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11 *Running head:* BEF relationships across scales

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13 **Scaling up biodiversity–ecosystem function relationships across space and over time**

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24 **ABSTRACT**

25 Understanding how to scale up effects of biological diversity on ecosystem functioning
26 and services remains challenging. There is a general consensus that biodiversity loss alters
27 ecosystem processes underpinning the goods and services upon which humanity depends. Yet,
28 most of that consensus stems from experiments performed at small spatial-scales for short time-
29 frames, which limits transferability of conclusions to longer-term, landscape-scale conservation
30 policies and management. Here we develop quantitative scaling relationships linking 374
31 experiments that tested plant diversity effects on biomass production across a range of scales.

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32 We show that biodiversity effects increase by factors of 1.68 and 1.10 for each 10-fold increase
33 in experiment temporal and spatial scales, respectively. Contrary to prior studies, our analyses
34 suggest that the time scale of experiments, rather than their spatial scale, is the primary source of
35 variation in biodiversity effects. But consistent with earlier research, our analyses reveal that
36 complementarity effects, rather than selection effects, drive the positive space-time interactions
37 for plant diversity effects. Importantly, we also demonstrate complex space-time interactions and
38 nonlinear responses that emphasize how simple extrapolations from small-scale experiments are
39 likely to underestimate biodiversity effects in real-world ecosystems. Quantitative scaling
40 relationships from this research are a crucial step towards bridging controlled experiments that
41 identify biological mechanisms across a range of scales. Predictions from scaling relationships
42 like these could then be compared with observations for fine-tuning the relationships and
43 ultimately improving their capacities to predict consequences of biodiversity loss for ecosystem
44 functioning and services over longer time-frames across real-world landscapes.

45
46 **Keywords:** BEF, plant diversity, ecosystem production, productivity, ecosystem service, spatial
47 scale, temporal scale, scaling function, landscape management

48 INTRODUCTION

49 We are living in an era that many are calling the “Anthropocene” – a period in which
50 humans and their activities dominate almost all ecosystems on the planet (Crutzen 2002, Ellis et
51 al. 2010). One of the most prominent consequences of anthropogenic environmental change in
52 the Anthropocene is changing biodiversity both on land and in water (Barnosky et al. 2011,
53 Pimm et al. 2014, Ceballos et al. 2015, Elahi et al. 2015). There is a growing recognition that
54 local biodiversity is increasing in some locations due to, for example, human-driven disturbance
55 or exotic species (Sax et al. 2002, Devictor and Robert 2009, Vellend et al. 2013). However,
56 recent studies suggest that declines in local biodiversity are common, averaging up to 14% of
57 species lost at terrestrial sites, with losses > 75% in the worst-affected habitats (Newbold et al.
58 2015). Declines in local biodiversity have raised substantial concerns about consequences for
59 ecosystem functioning and services such as food, clean water, disease control, and climate
60 regulation, all of which underpin human wellbeing (Balvanera et al. 2006, Cardinale et al. 2012,
61 Bennett et al. 2015). Yet accurately predicting effects of biodiversity change remains
62 challenging, because there is a mismatch between large scales at which species are lost and

63 ecosystem services are provided, and small scales where most knowledge on the functional
64 consequences of species loss is derived (Isbell et al. 2018). Such understanding is, nonetheless,
65 crucial for the ongoing management and policy initiatives, including the Intergovernmental
66 Platform on Biodiversity and Ecosystem Services (IPBES) for assessing regional and global
67 changes in biodiversity and ecosystem services (Larigauderie and Mooney 2010), and the United
68 Nations Sustainable Development Goals for halting biodiversity loss (Griggs et al. 2013).

69 Over the past two decades, remarkable theoretical and empirical advances have been
70 made towards understanding ecological and societal consequences of biodiversity change
71 (Loreau et al. 2001, Hooper et al. 2005, Balvanera et al. 2006, Tilman et al. 2014, Isbell et al.
72 2017). Ecological theories and mathematical models predict that biodiversity should increase the
73 efficiency by which ecological communities capture biologically essential resources, produce
74 biomass, decompose and recycle nutrients (Tilman et al. 1997, Loreau 2010). Possible
75 mechanisms include: (1) *niche complementarity* – coexisting species differ in their use of
76 biologically limiting resources in space and/or time, thus reducing interspecific competition
77 relative to intraspecific competition and leading to greater total exploitation of resources (Tilman
78 1999); (2) *facilitation* – positive species interactions increase efficiency by which communities
79 utilize resources and/or the total magnitude of resource use (Mulder et al. 2001, Bruno et al.
80 2003); (3) *sampling* or *selection effects* – more diverse communities have a higher probability
81 that species with particularly effective functional traits will be present and, through competition,
82 dominate the community, thus enhancing ecosystem functions (Huston 1997, Hector et al. 2002);
83 and (4) *intra-guild predation* – killing/eating of species occupying the same functional group and
84 sharing similar limiting resources can mediate cascading effects of predator diversity on plant
85 biomass, thus altering resources consumption of primary producers (Finke and Denno 2005).

86 A proliferation of > 600 experiments, along with quantitative syntheses, have collectively
87 confirmed the predictions that biodiversity enhances resource-use efficiency and biomass
88 production of ecological communities; although tests of how biodiversity influences the rate of
89 decomposition and nutrient recycling have been less conclusive (Balvanera et al. 2006, Worm et
90 al. 2006, Srivastava et al. 2009, Quijas et al. 2010, Cardinale et al. 2011, Handa et al. 2014,
91 Boyero et al. 2016). Nevertheless, most of this body of work stems from experiments performed
92 at small spatial-scales for short time-frames. There has been debate over whether small-scale
93 experiments represent biodiversity–ecosystem function (i.e., BEF) relationships in ‘real-world’

94 ecosystems (Srivastava and Vellend 2005, Wardle 2016). As such, numerous empirical studies
95 and syntheses have recently begun to explore how biodiversity affects ecosystem functioning,
96 such as the production of biomass, in larger and more natural systems (Grace et al. 2007,
97 Paquette and Messier 2011, Mora et al. 2011, Gamfeldt et al. 2013, Liang et al. 2016, Duffy et al.
98 2017, Felipe-Lucia et al. 2018). Of those that statistically controlled for abiotic covariates that
99 can affect biomass production, most have demonstrated that biodiversity effects are common in
100 nature, and qualitatively consistent with findings in small-scale experiments. Nonetheless, these
101 studies have also indicated that, if anything, small experiments have probably underestimated the
102 effects of biodiversity on productivity in natural ecosystems (Duffy et al. 2017). Hence, while
103 small-scale experiments have been instrumental for identifying biodiversity effects on ecosystem
104 functioning and for confirming mechanisms, results of these experiments have yet been fully
105 used to improve inferences and predictions on the consequences of biodiversity change at
106 landscape scales that are more relevant for policy, conservation and management.

107 There are several non-exclusive reasons why biodiversity effects tend to be stronger in
108 nature than in small-scale experiments. In natural systems characterized by larger spatial scales
109 and greater temporal fluctuations, more environmental heterogeneity may increase opportunities
110 for species to exploit a greater variety of niches (Cardinale et al. 2004, Tschamntke et al. 2005,
111 Reich et al. 2012). For example, a recent study by Isbell et al. (2018) showed that net diversity
112 effects were mostly explained by complementarity that tended to increase with spatial scales.
113 Regional processes such as dispersal or disturbance, which control species abundances in nature
114 but are absent from most experiments, can interact with local processes to amplify biodiversity
115 effects (Tschamntke et al. 2005). Whether or not these, or other hypotheses explain the disparity
116 between experimental results and observations in real ecosystems, the key to reconciling such
117 disparities is to first develop quantitative scaling relationships based on BEF experiments.
118 Indeed, prior studies (e.g., Reich et al. 2012, O'Connor et al. 2017, Isbell et al. 2017) have
119 explored the magnitude of diversity effects as a function of the scale of experiments, and also
120 provided several theoretical expectations on the scale dependence of diversity effects (e.g.,
121 Thompson et al. 2018). These empirical studies have generally found that diversity effects did, in
122 fact, increase with the scales at which experiments were conducted.

123 However, studies to date that have examined how diversity effects change with spatial
124 and temporal scale have not gone beyond correlations to generate quantitative scaling

125 relationships, nor have they separated the effects of space from time, and explicitly addressed
126 their interactions. These more detailed scaling relationships are an important step towards
127 quantifying biodiversity effects across space and over time, and linking mechanisms supported in
128 small experiments with large-scale patterns observed across landscapes. Specifically, the scaling
129 relationships developed from experiments can be first used to provide an initial predicted
130 biodiversity effect for a given spatial or temporal scale; the prediction can then be compared
131 against observations of real ecosystems at equivalent scales to inform parameter adjustments and
132 further hone the predictions of scaling relationships. Through such an iterative process, the
133 predictive capacities of scaling relationships can thus be improved. Developing these scaling
134 relationships is critical, especially given the well-recognized logistic challenges and/or ethical
135 concerns that are likely to prevent us from doing controlled, manipulative biodiversity
136 experiment at the scale of whole ecosystems (e.g., an entire island, lake or forest). Scaling
137 relationships are also fundamental to developing mechanistic models to predict real-world
138 consequences of biodiversity loss for ecosystem functioning and services across dynamic
139 landscapes (Brose and Hillebrand 2016, Isbell et al. 2017).

140 Here we attempted to develop improved BEF scaling relationships. We focused on
141 experiments that have examined plant diversity effects on biomass production, because (i) this
142 subset offers the largest number of studies ($N=374$); (ii) the range of spatial/temporal scales
143 represented in these experiments spans many orders of magnitude; and (iii) the production of
144 ecosystems is a fundamental function underpinning many ecosystem goods and services
145 (O'Connor et al. 2017). We used species richness as the measure for biodiversity, as this measure
146 is most widely adopted in the literature. Aside from the null hypothesis that biodiversity effects
147 on biomass production are scale-invariant, two hypotheses have been proposed (**Appendix S1:**
148 **Fig. S1**): plant diversity effects on biomass production: (1) increase with spatial/temporal scales,
149 which might occur if, for example, greater environmental variations allow for more niche
150 partitioning (Tscharrntke et al. 2005, Tylianakis et al. 2008, Duffy 2009), or (2) decline with
151 spatial/temporal scales if, for example, abiotic factors overwhelm biodiversity effects (Srivastava
152 and Vellend 2005, Wardle and Zackrisson 2005, Grace et al. 2007, Wardle 2016). As we show,
153 plant diversity effects increase with spatial and temporal scales, and the time scale of experiment
154 is the main source of variation in diversity effects. Our results also reveal the positive space-time
155 interactions for plant diversity effects, likely driven by complementarity effects.

MATERIALS AND METHODS

156

157 Selection of case studies

158 We used the database by Cardinale et al. (2009), which summarized results of BEF
159 relationships from 164 experiments (reported in 84 publications) through 2006. As part of a
160 National Center for Ecological Analysis and Synthesis Working Group, this dataset was updated
161 with additional peer-reviewed papers published through September 2009. While additional
162 experiments have been published over the past decade, updating this dataset with more recent
163 literature can be an enormous undertaking (e.g., collation of the original dataset has taken almost
164 a decade). We thus chose to use this dataset, which is still by far one of the largest existing
165 datasets of BEF studies, and selected a subset (see *selection criteria* below) for our analyses.

166 All studies included in this database experimentally manipulated species richness of a
167 given trophic group, and measured effects of species richness on (1) standing stock abundance or
168 biomass of all species within a focal trophic group t ; (2) standing stock of resources used by t ; and
169 (3) total resources depleted by t . Details on the methods of data collection were summarized in
170 Cardinale et al. (2009). For the purpose of this paper, we extracted records that describe how
171 species richness of terrestrial plants impacts biomass or density of plants. Our selection criteria
172 resulted in a total of 374 independent experiments (from 54 published studies) that vary in
173 diversity effect sizes by > three-fold (**Appendix S1: Fig. S2A**) and differ in spatial and temporal
174 scales by 6.5 and 2.4 orders of magnitude, respectively (**Appendix S1: Fig. 2B**). This subset
175 included experiments conducted in wetland (13 total), temperate grassland (331), forest (20),
176 bryophyte (2), agriculture (2) and tundra (6). The fundamental response for all experiments was
177 total plant biomass (mass per area) or abundance (density) summed across all species, reported
178 across a set of species richness treatments with all other factors controlled.

179 Analysis of diversity effect sizes

180 We used two complementary analyses to quantify diversity effect sizes in each
181 experiment. First, we used log response ratios to quantify the proportional change in plant
182 biomass/density between the highest vs. lowest levels of species richness used in each
183 experiment. The log response ratio is a widely used metric for measuring effect sizes in meta-
184 analysis (Hedges et al. 1999, Koricheva et al. 2013), because (1) it is dimensionless, and thus
185 allows for comparing effect sizes among studies where independent and dependent variables
186 differ in scale, and (2) its sampling properties are known to be approximately normal and

187 relatively robust to bias from small sample sizes (Hedges et al. 1999). Specifically, for our
188 purposes, the log ratio, LR_{net} , was calculated as proportional difference between the average
189 productivity/density of all replicates from most species rich polyculture (y_p), and the average of
190 these same species grown in monoculture (y_m), using equation: $\ln(y_p/y_m)$.

191 Although log response ratios can be calculated for nearly every experiment in the dataset,
192 one limitation is that these ratios only compare the most diverse polyculture to the monocultures.
193 In other words, they provide no further information about the functional form of diversity effect
194 in-between these two extremes. Hence, we complemented our analyses of log response ratios
195 with a second analysis that fits data to the power function for experiments that manipulated three
196 or more levels of plant species richness. Prior research (e.g., Reich et al. 2012) has demonstrated
197 that power function is a good descriptor of BEF relationships from experiments, and ranks
198 among the highest statistical models in terms of explanatory power. In addition, the coefficient b
199 from power function is easy to interpret and compare among studies. Specifically, in our
200 analyses, the power function was mathematically expressed as: $\ln\left(\frac{Y_s}{Y_m}\right) = a + b \times \ln(Sp)$, where
201 Y_s is the biomass/density at species richness Sp , Y_m is the mean biomass/density of monoculture
202 of all species, a is the constant and b is the power exponent. Thus, when $b = 0$ there is no
203 diversity effect, when $b = 1$ the proportional increase in biomass/density across levels of species
204 richness is linear, and for all $0 < b < 1$, the proportional increase in biomass/density across levels
205 of species richness is nonlinear and decelerating.

206 Loreau and Hector (2001) developed a technique to statistically partition the net effects
207 of diversity into two components: *sampling/selection effects* (SE) and *niche complementarity*
208 *effects* (CE). SE represents the proportion of diversity effects on polyculture biomass that can be
209 attributable to the productivity of individual species, such as those that occur when the most
210 productive species dominate the biomass of diverse polyculture. In contrast, CE represents the
211 portion of diversity effects that cannot be attributed to any single species, and thus denotes the
212 balance of all forms of niche partitioning that might influence biomass and all forms of indirect
213 and non-additive species interactions. The Cardinale et al. (2009) dataset used for our analyses
214 included estimates of SE and CE that were calculated from published studies, or provided by the
215 study authors. This allows us to examine how CE and SE change with spatial and temporal
216 scales of the experiments. While CE and SE do not, by themselves, provide unambiguous

217 evidence of biological mechanisms, they do tell us how the relative importance of single-species
218 (i.e., SE) vs. multi-species (i.e., CE) processes changes with scales.

219 **Spatial and temporal scales**

220 To allow comparison of studies performed at very different spatial scales using organisms
221 of vastly different sizes, we standardized spatial scales (S) by calculating the log ratio of the area
222 or volume of the experimental unit divided by mean body mass of the focal taxa, i.e., $S =$
223 $\ln(S_{\text{experiment}}/S_{\text{organism}})$. To allow comparison of studies that varied in their time-scales using
224 organisms with vastly different generation times, we standardized temporal scales (T) as the log
225 ratio of the duration of studies divided by mean generation time of the organism, i.e., $T =$
226 $\ln(D_{\text{study}}/G_{\text{organism}})$, which represents the number of generations an experiment was run. Log
227 ratios were used because the untransformed ratios varied 2.4 – 6.5 orders of magnitude across all
228 experiments. Details on how the information regarding spatial and temporal scales was collected
229 from experiments were described in Cardinale et al. (2009).

230 **Statistical analyses**

231 General linear mixed-effects models were used to quantify how effects of plant species
232 richness on biomass production vary across spatial and temporal scales. Analyses were done
233 separately for diversity effects quantified by log response ratio, and for parameter estimates from
234 the fitting of power function. The general statistical model was $y_i = \mu + S_i + T_i + S_i * T_i + e_i +$
235 ε_i , where y_i is either LR_{net} or scaling exponent b from curve fitting, S_i , T_i and $S_i * T_i$ are fixed
236 effects of spatial scale, temporal scale and their interactions, e_i is the random effects with which
237 each experiment was associated with independent errors following normal distribution, $N[0, \sigma_b^2]$,
238 and ε_i is the residual error. Random effects were included in the model to account for potential
239 systematic variations among experiments resulting from factors such as climatic differences
240 among sites, site-specific environmental parameters (e.g., soil), ecosystem types, taxonomic
241 groups, species or functional trait composition within those groups or other ecological and
242 scientific particularities that varied among different experiments (O'Connor et al. 2017). General
243 linear mixed-effects models were used for three reasons: (1) multicollinearity between spatial
244 and temporal scales was reasonable in all models (with all variation inflation factors, VIFs <
245 3.0); (2) random effects can be included; and (3) interaction term between spatial and temporal
246 scales can be readily included in the model. We included the interaction term because the models
247 with the interaction had lower Akaike information criterion (AIC) values compared to their

248 counterparts without the interaction term. Heterogeneity of residuals and normality of errors
249 were assessed for the full models, and no violations were detected. We also explored
250 heterogeneity of effect sizes across ecosystems, and examined non-independence of effect sizes
251 and publication bias (i.e. selective publication of significant over non-significant findings) (see
252 **Appendix S2**), and found no systematic bias.

253 We performed additional analyses using the same linear mixed-effects models with
254 absolute (raw, or non-standardized) spatial and temporal scales from each experiment (i.e.,
255 experimental unit size or study duration) to assess whether our results were driven by spatial and
256 temporal scale *per se*, or were driven by organismal traits like generation time and body size (see
257 **Appendix S3**). Our first analyses were suggested by a referee to analyze how diversity effects
258 across all studies in the dataset varied as a function of the raw (non-standardized) spatial and
259 temporal scales of the experiment, and the generation time and body size. While this approach
260 maximizes the use of data, it potentially suffers from confounding factors that could hinder the
261 interpretation. This is because, for example, studies of microalgae growing on a time-scale of
262 days in milliliter scale laboratory flasks differ from those of large plants grown for a decade in
263 100-m² field plots in a multitude of ways beyond just biological traits (e.g., experimental units
264 and conditions, methods, measurements, etc.), and thus may not be directly comparable without
265 standardization. Because these confounding factors cannot be directly controlled with the
266 existing data, we performed second analyses that were focused on all grassland studies. Not only
267 are these grassland studies more comparable to one another, they also dominate the dataset.

268 To explore how single- vs. multi-species processes contribute to changes in BEF
269 relationships across scales, we first assessed how CE and SE metrics varied with standardized
270 spatial and temporal scales. Based on the distribution of scales in the original dataset, we further
271 categorized the experiments into three subgroups: (1) *large* temporal and spatial scales (i.e., both
272 >90th percentile); (2) *large* temporal (i.e., >90th percentile) but *small* spatial scales (i.e., <60th
273 percentile); and (3) *large* spatial (i.e., >90th percentile) but *small* temporal scales (i.e., <60th
274 percentile). We then performed the same linear mixed-effects models to test for differences in
275 CE and SE values between these deliberately grouped experiments. Such subgrouping allows us
276 to explicitly attribute the extent to which CE or SE contributes to enhanced diversity effects from
277 increasing spatial scales while the temporal scales of experiments are large (i.e., comparing
278 subgroup 1 and 2), or vice versa (comparing subgroup 1 and 3). In other words, such analyses

279 could shed light into whether CE or SE derives the interactions between spatial and temporal
280 scales on diversity effects. All statistical analyses were performed in the R statistical software 3.3
281 (R Core Team 2016). We used ‘lmer’ function in ‘lme4’ package (Bates et al. 2015) for general
282 linear mixed-effects models, and significance of fixed effects was evaluated using the
283 Satterthwaite’s approximation for degrees of freedom in the ‘lmerTest’ package (Kuznetsova et
284 al. 2015). We used ‘vif.lmer’ function for calculating VIF in the linear mixed-effects model.

285 RESULTS

286 Scaling up net plant diversity effects

287 Among 374 experiments, the net plant diversity effects on biomass production, LR_{net} ,
288 ranged -0.73 to 1.51, with 89% showing positive effects (**Appendix S1: Fig. S2**). Individually,
289 LR_{net} showed positive relationships with standardized temporal (**Fig. 1A**) and spatial scales (**Fig.**
290 **1B**) (both $P < 0.001$). A general linear mixed-effects model revealed that spatial and temporal
291 scales also interacted to affect LR_{net} ($\beta_{int} = 0.015$, $P = 0.014$; **Table 1**). In other words, the
292 influences of spatial scale on plant diversity effects were contingent upon temporal scale, and
293 vice versa. Additional analyses using non-standardized temporal and spatial scales (with the full
294 dataset, as well as a subset of grassland studies) showed qualitatively similar results, with
295 significant positive pairwise correlations with LR_{net} (both $P < 0.001$; **Appendix S3: Fig. S1, S2**),
296 as well as positive space-time interactions ($P = 0.013$; **Appendix S3: Table S1**). We further found
297 no significant correlations between LR_{net} and body size and generation time of focal organisms
298 (**Appendix S3: Fig. S1, S2**), suggesting that it is the scale of experiments *per se* (rather than the
299 functional traits of organisms) that drives the scaling relationships of plant diversity effects.

300 To examine the interaction between spatial and temporal scale, we estimated how plant
301 diversity effects changed with temporal scale while holding spatial scales constant at the
302 minimum and maximum values in the dataset. Specifically, at the minimum spatial scale in the
303 dataset, LR_{net} remained positive irrespective of temporal scale (red line in **Fig. 2A**). However, at
304 the maximum spatial scale, the effects of temporal scale increased LR_{net} from $e^{-0.34}$ (i.e., the most
305 diverse polycultures achieved $0.71 \times$ the biomass of average monoculture) to $e^{0.90}$ (i.e., the most
306 diverse polycultures achieved $2.46 \times$ the biomass of average monoculture) (blue line in **Fig. 2A**).
307 Thus, effects of plant species richness on biomass production changed both qualitatively (from
308 negative to positive) and quantitatively ($e^{-0.34}$ to $e^{0.90}$) through time, and this variation required at
309 least four generations of population growth, if not more, to be realized (x-axis in **Fig. 2A**).

310 We similarly examined how plant diversity effects changed with spatial scale while
311 holding temporal scales constant at the minimum and maximum values in the dataset. At the
312 minimum temporal scale in the dataset, LR_{net} declined from $e^{0.24}$ to $e^{-0.35}$ as spatial scale increased
313 (red line in **Fig. 2B**). At the maximum temporal scale in the dataset, the effects of spatial scale
314 increased LR_{net} from $e^{0.29}$ to $e^{0.91}$ (blue line in **Fig. 2B**). Again, these results demonstrated that
315 effects of plant species richness on biomass production changed both qualitatively (from
316 negative to positive) and quantitatively ($e^{-0.35}$ to $e^{0.91}$) across several orders of magnitude of
317 spatial scales as represented in the experiments (x-axis in **Fig. 2B**).

318 The complex space-time interactions can also be portrayed in a different manner. In **Fig.**
319 **2C**, effects of temporal scale on plant diversity effects, LR_{net} (shown on y-axis) rose quickly as
320 the spatial scale of experiments (i.e., x-axis) increased. However, beyond a spatial scale of ~ 12 ,
321 effects of temporal scale on LR_{net} decelerated towards a maximum of $e^{0.27}$. In contrast, in **Fig.**
322 **2D**, effects of spatial scale on LR_{net} (shown on y-axis) were much smaller, and also decelerated
323 towards a maximum of $e^{0.044}$ when the experiments were run for ~ 4 generations.

324 **Scaling up the functional form of plant diversity effects**

325 Our complementary analysis detailing the functional form of plant diversity effects on
326 biomass production was constrained to experiments that manipulated three or more levels of
327 plant species richness ($N=227$) (**Appendix S1: Fig. S3**). Among this subset, the fitted power
328 exponent b ranged from -0.70 to 0.63 (mean = 0.19 ± 0.17), with 92% showing positive b values.
329 Pairwise correlations suggested that, individually, the power exponent b tended to increase as
330 spatial and/or temporal scales of experiments increased (both $P < 0.001$).

331 Consistent with results from analyses of LR_{net} , we found significant interactive effects
332 between spatial- and temporal-scale of experiments on the power exponent b ($\beta_{int} = 0.008$, $P =$
333 0.02 ; **Table 1**). Increasing spatial and temporal scales interacted to make the form of plant
334 diversity–productivity relationships more linear and less saturating as b approached its maximum
335 of ~ 0.40 (**Fig. 3**). Specifically, at the minimum spatial scale in the dataset, the exponent b was
336 uniformly positive but independent of temporal scale; in contrast, at the maximal spatial scale in
337 the dataset, b was negative at small temporal scales but increased to positive as temporal scale of
338 experiments increased (**Fig. 3A**). On the other hand, at the minimum temporal scale, b decreased
339 from 0.13 to -0.24 as spatial scale increased (**Fig. 3B**); in contrast, at the maximal temporal scale,
340 b increased nonlinearly towards its saturation point. In other words, effects of temporal scale on

341 exponent b increased from negative to positive in a nonlinear and concave-down manner at large
342 spatial scales (**Fig. 3C**). Likewise, effects of spatial scale on b also increased from negative to
343 positive as temporal scale increased (**Fig. 3D**), though the magnitude of effects of spatial scale
344 tended to be smaller than those of temporal scales.

345 **Factors driving plant diversity effects across scales**

346 In determining factors that drive plant diversity effects across scales, we found that CE
347 positively correlated with temporal scale ($P < 0.001$), whereas SE negatively correlated ($P = 0.02$)
348 (**Fig. 4A, 4C**). Spatial scale, however, shows non-significant correlations with either SE or CE
349 (**Fig. 4B, 4D**). These results indicated that changes in the magnitude of CE were most likely the
350 reason why plant diversity effects increased across scales. We further examined whether CE or
351 SE were the primary factor underlying positive space-time interactions for plant diversity effects.
352 We found that, in experiments characterized as large temporal scales, CE were substantially
353 greater with increasing spatial scales (**Fig. 5A**), whereas SE showed the opposite pattern (**Fig.**
354 **5B**). Similarly, in experiments of large spatial scales, CE increased as the temporal scales
355 increased (**Fig. 5C**), but no significant difference was found for SE (**Fig. 5D**).

356 **DISCUSSION**

357 On the basis of >370 experiments spanning 2.4 – 6.5 orders of magnitude in scales and
358 across a range of terrestrial ecosystems, we have developed a set of scaling relationships that
359 relate plant diversity effects on biomass productivity across space and over time (**Table 1**). By
360 explicitly accounting for space-time interactions, our analyses showed that: (1) the spatial and
361 temporal scales of experiments interacted to control the qualitative form of how plant species
362 richness affects biomass production, as well as the magnitude of effects; (2) within the range of
363 the dataset, LR_{net} and the power exponent b increased by factors of 1.68 and 0.27, respectively,
364 for each 10-fold increase in the number of generations run in experiments (while statistically
365 holding spatial scale as constant), and by factors of 1.10 and 0.04, respectively, for each 10-fold
366 increase in the spatial scale of experiment (while statistically holding temporal scale as constant);
367 (3) plant diversity effects on biomass production changed with both spatial and temporal scale of
368 experiments in a nonlinear manner, precluding simple linear interpolation or extrapolation from
369 one scale to another; and lastly (4) the temporal scale of experiments appeared to have a
370 substantially greater influence on biodiversity effects than did the spatial scale. Predictions from
371 these scaling relationships can be compared with the ever-increasing observations to further fine-

372 tune the relationships and advance their predicative capacities on the consequences of
373 biodiversity loss for ecosystem functioning and services across real-world landscapes.

374 Across the dataset, the power exponent b increased by 0.27 for each 10-fold increase in
375 the number of generations run in an experiment (note: this is similar to the range reported in
376 Reich et al. 2012), and increased by 0.04 for each 10-fold increase in the spatial scale of an
377 experiment. These results reinforce the caution by prior authors who have suggested that the
378 results of small-scale, short time-frame experiments are likely to be overly conservative, and
379 probably underestimate the influences of biodiversity on ecosystem functioning and services in
380 real-world landscapes. Our results corroborate other studies (Dimitrakopoulos and Schmid 2004,
381 Griffin et al. 2013) that have separately assessed the role of spatial scales and time scales in
382 affecting BEF relationships. We found that the power exponent b reached its saturation point of
383 ~ 0.40 at the extremes of spatial and temporal scales captured in experiments (**Fig. 3**). While the
384 estimate of 0.40 from our study is close to the value of b reported in natural grasslands (i.e., $b =$
385 0.53 in Duffy et al. 2017), there is still a good amount of disparity between experiments and
386 natural systems ($b = 0.40$ vs. $b = 0.53$). Since our dataset was dominated by grassland
387 experiments, we suspect that this gap in exponent b is due to differences in ecosystems, but may
388 be influenced by some mechanism(s) that control the BEF relationships in natural systems,
389 which have yet to be fully incorporated into experiments. Understanding how this gap of
390 biodiversity effects can be bridged (empirically or theoretically) and integrated into scaling
391 relationships is an area that requires more work, and will be instrumental in linking biological
392 and ecological mechanisms of biodiversity effects with broad-scale patterns.

393 Our study further explored how single- vs. multi-species contributions to the BEF
394 relationship change with scale, and why space and time interacted to affect the effects of plant
395 diversity on biomass production. We found that, consistent with other studies (e.g., Cardinale et
396 al. 2007, Isbell et al. 2018), the net diversity effects increased through time as a consequence of
397 complementarity becoming stronger as experiments are run longer (**Fig. 4**). Selection effects, on
398 the other hand, declined with the duration of experiments, indicating that selection effects are
399 unlikely the mechanism driving the positive effects of temporal scale on BEF relationships.
400 Similar findings were also reported in Reich et al. (2012), who suggested that complementarity
401 effects accumulated over time, causing species-rich polycultures that are functionally redundant
402 earlier to become more functionally unique through successional time. As for the spatial scale,

403 our results revealed that, both complementarity and selection effects did not change significantly
404 with spatial scale – results that contrast with those of other studies (e.g., Dimitrakopoulos and
405 Schmid 2004) showing that complementarity effects can be amplified when more space is
406 provided. We suspect that this discrepancy results from the interactions between spatial and
407 temporal scales that were not explicitly addressed in prior studies, which could mask the
408 individual effects of spatial scales.

409 One thing that is unique about our study relative to others that have considered scaling
410 relationships is that, we explicitly analyzed the effects of both spatial and temporal scale
411 simultaneously (as opposed to examining the influence of one scale at a time) and found
412 significant interactions (**Table 1**). Our analyses suggest that increasing spatial and temporal
413 scales can have facilitative effects on one another to alter plant diversity effects, and sometimes
414 simply changing one scale might have limited influences on plant diversity effects. In extreme
415 cases, for example, plant diversity effects can be independent of time when spatial scale is very
416 small, or even decline with spatial scales when a study fails to allow reproduction to occur (< 1
417 generation, **Figs. 2, 3**). We further explored possible factors responsible for synergistic space-
418 time interactions, and found that CE was likely the main factor driving positive interactions
419 between spatial and temporal scales for plant diversity effects (**Fig. 5**). Specifically, temporal
420 complementarity effects could be more enhanced when experiments are conducted across a
421 sufficiently large, heterogeneous environment that allows species specialization to be expressed
422 (as compared to experiments at small spatial scales) (**Fig. 5A, 5B**), as also shown in Stachowicz
423 et al. (2008). Similarly, spatial complementarity and resource partitioning could be more fully
424 utilized when experiments are run over a large number of generations that allows for sufficient
425 species interactions and exploration of all potential niches (**Fig. 5C, 5D**). In tandem, our results
426 provide evidence that increasing spatial and temporal scales and associated heterogeneity could
427 regulate the performance of species and offer more niche opportunities for species to exploit in
428 ways that are complementary in time and space (Loreau et al. 2003). Space-time interactions also
429 underline the importance of adopting a dynamic and landscape lens in understanding biodiversity
430 effects on ecosystem functioning and services, and informing conservation and management
431 (Tscharrntke et al. 2005, Brose and Hillebrand 2016).

432 For our primary analyses, we used spatial scales that were standardized to the mean body
433 mass of the focal organisms, and temporal scales that were standardized to their mean generation

434 time. Scale standardization is vital in order to synthesize diversity effects across studies that used
435 organisms of different sizes and life-spans (e.g., grass vs. tree vs. fish vs. bird), and in different
436 systems. However, it may also face potential challenges, such as (1) making direct inferences in
437 regards to effects of altering raw scales (e.g., area or duration) for conservation and management;
438 (2) obtaining accurate estimates of mean body mass or generation time for species that may have
439 limited information or are heterogeneous with high levels of intra- or inter-specific variations.
440 Nonetheless, our conclusions were robust regardless of standardization, as additional analyses
441 using raw, or non-standardized scales for grassland studies revealed qualitatively similar results.
442 Our study did also demonstrate that it is possible to perform analyses using raw scales in order to
443 draw direct inferences, but perhaps only for the same functional group of species at a time.

444 Our research points to several avenues for future research. First, our analysis is based on
445 experiments that used species richness as the measure of biodiversity. A growing number of
446 studies have focused on other dimensions of biodiversity, such as phylogenetic or functional
447 diversity, and some have argued that alternative metrics of biodiversity might be better predictors
448 of ecosystem functioning or services (Purvis and Hector 2000, Isbell et al. 2017). Thus, scaling
449 relationships may be improved and more universal (e.g., across trophic groups) if other
450 dimensions of biodiversity are considered. Second, our study is focused on experiments of plant
451 diversity effects on biomass production, in which grasslands dominate the dataset. Hence, there
452 is a need to determine (i) whether scaling relationships revealed here are broadly applicable to
453 other ecosystem functions or services that are more relevant for human well-being (e.g., water
454 quality, pest control, pollination) (Lefcheck et al. 2015); and (ii) whether scaling relationships
455 are consistent across ecosystems, especially in non-terrestrial ecosystems (e.g., freshwater and
456 marine). Moreover, it is important to note that the maximum temporal and spatial scales in the
457 dataset that we analyzed are 4.63 generations and 20,000 m², respectively (**Appendix S1: Fig.**
458 **S2**), which may be relevant to many policy and conservation needs. Yet the extent to which our
459 scaling relationships can be extrapolated beyond these scales warrants future work and validation
460 when there are sufficient large-scale observational and remote sensed studies. Such validations
461 are also helpful to fine-tune the scaling relationships and ultimately improve their predictions in
462 real-world landscapes. One roadmap for doing so is to first use scaling relationships to predict
463 diversity effects at larger spatial and temporal scales, and then the predictions can be confirmed
464 or refined (e.g., via parameter adjustments) by comparing with BEF relationships derived from

465 equivalent observational scales. Finally, our analysis demonstrates strong space-time interactions
466 on plant diversity–ecosystem function relationships, and also explores possible driving factors of
467 such interactions. Future research designed to explicitly and accurately measure and quantify the
468 relative importance of different mechanisms, and conditions under which they operate is needed.
469 Such mechanistic understanding is crucial for developing landscape models that more accurately
470 predict changes in multiple ecosystem services and their tradeoffs due to biodiversity losses (Qiu
471 and Turner 2013, O’Connor et al. 2017, Qiu et al. 2018a).

472 The rapid pace of species extinction amid the Anthropocene has prompted substantial
473 concerns and efforts to determine their ecological, social and economic consequences (Naeem et
474 al. 2016, Hungate et al. 2017, Qiu et al. 2018b). Of particular interest is the extent to which
475 species losses undermine continued functioning of ecosystems and their long-term resilience to
476 deliver ecosystem services (Oliver et al. 2015). There is still a good window of opportunity to
477 safeguard biodiversity and sustain goods and services essential for human society. However,
478 accomplishing these goals requires sound knowledge to forecast real-world consequences of
479 biodiversity change in landscapes where concerted societal actions can be motivated. Our
480 research develops useful scaling relationships that quantify and scale up biodiversity effects on
481 productivity across space and over time. Results of nonlinear responses of biodiversity effects,
482 along with complex space-time interactions suggest that simple linear extrapolation of results
483 from small-scale, controlled experiments to large-scale landscapes without proper scaling
484 functions will likely underestimate biodiversity effects. Our study moves us one step closer to
485 use results of small-scale experiments to help predict the consequences of biodiversity change in
486 more natural ecosystems. Findings from this study will be relevant for designing conservation
487 strategies, and can be integrated into predictive models to more accurately examine
488 consequences of realistic extinction scenarios in a changing and uncertain future.

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493 **Supporting Information**

494 Additional supporting information may be found online at: [link to be added in
495 production].

496

497

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678 **Tables**

679 **Table 1.** General linear mixed-effects model results showing how standardized spatial (S) and
680 temporal scales (T) influence plant diversity effects – LR_{net} , and parameters a and b derived from
681 curve fitting of the power function. Power function is mathematically expressed as: $\ln\left(\frac{Y_s}{Y_m}\right)$
682 $= a + b \times \ln(S)$, where Y_s is the biomass/density at species richness S , Y_m is the mean
683 biomass/density of monoculture of all species, a is the constant and b is the exponent. Spatial and
684 temporal scales were log-transformed prior to analysis. Model was fitted by restricted maximum
685 likelihood (REML), and significant test was performed with the Satterthwaite approximations.
686 All predictors had variance inflation factors (VIF) < 2.8 , and all model assumptions were met
687

		Estimated β	SE	t -value	Prob. ($> t $)
LR_{net}	Intercept	0.448	0.031	14.44	<0.001
	S	0.019	0.011	1.69	0.091
	T	0.141	0.027	5.21	<0.001
	$S:T$	0.015	0.006	2.48	0.014
Parameter a	Intercept	0.02	0.012	1.60	0.11
	S	-0.005	0.004	-1.24	0.22
	T	0.003	0.012	0.30	0.77
	$S:T$	-0.001	0.002	-0.46	0.65
Parameter b	Intercept	0.19	0.026	7.54	<0.001
	S	0.006	0.007	0.86	0.39
	T	0.07	0.017	4.15	<0.001
	$S:T$	0.008	0.003	2.35	0.02

688

689

Figure Captions

690 **Fig. 1.** Pairwise correlations between net effects of plant diversity on biomass production and
691 standardized (A) temporal scale (i.e., natural log of $D_{study}/G_{organism}$, where D_{study} represents
692 study duration and $G_{organism}$ as the organism generation time), and (B) spatial scale (i.e., natural
693 log of $S_{experiment}/S_{organism}$, where $S_{experiment}$ represents experimental unit size, and $S_{organism}$ as
694 organism body mass). Red solid lines are derived from linear regressions fitted to the data, with
695 the 95% confidence intervals shown in grey band.

696

697 **Fig. 2.** Interactive effects of scales on altering plant diversity effects on biomass production: (A)
698 how plant diversity effects, LR_{net} , vary in response to temporal scale (x-axis) while spatial scales
699 are held constant at two extremes (i.e., minimum and maximum, in red and blue color
700 respectively); (B) how plant diversity effects, LR_{net} , vary in response to spatial scale (y-axis)
701 while temporal scales are held constant at two extremes (i.e., minimum and maximum, in red and
702 blue color respectively); (C) estimated slope β of temporal scales (i.e., effects of temporal scales
703 on LR_{net}) in responses to spatial scales; (D) estimated slope β of spatial scales (i.e., effects of
704 spatial scales on LR_{net}) in responses to temporal scales.
705

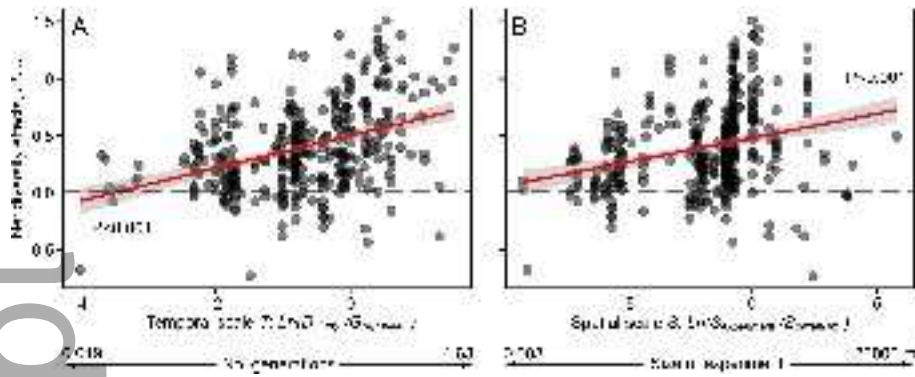
706 **Fig. 3.** Interactive effects of scales on the form of plant diversity–biomass relationships,
707 quantified by exponent b from power function fit: (A) how exponent b varies with temporal scale
708 while spatial scales are held constant at two extremes (i.e., minimum and maximum, in red and
709 blue color respectively); (B) how exponent b varies with spatial scale while temporal scales are
710 held constant at two extremes; (C) estimated slope β of temporal scales (i.e., effects of temporal
711 scales on exponent b) in responses to spatial scales; (D) estimated slope β of spatial scales (i.e.,
712 effects of spatial scales on exponent b) in responses to temporal scales. In Panel A and B,
713 horizontal dashed green lines represent mean exponent b estimated in natural grassland
714 ecosystems from Duffy et al. (2017).
715

716 **Fig. 4.** Pairwise correlations between partitioned complementarity effects (CE) vs. standardized
717 temporal (A) and spatial (B) scales, as well as partitioned selection effects vs. standardized
718 temporal (C) and spatial (D) scales. Color gradient represents the magnitude of net plant
719 diversity effects. Black solid lines are derived from linear regressions fitted to the data, with the
720 95% confidence interval shown in grey band.
721

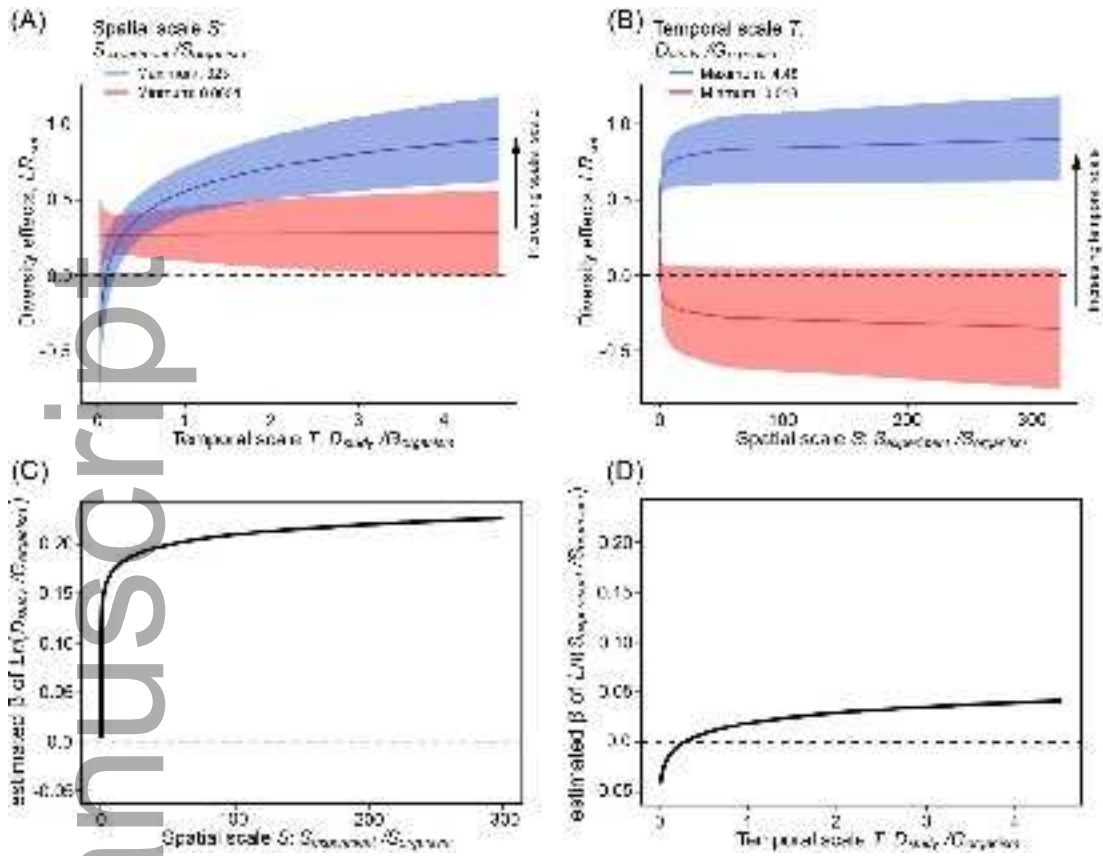
722 **Fig. 5.** Boxplots showing the complementarity effects (A) and selection effects (B) between
723 experiments categorized into *large* temporal and spatial scales (i.e., both >90th percentile) vs.
724 *large* temporal (>90th percentile) but *small* spatial scales (<60th percentile). Additional two
725 boxplots showing the complementarity effects (C) and selection effects (D) between experiments
726 categorized into *large* spatial and temporal scales (i.e., both >90th percentile) vs. *large* spatial
727 (>90th percentile) but *small* temporal scales (<60th percentile). Please note that: (1) y-axes for

728 panels A vs. C, and B vs. D are in different scales; (2) *P*-values denote the significant differences
729 between groups of experiments estimated from the linear mixed-effects models; (3) the purpose
730 of our deliberate comparisons is to highlight the contributions of complementarity effects vs.
731 selection effects at high spatial scales while increasing temporal scales, or vice versa.

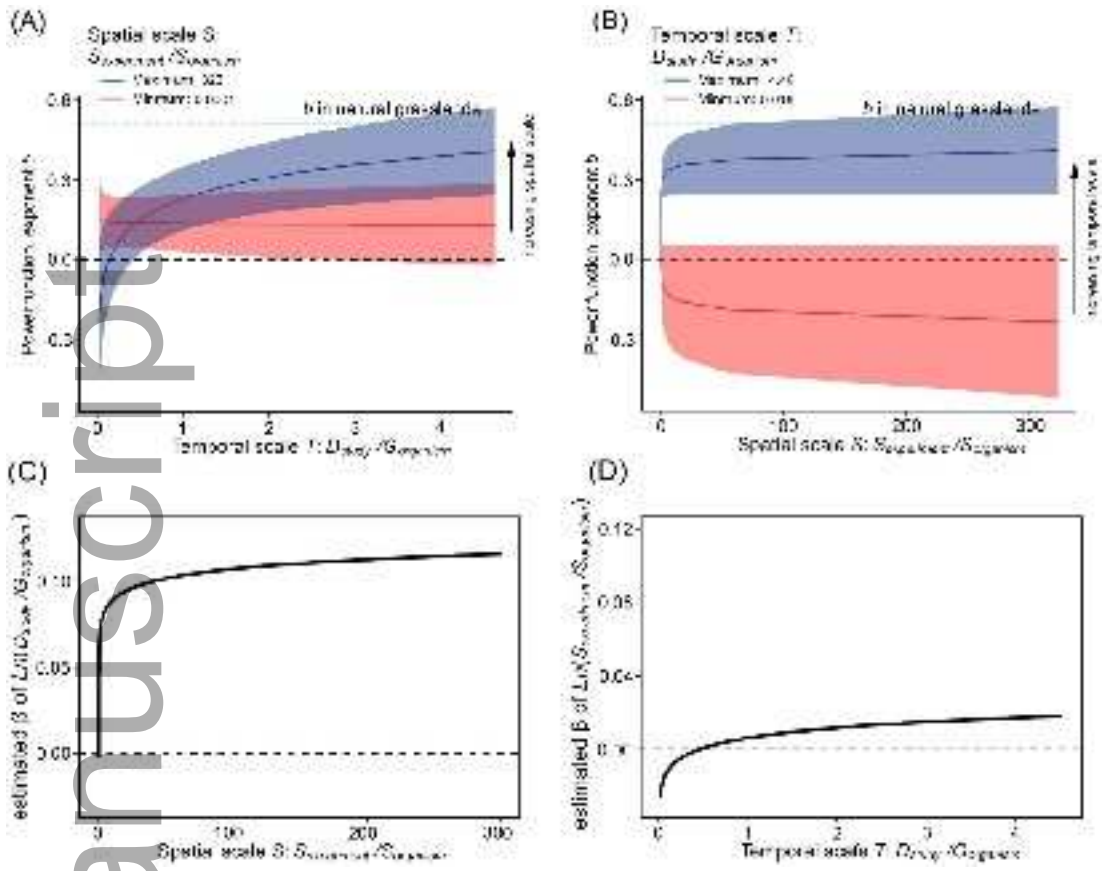
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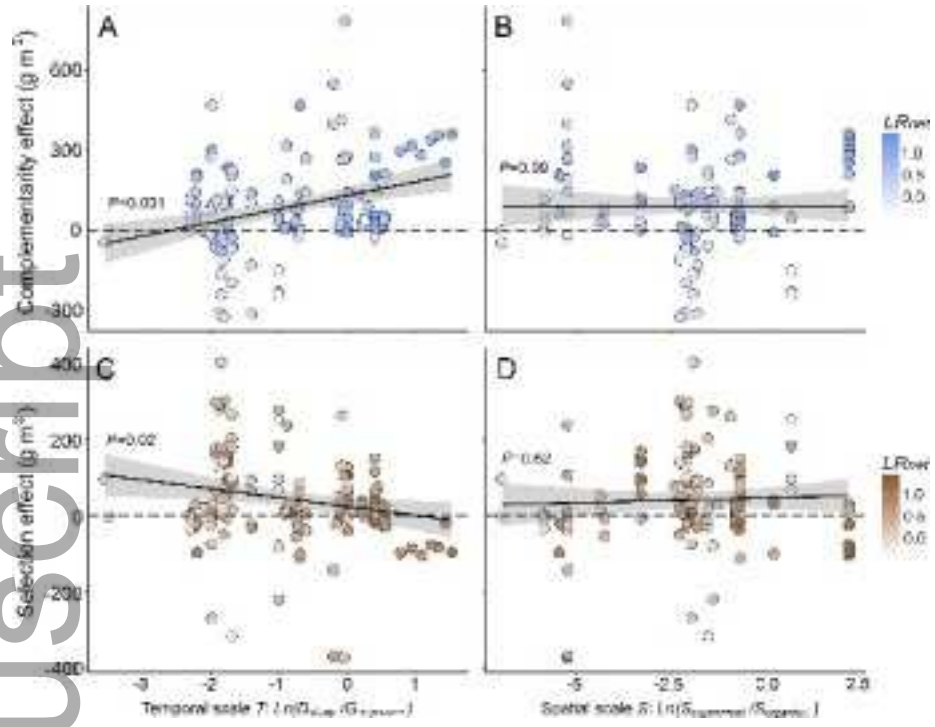
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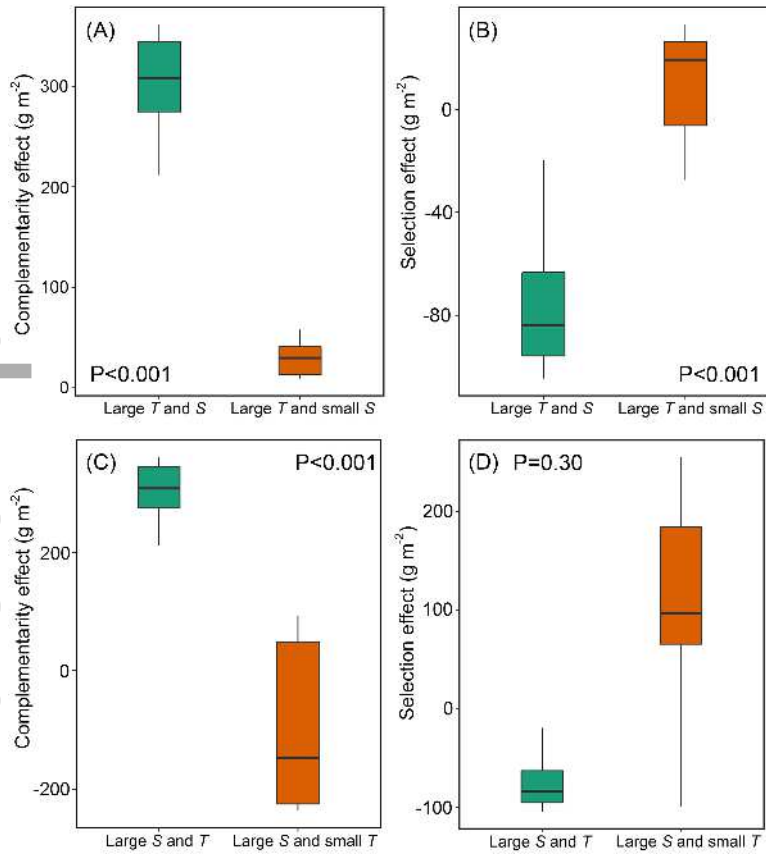
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