161 thus the potential for niche partitioning, is predicted to be greater in resource-limited
162 environments (Harpole *et al.* 2016). Following this reasoning, a greater potential for niche
163 partitioning should promote higher levels of ecosystem functioning in conditions less
164 favourable for growth. Forest stands with poor soil quality have been found to exhibit
165 stronger positive diversity effects than stands on highly fertile soils (Pretzsch *et al.* 2013a;
166 Toigo *et al.* 2015). In addition, along broad climatic gradients B-EF relationships have been
167 reported to be strongest in conditions less favourable for growth (e.g. Paquette & Messier
168 2011; Ratcliffe *et al.* 2016); (ii) *Resource heterogeneity*: niche partitioning between species
169 can be promoted by spatial heterogeneity of resources (Pacala & Tilman 1994; Cardinale *et al.*
170 *et al.* 2000) and diversity may be more important to guarantee functioning in heterogeneous
171 environments, due to spatial insurance effects (Loreau *et al.* 2003). Heterogeneity of soil
172 nutrients has been found to promote aboveground biomass production in experimental
173 grassland communities through increased resource partitioning (Wacker *et al.* 2008); (iii)
174 *Biotope space*: an increase in biotope space (i.e. the physical space associated with a species'
175 niche) could also lead to more pronounced diversity effects, as demonstrated in experimental
176 grasslands where greater soil depth and rooting space increased biodiversity effects on

177 biomass production, due to greater differentiation of rooting architectures through the soil
178 profile (Dimitrakopoulos & Schmid 2004); and (iv) *Species functional dissimilarity*: niche
179 partitioning requires coexisting species to have different attributes that enable them to utilise
180 available resources in different ways (Díaz & Cabido 2001). B-EF relations are therefore
181 predicted to be stronger where coexisting species are more functionally dissimilar (Chesson
182 2000), for example via phenological differences (Sapijanskas *et al.* 2014) or heterogeneity in
183 rooting or canopy architectures and shade tolerance (Brassard *et al.* 2013; Jucker *et al.*
184 2015).

185

186 How multiple functions co-vary in their response to diversity across complex environmental
187 gradients is rarely investigated (Cardinale *et al.* 2013; Dooley *et al.* 2015; Ruiz-Benito *et al.*
188 2017). However, identifying patterns in these responses is a key step towards understanding
189 the mechanisms that give rise to general patterns of B-EF. Using a continent-wide forest
190 research platform (FunDivEUROPE; Baeten *et al.*, 2013) in six European regions with
191 differing climatic, edaphic and biotic conditions, we tested the extent and potential drivers of
192 context dependency of species richness effects on 26 ecosystem functions (EFs). In a first
193 step, we quantified the proportion of total variation in functioning attributable to
194 interregional differences in species richness effects. We did this to determine the importance
195 of species richness relative to other potential drivers, and to evaluate the extent of context
196 dependency in B-EF. Subsequently, we explored the environmental modulators of species
197 richness effects for each EF. For this we designed a hierarchical approach, which first tested
198 the strength and direction of EF responses to species richness, and then identified key drivers
199 of variation in any response (hereafter ‘context variables’). This allowed us to identify the
200 functions that were most strongly promoted by tree species richness and the environmental
201 conditions in which the effect was strongest. We expected B-EF relations to vary between
202 the six regions and hypothesised that species richness effects on individual functions will
203 increase along one or more of the following gradients:

204

205 (H1) decreasing resource availability, such as low water availability and poor soil fertility;

206 (H2) increasing soil resource heterogeneity;

207 (H3) increasing biotope space, such as increasing soil volume; and

208 (H4) increasing functional dissimilarity of the regional tree species pool.

209

210 **Methods**

211 *FunDivEUROPE Exploratory Platform*

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

227

228 *Ecosystem functions*

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

236

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

244

245 *Plot-level predictors*

246 To explain plot-level variation in EFs and multifunctionality, we used target species richness
247 as a continuous variable. Non-target species made up 5% of the basal area across all the plots
248 and given that their contribution to ecosystem functioning is likely to be low, they were not
249 included in the species richness measure. Plot species composition (a categorical variable
250 with 92 levels, where each level reflects a unique combination of target species), total tree
251 basal area (the sum of the basal area of all trees per plot, m²) and the proportion of conifers
252 were included as covariates. Species composition was included to account for the identity of
253 the species, which can greatly influence ecosystem functioning (Hooper *et al.* 2005). Basal
254 area was included to account for within-region variability due to historical management
255 effects and natural disturbances and the proportion of conifers was included to account for
256 within-region functional effects of the two highly dissimilar clades (Stahl *et al.* 2013), which
257 are known to be important for several of the EFs (e.g. Guyot *et al.* 2016; Dawud *et al.* 2017).

258

259 *Regional context variables*

260 To test our four hypotheses, we chose context variables that describe the climatic, edaphic
261 and biotic conditions of each region. All context variables were measured on site except for
262 the climate variables. **(H1)**: Differences in the abiotic conditions between the regions were
263 described using a water availability index (WAI = (precipitation–potential
264 evapotranspiration)/potential evapotranspiration), actual evapotranspiration (AET, mm),
265 annual growing season length (GSL, number of days above 10 °C, following Pretzsch *et al.*
266 (2014)), soil sand content (SAND, %) and soil pH (pH). WAI and GSL were both calculated
267 from AGRI4CAST (<https://ec.europa.eu/jrc/en/mars>) using daily data from 1997 to 2011.
268 AET was derived from the water balance model BILJOU (Granier *et al.*, 1999;
269 <https://appgeodb.nancy.inra.fr/biljou/>). WAI reflects the potential drought stress experienced
270 by plants, whilst AET reflects the magnitude and length of conditions favourable to plant
271 growth (Stephenson 1998). Both GSL and AET are measures of potential climate influence
272 on the productivity of the region, however they were weakly correlated (Pearson correlation:
273 $r = 0.13$; $p=0.80$) and we used both in the analyses. SAND was used to describe soil nutrient
274 and water retention potential, which declines as the percentage of sand increases (Brady
275 1984), and the pH of the top 10 cm mineral soil layer was used as an indicator of the soil
276 nutrient status.

277

278 (H2): Soil resource heterogeneity was quantified as the coefficient of variation of soil
279 moisture in each plot (M_{VAR}). (H3): The volumetric stone content (STONES) in the upper 30
280 cm of mineral soil was used as an indicator of the available belowground growing space or
281 biotope space (see Appendix S1.3). We did not use soil depth because of the lack of a
282 precise measurement in each plot; however, soils with high rock content are typically also
283 shallower.

284
285 (H4): The functional diversity of the species pool (FD_{pool}) in each region was used to
286 describe the dissimilarity in traits of the tree species and thus their potential for niche
287 partitioning. The use of FD_{pool} assumes that the propensity for complementarity between
288 species has more to do with their functional traits than with their biogeographic origin, for
289 instance, if complementarity between native and non-native species is reduced due to the
290 lack of mutualists (Tobner *et al.* 2014). FD_{pool} was calculated using the mean dissimilarity
291 index of Pavoine & Bonsall (2011) based on seed mass (mg), maximum height (m),
292 maximum life span (yrs), leaf nitrogen content ($mg\ g^{-1}$), litter lignin/nitrogen ratio, litter
293 SLA and wood density ($g\ cm^{-3}$). These are key functional traits that are indicative of species'
294 ecological strategies of resource acquisition, growth and litter quality (Westoby *et al.* 2002;
295 Appendix S1.3). ANOVA indicated significant ($p < 0.05$) differences in all the context
296 variables between the regions (Figure S1.3).

297 298 *Statistical methods*

299 Variance partitioning was used to quantify the proportion of total variation in functioning
300 attributable to species richness, interregional differences in the effect of species richness and
301 other potential drivers of ecosystem functioning. Using the same base model, we then
302 explored how species richness effects varied between the regions and what factors could
303 explain this variation. The analyses were run in a Bayesian framework using the Stan
304 probabilistic modelling language, called from R (version 3.2.4) using the *rstan* package
305 (Stan Development Team 2016). All models were run for 5000 iterations of both warm up
306 and sampling. We tested for model convergence by running three MCMC chains with
307 different starting values and checked the trace plots and Rhat statistics (Gelman & Hill
308 2007).

309 310 *Variance partitioning*

311 For each EF and multifunctionality measure, we partitioned the total variance into several
312 components using a multilevel analysis of variance (Gelman & Hill 2007; Hector *et al.*
313 2011). Between-plot variation was attributed to: i) region effects; ii) species richness effects;
314 iii) region \times species richness interaction effects; iv) species composition effects; v) other
315 plot-level effects (basal area and proportion of conifers); and vi) residual variation, in the
316 following model:

$$318 \quad EF_i = \beta^0 + \beta_{j(i)}^{region} + \beta_{j(i)}^{sr} \cdot SR_i + \beta_{k(i)}^{mix} + \beta_i^{ba} \cdot BA_i + \beta_i^{cp} \cdot CP_i + \varepsilon_i \quad (1)$$

319
320 where EF_i is the predicted ecosystem function in plot i , β^0 is the grand mean for the EF,
321 $\beta_{j(i)}^{region}$ is the effect of region ($j = 1, \dots, 6$), $\beta_{j(i)}^{sr}$ is the region-specific slope of the species
322 richness effect, i.e. the interaction between region and species richness, $\beta_{k(i)}^{mix}$ is the effect of
323 species composition ($k = 1, \dots, 92$), and β_i^{ba} and β_i^{cp} are the slopes for the effects of basal
324 area (BA) and proportion of conifers (CP), respectively. Plot-level residual error was
325 modelled from a normal distribution ($\varepsilon_i \sim N(0, \sigma^2)$) and the region, region \times species richness
326 interaction and composition effects were modelled from separate zero-mean normal
327 distributions (e.g., $\beta_{j(i)}^{region} \sim N(0, \sigma_{region}^2)$, with σ_{region}^2 a super-population variance). EF
328 values were transformed where necessary to meet assumptions of normality and were
329 centred on 0 and scaled by their standard deviation. Following Gelman & Hill (2007) and
330 Hector *et al.* (2011), the variance components were estimated as the standard deviation of
331 the β s (e.g., σ_{region} , the finite population standard deviation of the region-level effects) and
332 are independent of the order of terms in the model. Plot-level basal area and proportion of
333 conifers were centred on their regional mean to reduce their influence on any context
334 variable effect (see the following section for more details) especially in the case where the
335 covariates and context variables were correlated (Bell & Jones, 2015). This form of scaling
336 allows for the within-region effects of the covariates to be accounted for in the model but
337 excludes any between-region effects. The variance partitioning analysis was repeated with
338 the dataset restricted to mixtures of up to three species, to check that the patterns were not
339 influenced by the different lengths of the species richness gradients in the different regions.

340
341 *Estimation of species richness effects and drivers of context dependency*

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

$$348 \beta_j^{SR} = \alpha_{sens} + \beta_{sens} \cdot CONTEXT_j + \varepsilon_j \quad (2)$$

350 where α_{sens} is the estimated intercept, β_{sens} is the sensitivity coefficient, $CONTEXT_j$ is the
351 context variable in region j and ε_j is the residual error (again modelled from a normal
352 distribution). The context variables were centred on 0 and scaled by the standard deviation.

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

370

371 **Results**

372 *Species richness effects and the degree of context dependency*

373 Species richness (SR) explained only 4% of the total variation across all the ecosystem
374 functions (EFs, Fig. 1). However, SR was more important for multifunctionality (assuming a

375 50% threshold) than for any of the individual EFs (explaining 11% of the total variation, Fig.
376 1). For most of the EFs the importance of SR varied between regions and the interaction
377 between region and SR explained more variance on average (10%) than the main effect of
378 SR (Fig. 1). For the individual variance components estimates see Fig. S2.1 and Table S2.1.
379 The interaction between region and SR explained the greatest variation in the resistance EFs
380 (13%) and the least in the production EFs (8%, Fig. S2.2); however, the differences were not
381 significant (ANOVA: $F=1.622$, $p=0.206$). At the highest threshold of multifunctionality
382 tested (70%) the interaction of region with SR variance component was larger than for any
383 of the individual EFs (25% of the total variation, Fig. S2.2). The magnitude of the interaction
384 of region with SR variance components, across the EFs, was generally supported when the
385 SR gradient was restricted to three species (Fig. S2.3). Species composition effects, on
386 average, explained only slightly more variation than the interaction of region with SR (14%
387 and 10% of the total variation, respectively, Fig. 1). For multifunctionality, species
388 composition was of comparable importance to SR and the interaction of region with SR
389 (11%, 11% and 8%, respectively, Fig. 1).

390
391 Across the EFs, the mean effect of SR was positive (mean effect size 0.06 ± 0.03 95% CIs;
392 Fig. 2) and there were no significant differences between the EF groups ($F=2.01$; $p = 0.129$;
393 Fig. S2.4). In addition, the mean effect of SR on multifunctionality (50% threshold and
394 average-based) was positive with 95% credible intervals that did not include zero. The
395 boreal forest (Finland) had the largest number of negative SR effects (46%) and the
396 temperate deciduous forest (Germany) the least (19%); consistent with this, SR effects on
397 multifunctionality (50% threshold) varied across the regions, from strongly positive in
398 Germany to neutral in Finland.

399 400 *Drivers of context dependency in species richness effects*

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

409 was more strongly related to the context variables in the resistance EFs (mean $|\beta_{sens}|$ $0.081 \pm$
410 0.02) than in the production and regeneration EFs (0.044 ± 0.01 and 0.047 ± 0.01 ,
411 respectively; ANOVA: $F = 5.363$; $p < 0.001$; Fig. S2.6). See Supplementary Material S3 and
412 Table S2.2 for the individual β_{sens} figures and estimates, and Fig. S2.7 for the variance
413 explained by each model. Species richness effects on multifunctionality (50% threshold)
414 were more positive in regions with high AET (Figs. S2.5 & S3.28). However, at higher
415 levels of functioning (70% threshold), and for average-based multifunctionality, SR effects
416 on multifunctionality were highly sensitive to WAI, GSL and sand content, becoming
417 negative in regions with shorter growing seasons, high sand content and high water
418 availability (i.e. Finland, Figs. S2.5 & S3.29 & S3.30).

419

420 *Co-variation in context dependency between ecosystem functions*

421 The largest amount of variation in the B-EF sensitivities was explained by water availability
422 and soil pH (PC1; 53.7%, Table 2 & Fig. S2.8); followed by actual evapotranspiration (PC2;
423 23.3%); and finally growing season length (PC3; 19.4%). The sensitivity of SR effects to the
424 main drivers of context dependency differed between the EFs (Fig. 4); however, there were
425 no significant differences between the EF groups (Fig. S2.9). With increasing water
426 availability, SR had increasingly positive effects on nutrient cycling processes but
427 increasingly negative effects on nutrient and carbon cycling drivers. Species richness effects
428 in both groups tended to decrease, and turn weakly negative, with increasing growing season
429 length, whilst the reverse was the case in the EFs related to regeneration and resistance (Figs.
430 4, S2.9 & S2.10).

431

432 **Discussion**

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

438

439 *Regional importance of species richness for forest ecosystem functioning*

440 Regional differences in species richness effects accounted for 10% of the variation in EFs
441 (ranging from 4% to 20%, Fig. 1), which is an important contribution across such broad
442 gradients in forest types, climates and soils. Thus, our study is in accordance with growing

443 evidence that biodiversity effects on ecosystem functioning can be substantially modified by
444 environmental conditions (Cardinale *et al.* 2000; Hättenschwiler *et al.* 2005; Paquette &
445 Messier 2011; Pretzsch *et al.* 2013a; Forrester 2014; Liang *et al.* 2016; Ratcliffe *et al.* 2016).
446 We also found that at a continental scale, across multiple functions, species richness was
447 comparable in importance to species composition for ecosystem functioning. We found a
448 clear tendency for more positive than negative species richness effects (Fig. 2). As a
449 consequence, our indices of multifunctionality were also positively related to tree species
450 richness in all regions (low or medium threshold), or were positive in most regions (high
451 threshold and average-based). Interestingly, no ecosystem function responded negatively to
452 increasing tree species richness in all regions. From a forest management perspective this
453 means that conversion of mono-specific stands to multi-species forests should generally
454 result in a higher delivery of ecosystem goods and services, thus supporting current policies
455 of forest conversion in several countries (Knoke *et al.* 2008).

456

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

467

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

469 From the set of context variables that we tested, water availability was the most important in
470 changing the relationship between species richness and forest functioning (Fig. 3 & Table 2).
471 We therefore found the greatest support for our first hypothesis (H1) that the positive effects
472 of species richness should increase with resource limitation, consistent with earlier studies
473 demonstrating the importance of abiotic gradients in modulating diversity effects (Pretzsch
474 *et al.* 2013a; Forrester & Pretzsch 2015; Ratcliffe *et al.* 2016). We acknowledge that water
475 availability and soil pH were highly correlated and that we cannot rule out that soil pH
476 contributed to context dependency. However, water availability loaded more strongly on

477 PC1 than soil pH and, in general, B-EF relations were more sensitive to water availability
478 than soil pH, especially for functions related to resistance and nutrient cycling. Water
479 availability explained the variability in species richness effects better than evapotranspiration
480 rates or growing season length, which suggests that species richness effects may be more
481 influenced by the length and severity of drought conditions than they are by the magnitude
482 and length of conditions favourable to plant growth (Seddon *et al.* 2016). In general, B-EF
483 relations tended to be more positive in water-limited regions (e.g. Spain) and to turn neutral
484 or negative in regions with high water availability (e.g. Finland). This is consistent with a
485 pan-European study of diversity effects on tree growth (Ratcliffe *et al.* 2016) and provides
486 further evidence, across multiple EFs, that niche partitioning may be particularly important
487 in water-limited forests (Grossiord *et al.* 2014).

488

489 Species richness effects, in some functions, were highly sensitive to evapotranspiration rate
490 (AET), especially in the regeneration and resistance functions. However, across the EFs
491 there was no general pattern in the direction of the sensitivity to AET. The only exception
492 was for the regeneration functions, in which species richness effects became more strongly
493 positive in regions with high AET (central Europe), in contrast to our expectations from H1.
494 Although growing season length was a weaker modulator of B-EF relations than water
495 availability, our synthesis revealed a tendency for B-EF relations to become more strongly
496 positive with increasing growing season length, especially in the resistance EFs. This also
497 contradicts our expectations from H1, and suggests that seasonal complementarity between
498 co-existing species may be an important underlying mechanism of positive species richness
499 effects where growing seasons are long enough (Hooper & Vitousek 1998; Sapjanskas *et al.*
500 2014).

501

502 Soil sand content, moisture variability and stone content were less important in modulating
503 species richness effects than climatic variables. One general pattern, which was in contrast to
504 our predictions from H1, was that tree species richness had stronger effects on functioning in
505 forests with soils that had higher nutrient and water-holding capacities (low sand content;
506 e.g. Germany and Romania), especially for the nutrient and carbon cycling processes, than in
507 soils with poor nutrient and water-holding capacities (e.g. Poland and Finland). It is likely
508 that the sensitivity of B-EF to soil sand content was an artefact of its correlation with several
509 other context variables. We found limited evidence that an increase in soil moisture
510 variability (H2), or biotope space (H3), promoted stronger positive species richness effects.

511 However, the ephemeral nature of soil moisture variability makes it challenging to generalise
512 from single point estimates. Our results provide some support for the hypothesis that a
513 greater tree species functional diversity promotes stronger B-EF relations (H4). Functional
514 diversity appeared particularly important for driving positive species richness effects in the
515 resistance EFs, consistent with studies on tree growth resilience to wildfires (Spasojevic *et al.*
516 *et al.* 2016) and associational resistance to herbivores (Castagneyrol *et al.* 2014).

517

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

529

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

545 that we detected only reflects environmental conditions in Europe. Larger scale studies are
546 needed to determine whether these same patterns hold true across wider climatic gradients.

547

548 **Conclusions**

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

565

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577

578 **Supplementary Materials**

579 S1 FunDivEUROPE Exploratory Platform and ecosystem functions, covariates and context
580 variable descriptions.

581 S2 Supplementary figures and tables

582 S3 Predicted sensitivity estimates

583 S4 Model scripts: a) variance partitioning; b) mean species richness effects; and c)
584 hierarchical context dependency.

585

586 **References**

587 1.Allan, E., Manning, P., Alt, F., Binkenstein, J., Blaser, S., Blüthgen, N., *et al.* (2015). Land
588 use intensification alters ecosystem multifunctionality via loss of biodiversity and changes to
589 functional composition. *Ecol. Lett.*, 18, 834–843

590

591 2.Baeten, L., Verheyen, K., Wirth, C., Bruelheide, H., Bussotti, F., Finér, L., *et al.* (2013). A
592 novel comparative research platform designed to determine the functional significance of
593 tree species diversity in European forests. *Perspect. Plant Ecol. Evol. Syst.*, 15, 281–291

594

595 3.Bauhus, J., Forrester, D.I., Gardiner, B., Jactel, H., Vallejo, R. & Pretzsch, H. (2017).
596 Ecological Stability of Mixed-Species Forests. In: *Mix. For. - Ecol. Manag.* Springer-Verlag,
597 Heidelberg, pp. 337–382

598

599 4.Bauhus, J. & Schmerbeck, J. (2010). Silvicultural options to enhance and use forest
600 plantation biodiversity. In: *Ecosyst. Goods Serv. from Plant. For.* (eds. Bauhus, J., van der
601 Meer, P. & Kanninen, M.). Earthscan, pp. 96–139

602

603 5.Bell, A. & Jones, K. (2015). Explaining Fixed Effects: Random Effects Modeling of Time-
604 Series Cross-Sectional and Panel Data. *Polit. Sci. Res. Methods*, 3, 133–153

605

606 6.Brady, N.C. (1984). *The nature and properties of soils*. 15th edn. Pearson Education

607

608 7.Brassard, B.W., Chen, H.Y.H., Cavard, X., Yuan, Z., Reich, P.B., Bergeron, Y., *et al.*
609 (2013). Tree species diversity increases fine root productivity through increased soil volume
610 filling. *J. Ecol.*, 101, 210–219

611

612 8.Byrnes, J.E.K., Gamfeldt, L., Isbell, F., Lefcheck, J.S., Griffin, J.N., Hector, A., *et al.*

- 613 (2014). Investigating the relationship between biodiversity and ecosystem multifunctionality:
614 challenges and solutions. *Methods Ecol. Evol.*, 5, 111–124
615
- 616 9.Cardinale, B.J., Gross, K., Fritschie, K., Flombaum, P., Fox, J.W., Rixen, C., *et al.* (2013).
617 Biodiversity simultaneously enhances the production and stability of community biomass,
618 but the effects are independent. *Ecology*, 94, 1697–707
619
- 620 10.Cardinale, B.J., Nelson, K. & Palmer, M.A. (2000). Linking species diversity to the
621 functioning of ecosystems: on the importance of environmental context. *Oikos*, 91, 175–183
622
- 623 11.Castagneyrol, B., Jactel, H., Vacher, C., Brockerhoff, E.G. & Koricheva, J. (2014).
624 Effects of plant phylogenetic diversity on herbivory depend on herbivore specialization. *J.*
625 *Appl. Ecol.*, 51, 134–141
626
- 627 12.Chesson, P. (2000). General theory of competitive coexistence in spatially-varying
628 environments. *Theor. Popul. Biol.*, 58, 211–237
629
- 630 13.Cleland, E.E., Chuine, I., Menzel, A., Mooney, H.A. & Schwartz, M.D. (2007). Shifting
631 plant phenology in response to global change. *Trends Ecol. Evol.*, 22, 357–365
632
- 633 14.Comita, L.S., Muller-Landau, H.C., Aguilar, S. & Hubbell, S.P. (2010). Asymmetric
634 density dependence shapes species abundances in a tropical tree community. *Science*, 329,
635 330–2
636
- 637 15.Dawud, S.M., Raulund-Rasmussen, K., Ratcliffe, S., Domisch, T., Finér, L., Joly, F.-X.,
638 *et al.* (2017). Tree species functional group is a more important driver of soil properties than
639 tree species diversity across major European forest types. *Funct. Ecol.*, 31, 1153–1162
640
- 641 16.Díaz, S. & Cabido, M. (2001). Vive la différence: plant functional diversity matters to
642 ecosystem processes. *Trends Ecol. Evol.*, 16, 646–655
643
- 644 17.Dimitrakopoulos, P.G. & Schmid, B. (2004). Biodiversity effects increase linearly with
645 biotope space. *Ecol. Lett.*, 7, 574–583
646

- 647 18.Dooley, Á., Isbell, F., Kirwan, L., Connolly, J., Finn, J.A. & Brophy, C. (2015). Testing
648 the effects of diversity on ecosystem multifunctionality using a multivariate model. *Ecol.*
649 *Lett.*, 18, 1242–1251
650
- 651 19.Forrester, D.I. (2014). The spatial and temporal dynamics of species interactions in
652 mixed-species forests: From pattern to process. *For. Ecol. Manage.*, 312, 282–292
653
- 654 20.Forrester, D.I., Bonal, D., Dawud, S.M., Gessler, A., Granier, A., Pollastrini, M., *et al.*
655 (2016). Drought responses by individual tree species are not often correlated with tree
656 species diversity in European forests. *J. Appl. Ecol.*, 53, 1725–1734
657
- 658 21.Forrester, D.I. & Pretzsch, H. (2015). Tamm Review: On the strength of evidence when
659 comparing ecosystem functions of mixtures with monocultures. *For. Ecol. Manage.*, 356,
660 41–53
661
- 662 22.Gamfeldt, L., Hillebrand, H. & Jonsson, P.R. (2008). Multiple functions increase the
663 important of biodiversity for overall ecosystem functioning. *Ecology*, 89, 1223–1231
664
- 665 23.Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., *et al.*
666 (2013). Higher levels of multiple ecosystem services are found in forests with more tree
667 species. *Nat. Commun.*, 4, 1–8
668
- 669 24.Gelman, A. & Hill, J. (2007). *Data Analysis Using Regression and*
670 *Multilevel/Hierarchical Models*. Cambridge University Press
671
- 672 25.Granier, A., Bréda, N., Biron, P. & Villette, S. (1999). A lumped water balance model to
673 evaluate duration and intensity of drought constraints in forest stands. *Ecol. Model.*, 116, 269–
674 283
675
- 676 26.Grossiord, C., Granier, A., Ratcliffe, S., Bouriaud, O., Bruehlheide, H., Chečko, E., *et al.*
677 (2014). Tree diversity does not always improve resistance of forest ecosystems to drought.
678 *Proc. Natl. Acad. Sci. U. S. A.*, 111, 14812–14815
679
- 680 27.Guyot, V., Castagneyrol, B., Vialatte, A., Deconchat, M. & Jactel, H. (2016). Tree

681 diversity reduces pest damage in mature forests across Europe. *Biol. Lett.*, 12, 20151037
682
683 28.Handa, I.T., Aerts, R., Berendse, F., Berg, M.P., Bruder, A., Butenschoen, O., *et al.*
684 (2014). Consequences of biodiversity loss for litter decomposition across biomes. *Nature*,
685 509, 218–221
686
687 29.Harpole, W.S., Sullivan, L.L., Lind, E.M., Firn, J., Adler, P.B., Borer, E.T., *et al.* (2016).
688 Addition of multiple limiting resources reduces grassland diversity. *Nature*, 537, 93–96
689
690 30.Hättenschwiler, S., Tiunov, A. & Scheu, S. (2005). Biodiversity and litter decomposition
691 in terrestrial ecosystems. *Annu. Rev. Ecol. Evol.*, 36, 191–218
692
693 31.Hector, A., Bell, T., Hautier, Y., Isbell, F., Kéry, M., Reich, P.B., *et al.* (2011). BUGS in
694 the analysis of biodiversity experiments: species richness and composition are of similar
695 importance for grassland productivity. *PLoS One*, 6, e17434
696
697 32.Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., *et al.* (2005).
698 Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol.*
699 *Monogr.*, 75, 3–35
700
701 33.Hooper, D.U. & Vitousek, P.M. (1998). Effects of plant composition and diversity on
702 nutrient cycling. *Ecol. Monogr.*, 68, 121–149
703
704 34.Jacob, D., Petersen, J., Eggert, B., Alias, A., Christensen, O.B., Bouwer, L.M., *et al.*
705 (2014). EURO-CORDEX: New high-resolution climate change projections for European
706 impact research. *Reg. Environ. Chang.*, 14, 563–578
707
708 35.Jactel, H., Bauhus, J., Boberg, J., Bonal, D., Castagneyrol, B., Gardiner, B., *et al.* (2017).
709 Tree Diversity Drives Forest Stand Resistance to Natural Disturbances. *Curr. For. Reports*
710
711 36.Jucker, T., Avăcărței, D., Bărnoaiea, I., Duduman, G., Bouriaud, O. & Coomes, D.A.
712 (2016). Climate modulates the effects of tree diversity on forest productivity. *J. Ecol.*, 104,
713 388–398
714

- 715 37.Jucker, T., Bouriaud, O., Avacaritei, D. & Coomes, D.A. (2014). Stabilizing effects of
716 diversity on aboveground wood production in forest ecosystems: linking patterns and
717 processes. *Ecol. Lett.*, 17, 1560–1569
718
- 719 38.Jucker, T., Bouriaud, O. & Coomes, D.A. (2015). Crown plasticity enables trees to
720 optimize canopy packing in mixed-species forests. *Funct. Ecol.*, 29, 1078–1086
721
- 722 39.Knoke, T., Ammer, C., Stimm, B. & Mosandl, R. (2008). Admixing broadleaved to
723 coniferous tree species: A review on yield, ecological stability and economics. *Eur. J. For.*
724 *Res.*, 127, 89–101
725
- 726 40.Liang, J., Crowther, T.W., Picard, N., Wiser, S., Zhou, M., Alberti, G., *et al.* (2016).
727 Positive biodiversity–productivity relationship predominant in global forests. *Science*, 354,
728 aaf8957
729
- 730 41.Loreau, M., Mouquet, N. & Gonzalez, A. (2003). Biodiversity as spatial insurance in
731 heterogeneous landscapes. *Proc. Natl. Acad. Sci. U. S. A.*, 100, 12765–70
732
- 733 42.Pacala, S.W. & Tilman, D. (1994). Limiting similarity in mechanistic and spatial models
734 of plant competition in heterogeneous environments. *Am. Nat.*, 143, 222–257
735
- 736 43.Paquette, A. & Messier, C. (2011). The effect of biodiversity on tree productivity: from
737 temperate to boreal forests. *Glob. Ecol. Biogeogr.*, 20, 170–180
738
- 739 44.Pavoine, S. & Bonsall, M.B. (2011). Measuring biodiversity to explain community
740 assembly: a unified approach. *Biol. Rev. Camb. Philos. Soc.*, 86, 792–812
741
- 742 45.van der Plas, F., Manning, P., Allen, E., Scherer-Lorenzen, M., Verheyen, K., Wirth, C.,
743 *et al.* (2016). “Jack-of-all-trades” effects drive biodiversity-ecosystem multifunctionality
744 relationships. *Nat. Commun.*, 7, 11109
745
- 746 46.Pretzsch, H., Biber, P., Schütze, G., Uhl, E. & Rötzer, T. (2014). Forest stand growth
747 dynamics in Central Europe have accelerated since 1870. *Nat. Commun.*, 5, 4967
748

- 749 47.Pretzsch, H., Bielak, K., Block, J., Bruchwald, A., Dieler, J., Ehrhart, H.-P., *et al.*
750 (2013a). Productivity of mixed versus pure stands of oak (*Quercus petraea* (Matt.) Liebl. and
751 *Quercus robur* L.) and European beech (*Fagus sylvatica* L.) along an ecological gradient.
752 *Eur. J. For. Res.*, 132, 263–280
753
- 754 48.Pretzsch, H., Schütze, G. & Uhl, E. (2013b). Resistance of European tree species to
755 drought stress in mixed versus pure forests: evidence of stress release by inter-specific
756 facilitation. *Plant Biol.*, 15, 483–495
757
- 758 49.Ratcliffe, S., Liebergesell, M., Ruiz Benito, P., Madrigal González, J., Muñoz Castañeda,
759 J.M., Kändler, G., *et al.* (2016). Modes of functional biodiversity control on tree productivity
760 across the European continent. *Glob. Ecol. Biogeogr.*, 25, 251–262
761
- 762 50.Richards, A.E., Forrester, D.I., Bauhus, J. & Scherer-Lorenzen, M. (2010). The influence
763 of mixed tree plantations on the nutrition of individual species: a review. *Tree Physiol.*, 30,
764 1192–1208
765
- 766 51.Ruiz-Benito, P., Ratcliffe, S., Jump, A.S., Gómez-Aparicio, L., Madrigal-González, J.,
767 Wirth, C., *et al.* (2017). Functional diversity underlies demographic responses to
768 environmental variation in European forests. *Glob. Ecol. Biogeogr.*, 26, 128–141
769
- 770 52.Sapijanskas, J., Paquette, A., Potvin, C., Kunert, N. & Loreau, M. (2014). Tropical tree
771 diversity enhances light capture through crown plasticity and spatial and temporal niche
772 differences. *Ecology*, 95, 2479–92
773
- 774 53.Seddon, A.W., Macias-Fauria, M., Long, P.R., Benz, D. & Willis, K.J. (2016). Sensitivity
775 of global terrestrial ecosystems to climate variability. *Nature*, 531, 229–232
776
- 777 54.Soliveres, S., van der Plas, F., Manning, P., Prati, D., Gossner, M.M., Renner, S.C., *et al.*
778 (2016). Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality.
779 *Nature*, 536, 456–459
780
- 781 55.Spasojevic, M.J., Bahlai, C.A., Bradley, B.A., Butterfield, B.J., Tuanmu, M.N., Sistla, S.,
782 *et al.* (2016). Scaling up the diversity-resilience relationship with trait databases and remote

783 sensing data: The recovery of productivity after wildfire. *Glob. Chang. Biol.*, 22, 1421–1432
784
785 56.Srivastava, D.S. & Vellend, M. (2005). Biodiversity-ecosystem function research: is it
786 relevant to conservation? *Annu. Rev. Ecol. Evol. Syst.*, 36, 267–294
787
788 57.Stahl, U., Kattge, J., Reu, B., Voigt, W., Ogle, K., Dickie, J., *et al.* (2013). Whole-plant
789 trait spectra of North American woody plant species reflect fundamental ecological
790 strategies. *Ecosphere*, 4, 1–28
791
792 58.Stan Development Team. (2016). Stan: A C++ Library for Probability and Sampling
793
794 59.Stephenson, N.L. (1998). Actual evapotranspiration and deficit: biologically meaningful
795 correlates of vegetation distribution across spatial scales. *J. Biogeogr.*, 25, 855–870
796
797 60.Tobner, C.M., Paquette, A., Reich, P.B., Gravel, D. & Messier, C. (2014). Advancing
798 biodiversity-ecosystem functioning science using high-density tree-based experiments over
799 functional diversity gradients. *Oecologia*, 174, 609–21
800
801 61.Toïgo, M., Vallet, P., Perot, T., Bontemps, J.-D., Piedallu, C. & Courbaud, B. (2015).
802 Over-yielding in mixed forests decreases with site productivity. *J. Ecol.*, 103, 502–512
803
804 62.Wacker, L., Baudois, O., Eichenberger-Glinz, S. & Schmid, B. (2008). Environmental
805 heterogeneity increases complementarity in experimental grassland communities. *Basic*
806 *Appl. Ecol.*, 9, 467–474
807
808 63.Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. & Wright, I.J. (2002). PLANT
809 ECOLOGICAL STRATEGIES: Some Leading Dimensions of Variation Between Species.
810 *Annu. Rev. Ecol. Syst.*, 33, 125–159
811

TABLES

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.

| 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 (Mg C) | 209 |

| | | |
|-------------------------------|--|-----|
| | ha ⁻¹ yr ⁻¹) | |
| 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 five 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 |

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. 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; and FD_{pool} : functional diversity of the species pool.

| | 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%.

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 (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 ($F=1.063$; $p = 0.389$).

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.

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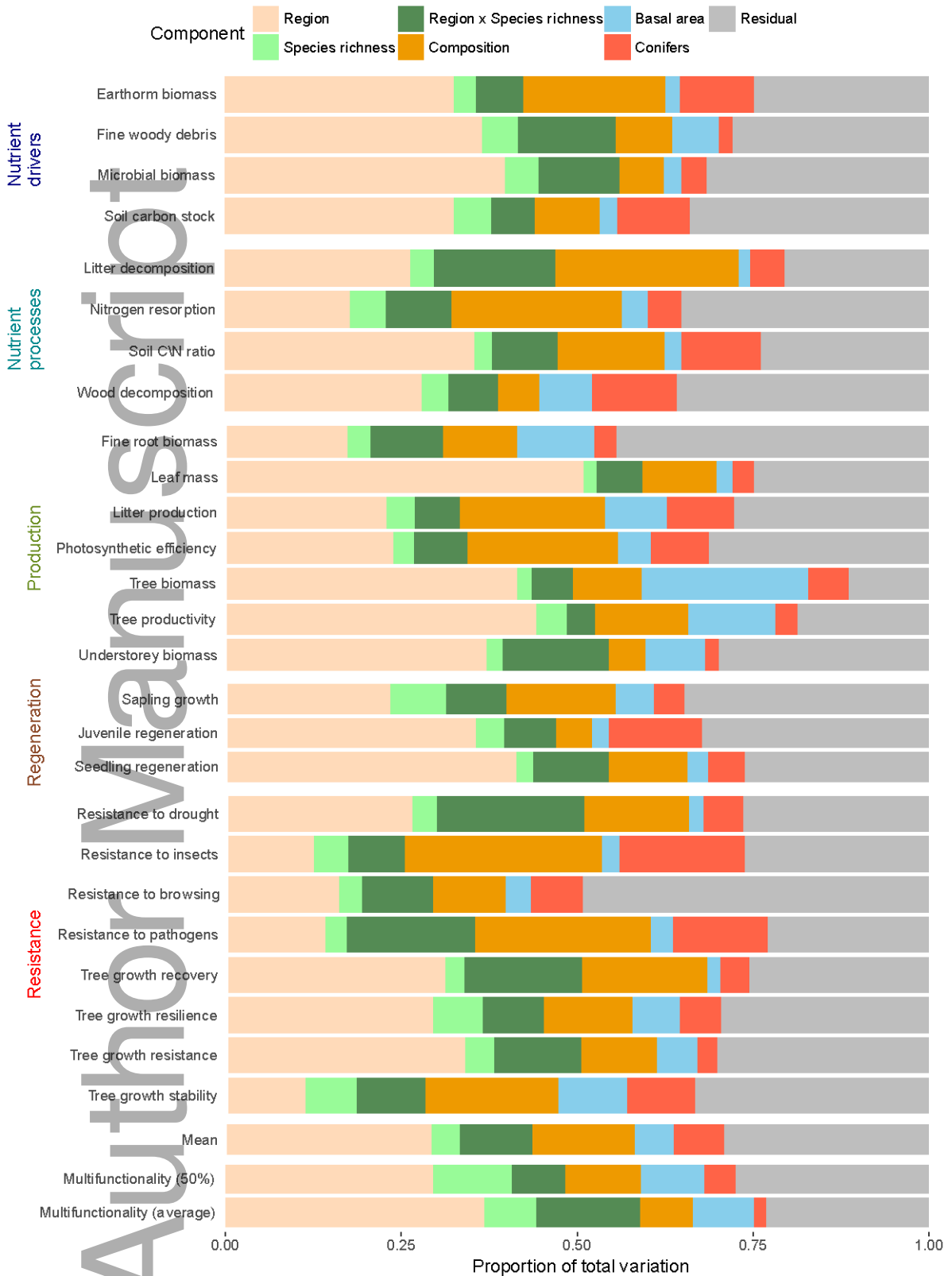


Figure 2.

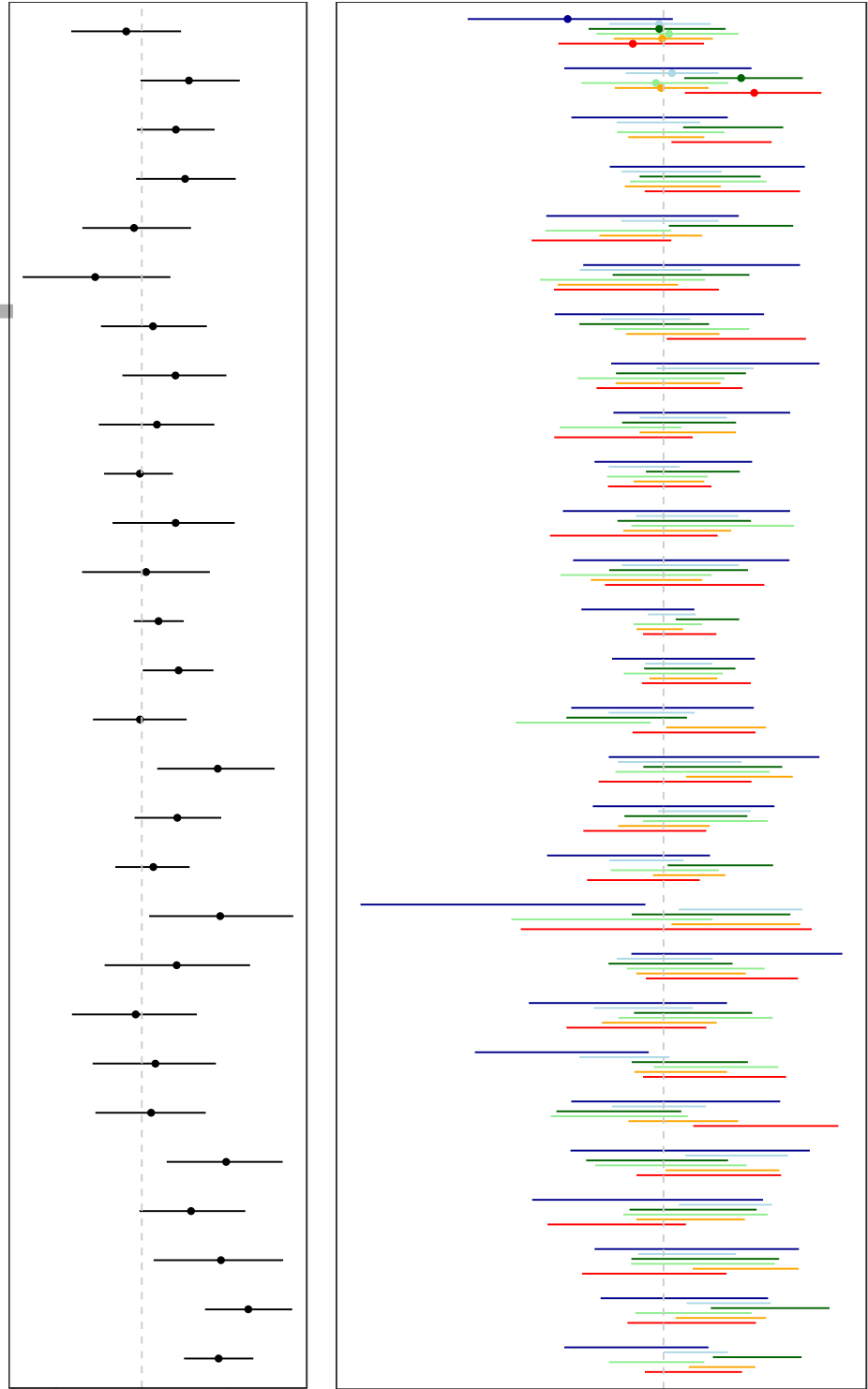


Figure 3.

Sensitivity of species richness effects (β_{sens})

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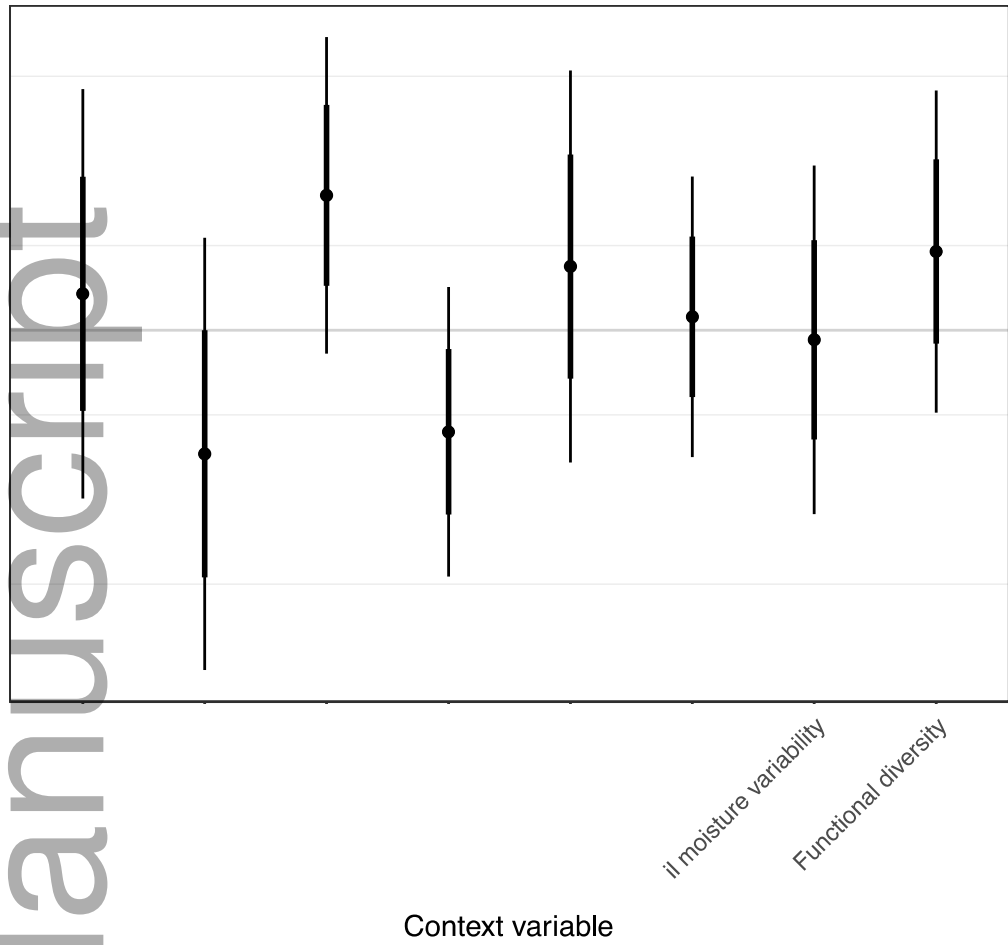
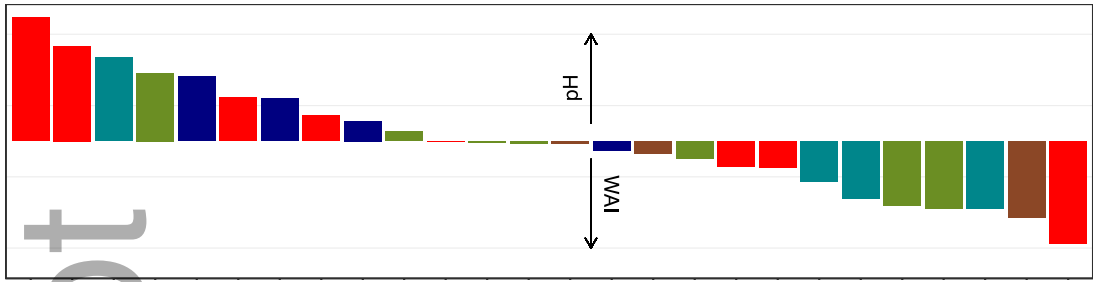
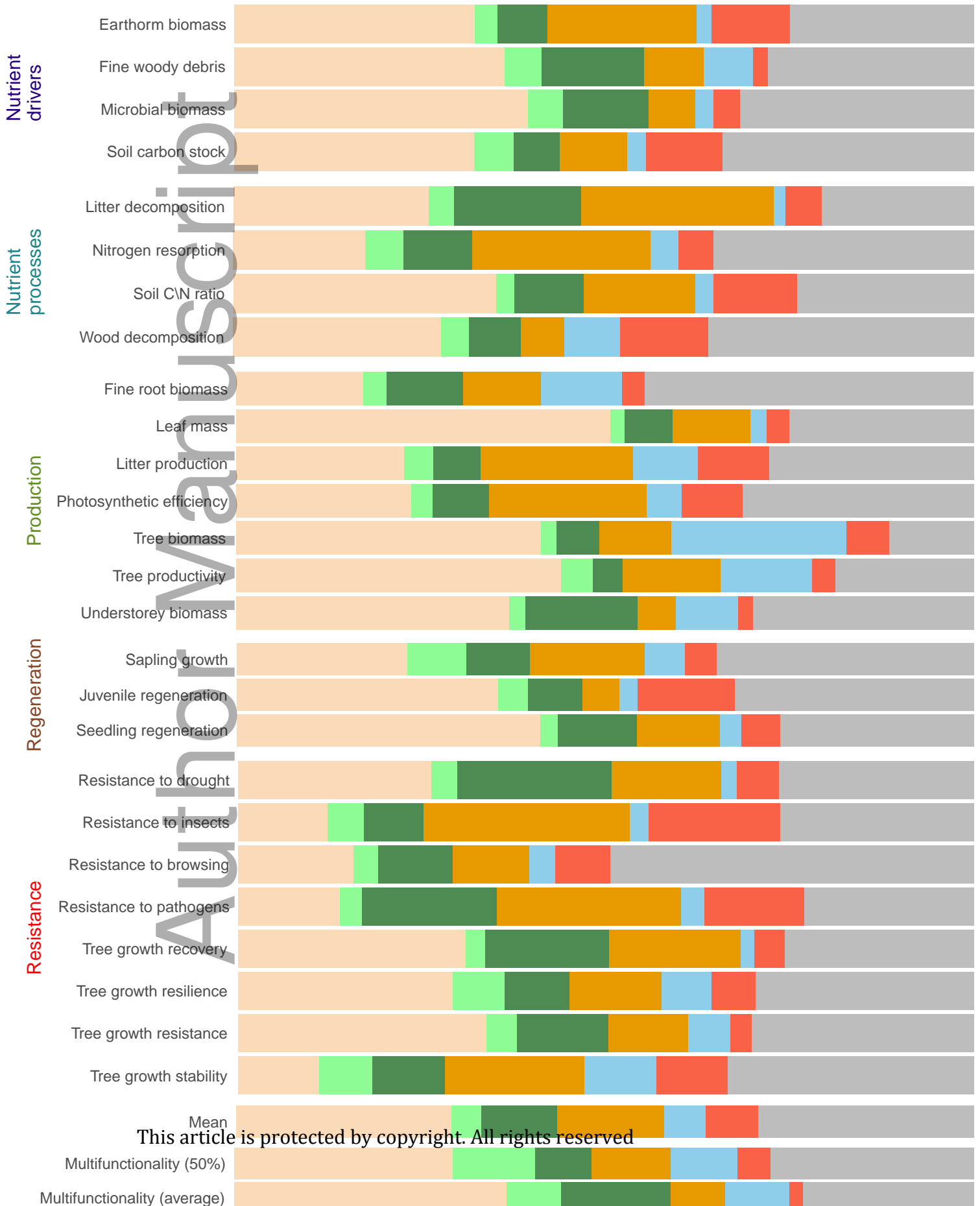
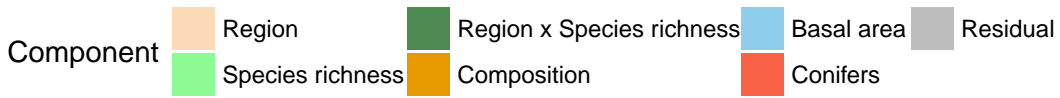


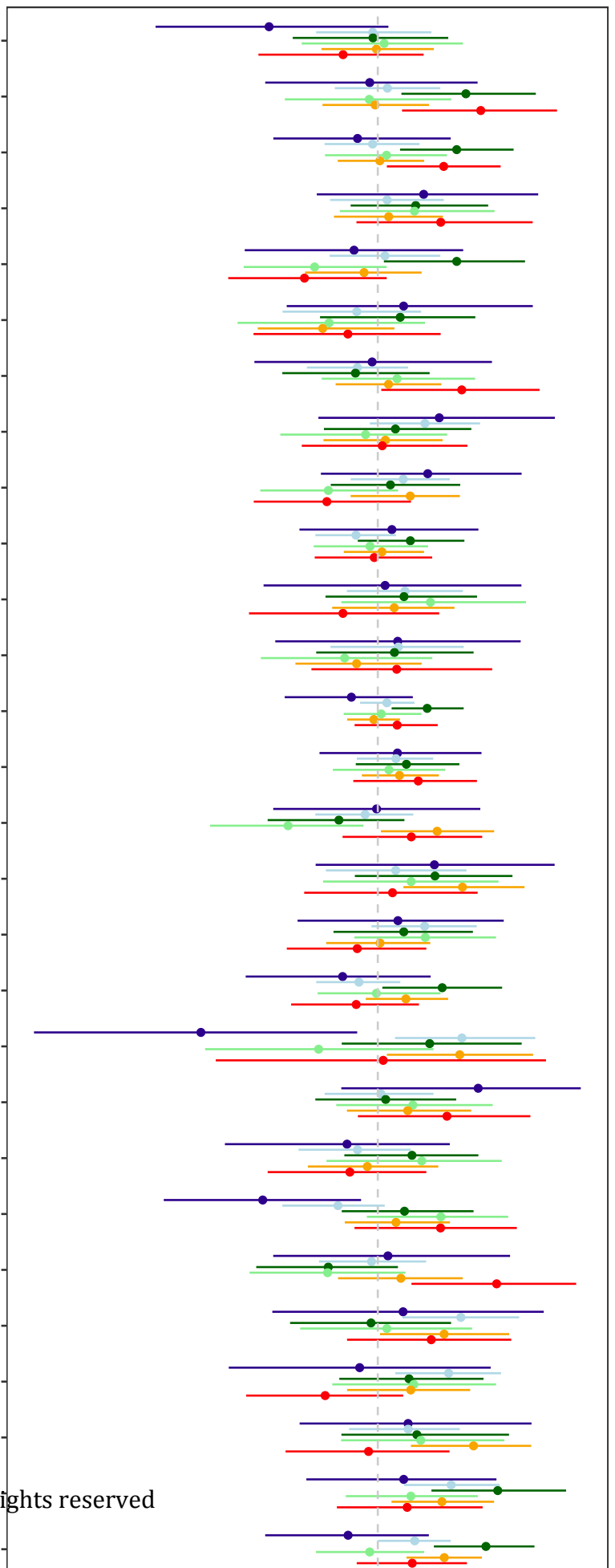
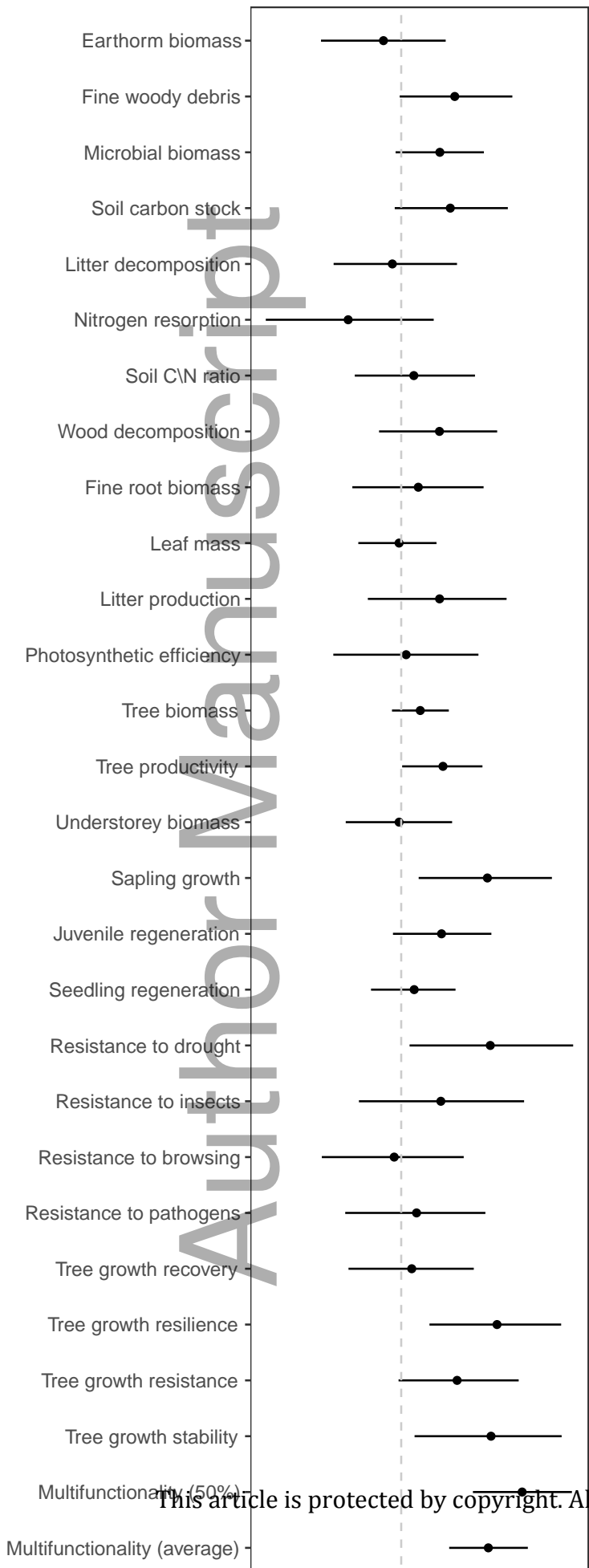
Figure 4.

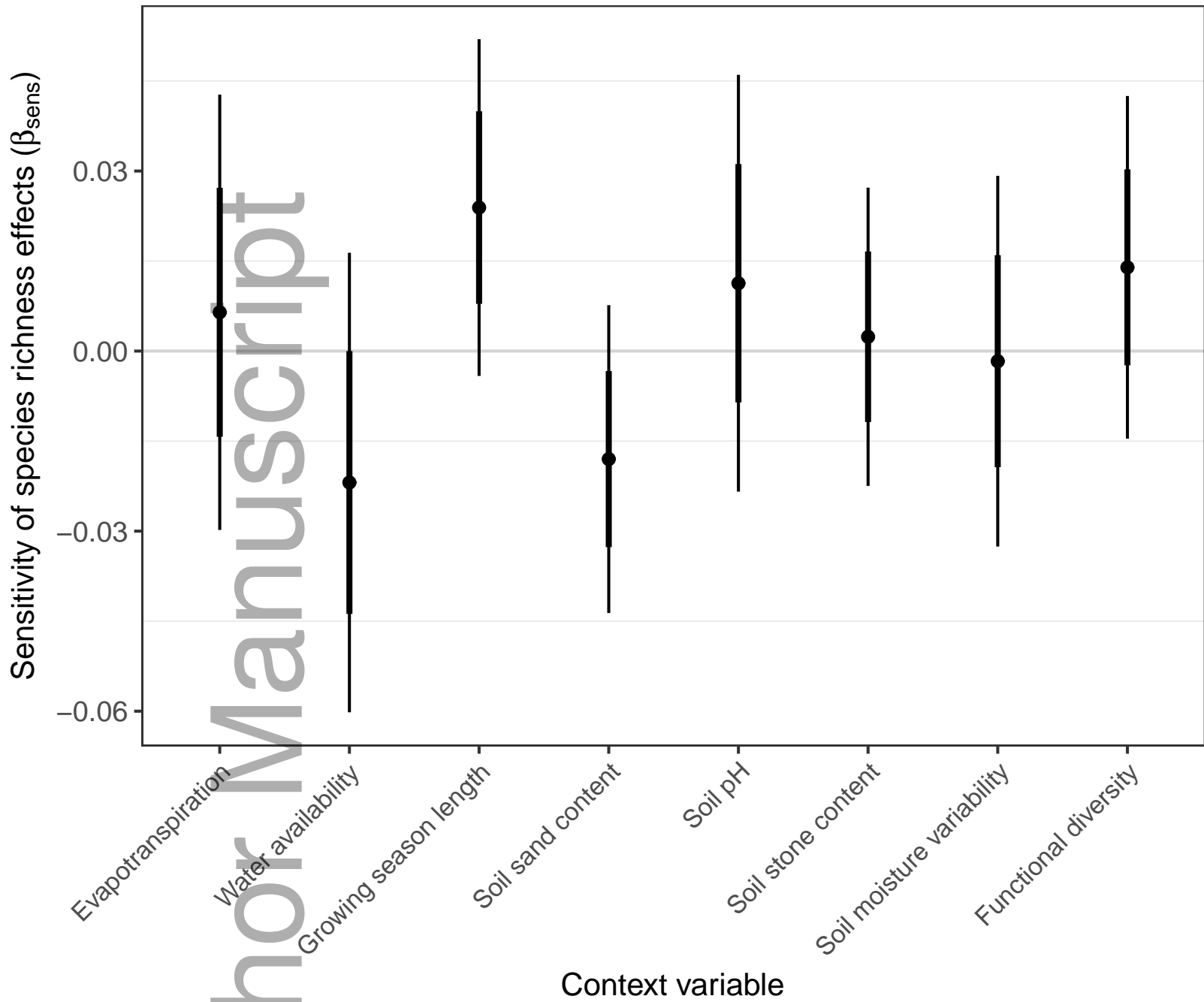


Nutrient cycling processes ivers Production Resistance
Regeneration



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