

1 **The influence of balanced and imbalanced resource supply on biodiversity-functioning relationship**  
2 **across ecosystems**

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51

## Summary

52 Numerous studies show that increasing species richness leads to higher ecosystem productivity. This  
53 effect is often attributed to more efficient portioning of multiple resources in communities with higher  
54 numbers of competing species, indicating the role of resource supply and stoichiometry for biodiversity-  
55 ecosystem functioning relationships. Here, we merged theory on ecological stoichiometry with a  
56 framework of biodiversity-ecosystem functioning to understand how resource use transfers into primary  
57 production. We applied a structural equation model to define patterns of diversity-productivity  
58 relationships with respect to available resources. Meta-analysis was used to summarize the findings  
59 across ecosystem types ranging from aquatic ecosystems to grasslands and forests. As hypothesized,  
60 resource supply increased realized productivity and richness, but we found significant differences  
61 between ecosystems and study types. Increased richness was associated with increased productivity,  
62 although this effect was not seen in experiments. More even communities had lower productivity,  
63 indicating that biomass production is often maintained by a few dominant species, and reduced  
64 dominance generally reduced ecosystem productivity. This synthesis, which integrates observational  
65 and experimental studies in a variety of ecosystems and geographic regions, exposes common patterns  
66 and differences in biodiversity-functioning relationships, and increases the mechanistic understanding of  
67 changes in ecosystems productivity.

68 Keywords: biodiversity-ecosystem functioning, stoichiometry, evenness, richness, productivity, Nutrient  
69 Network (NutNet)

70 **Introduction**

71 The correlation between primary producer diversity and ecosystem productivity is a fundamental and  
72 broadly studied relationship in ecology. This relationship has been addressed mainly using bivariate  
73 approaches, either envisioning diversity as an emergent property of productivity gradients, or proposing  
74 a functional influence of diversity on productivity. The latter reasoning has been advanced by numerous  
75 empirical studies showing that increasing richness (number of species) drives higher productivity of  
76 terrestrial and aquatic ecosystems [1–3]. This effect is attributed to more complete resource use in  
77 communities with a higher number of competing species [4,5] or to a greater chance of including a  
78 highly productive species in a more diverse community [6]. The influence of productivity on diversity, on  
79 the other hand, has a long history of debate in ecology, in particular regarding the general presence or  
80 absence of hump-shaped patterns of biodiversity across gradients of productivity [7–12].

81 Profitable solutions to reconcile both relationships, the effect of diversity on productivity and vice versa,  
82 have been proposed by models [13] and empirical work [5,14,15]. These studies suggest that we can  
83 advance our understanding of the relationships between productivity and diversity by (i) recognition  
84 that “productivity” refers to different kinds of productivity when invoked for the diversity-productivity  
85 or the productivity-diversity relationship, and (ii) advancing to multivariate approaches which account  
86 for multiple mechanisms acting simultaneously [9,16].

87 Concerning (i): producer diversity responds not only to the availability of resources (i.e., the potential  
88 productivity), but it also influences the realized productivity, because more diverse communities can use  
89 the resources more completely. With respect to potential productivity, more species can coexist at  
90 higher levels of resource supply if the resources are provided in balanced ratios [13,15]. Stoichiometric  
91 imbalance in resource supply leads to exclusion of poor competitors for the most limiting resource  
92 [15,17] restricting the number of species that can coexist [18]. Indeed, more balanced resource supply  
93 ratios are expected to enhance the chance for coexistence by allowing trade-offs in resource acquisition  
94 to play out [19]. By this theory, changes in absolute and relative availability of resources, not the rate of  
95 biomass production itself, alters producer biodiversity. Conversely, the number and identity of  
96 coexisting species affects how efficiently the available resources are transferred into biomass  
97 production and hence realized productivity. At the same time, an overall increase in resource supply also  
98 will affect the realized productivity directly, with or without changes in biodiversity, a mechanism  
99 underlying the yield increase from agricultural fertilization or the response of ecosystems to  
100 eutrophication.

101 Concerning (ii): the evidence that biodiversity responds to potential productivity but also influences  
102 realized productivity [13,14] negates the relevance of simple bivariate analyses, although they are still  
103 commonly used in ecology [8,9]. Instead, multivariate frameworks with resource availability (potential  
104 productivity), biodiversity, and realized productivity as causally-connected components promise greater  
105 mechanistic insight regarding biodiversity-productivity relationships. Cardinale et al. [15] developed a  
106 structural equation model (SEM) to illustrate a multivariate approach, in which availability of multiple  
107 resources is decomposed into two independent components: overall resource availability and the  
108 degree of imbalance among these resources. Their suggested framework was tested with a single  
109 freshwater phytoplankton dataset, which – as predicted – found increased species richness and biomass  
110 with higher resource availability, reduced richness and productivity with increasing resource imbalance,  
111 and greater biomass with increasing richness.

112 Diversity is comprised of not just the number of species but also their relative abundances: greater  
113 evenness of species relative abundance contributes to greater diversity. Evenness has been less  
114 frequently analyzed in studies on biodiversity-functioning relationships [20], but theory suggests that at  
115 the local scale, dominance by a single species (i.e. low evenness) can result in high biomass production  
116 when the dominant species has a high resource use efficiency [21]. If dominance by this species is  
117 reduced in a more even community, productivity should decrease since any other species will perform  
118 less efficiently. This phenomenon has been confirmed for aquatic [22,23] and terrestrial [24]  
119 ecosystems. Furthermore, a meta-analysis by Hillebrand et al. [25] showed that increased nutrient  
120 supply generally decreases evenness in both terrestrial and aquatic ecosystems, whereas the responses  
121 of species richness were more dependent on context and system.

122 In this study, we present the first general test of the multivariate framework proposed by Cardinale et  
123 al. [15] across ecosystems (marine, freshwater and terrestrial), and approaches (field observational  
124 studies and experiments). We combined structural equation modelling with meta-analysis, using the  
125 analytical framework proposed by Cardinale et al. [15] for each single study and derived the  
126 standardized path coefficients as effect sizes for the meta-analysis [26]. In addition to the effects of  
127 richness on resource use, we also analysed effects of evenness within the same framework across  
128 systems. Our study, which merges the theory of ecological stoichiometry (ES) with the framework of  
129 biodiversity-ecosystem functioning (BEF), aims to increase the mechanistic understanding of how  
130 resource use transfers into primary production.

131 We hypothesized that resource availability would increase realized productivity and species richness  
132 ( $H_1$ ), that resource imbalance would decrease realized productivity and diversity (richness and evenness)  
133 ( $H_2$ ), and that an increased richness would have a positive impact on biomass production ( $H_3$ ).  
134 Furthermore, we expected evenness to have a negative impact on realized productivity ( $H_4$ ), if biomass  
135 production is maintained by few, highly productive dominant species.

## 136 **Methods**

### 137 *Data sources*

138 We assembled 78 datasets comprising terrestrial, freshwater and marine studies that included  
139 information on available resources and producer diversity. This database contains data from published  
140 experimental and field observational studies across a broad range of habitats and geographic regions  
141 (Table 1), amended by the authors' own data. All studies provided the number of species (richness) and  
142 69 studies provided evenness, as Pielou's index [27]. We did not consider experimental studies which  
143 manipulated species richness or composition as this could bias our model results, but we included  
144 experiments that manipulated resource supply (Table S1). To be included in the analysis, studies needed  
145 to contain information on total biomass of producers (realized productivity), producer diversity (at least  
146 richness) and supply of at least two resources. From 78 datasets, 46 contained information on the  
147 supply of three or more resources, mostly nitrogen, phosphorus and potassium (Table S1,  
148 Supplementary Material). Depending on the producer community, realized productivity was measured  
149 as concentration of chlorophyll a, biovolume, aboveground plant biomass, or total carbon content of the  
150 plant tissue. The measurements of resources included photosynthetically active radiation (PAR) and  
151 concentrations of total nitrogen, phosphorus, potassium and other elements in water or soil. The total  
152 amount of each element was estimated as the sum of organic and inorganic bioavailable fractions. Table  
153 S1 contains information on the resources and the biomass measurement for each study.

### 154 *Structural equation model (SEM)*

155 To quantify resource availability and imbalance we followed the geometric approach of Cardinale et al.  
156 [15]. To compare resources, we rescaled resource measurements within each study to have a mean of  
157 zero and standard deviation of one. Thus, changes on the multidimensional coordinate system (Fig. 1)  
158 are in units of standard deviation from the mean value of all sampling points within each study. We then  
159 defined a reference vector  $y$ , where the change in standard deviation of one resource corresponds to  
160 the equal change in all other resources on the multidimensional coordinate system (Fig. 1). For two

161 resources, vector  $y$  represents the 1:1 proportion. No specific stoichiometric requirements (e.g. Redfield  
162 ratio of N:P = 16:1) are considered.

163 The total amount of resources (resource availability,  $a$ ) was calculated after Cardinale et al. (2009a) as

$$a = \frac{\sum_{i=1}^k R_i y_i}{\|y\|}$$

164 (1)

165 where  $y$  is the reference vector (Fig. 1), and  $r$  is the resource vector which can be calculated for any  $k$   
166 number of resources ( $R$ )

$$\|r\| = \sqrt{\sum_{i=1}^k (R_i)^2}$$

167 (2)

168 The  $a$  value represents the total amount of available resources. The value is greater than zero when the  
169 covariance of two resources is positive and below zero if the covariance is negative. Positive  $a$  values  
170 represent abundant resources and negative  $a$  values represent scarce resources within each study.

171 In this study, we defined resource imbalance as a degree of deviation in resource supply from the  
172 reference state in given system. This value was calculated as a perpendicular distance  $b$  from the  
173 reference vector  $y$  (Fig. 1)

$$b = \begin{cases} \arccos\left(\frac{a}{\|r\|}\right) & a \geq 0 \\ 180^\circ - \arccos\left(\frac{a}{\|r\|}\right) & a < 0 \end{cases}$$

174 (3)

176 To quantify the direct and indirect effects of resource availability and imbalance on realized productivity,  
177 we followed the set of causal relationships proposed by Cardinale et al. [15]. In this model, resource  
178 availability and imbalance each have a direct as well as indirect impact (mediated through diversity) on  
179 the realized productivity. The model was evaluated separately for each study in our dataset using  
180 species number (richness) or Pielou's evenness as diversity variables. Model fitting was performed using

181 maximum likelihood estimation with robust standard errors in the *lavaan* package [28] of R statistical  
182 software (R version 3.1.1., R core development team, 2015). Prior to fitting the model, we tested  
183 bivariate relationships between variables to check for nonlinear relationships. Because we found no  
184 significant nonlinearities, no polynomial terms were included in the models. For time series, we first  
185 fitted autoregressive models to the data and used lagged values in SEM. The relative importance of  
186 paths was compared using Fisher's z-transformed standardized coefficients ( $\gamma$ ). A chi-square test was  
187 used to quantify the overall fit of the model. To enable comparison of all the studies in the meta-  
188 analysis, no attempt was made to select a best fitting model. Only the models which were not  
189 statistically different from our theoretical model ( $p(\chi^2) > 0.05$ ) were used in the meta-analysis and are  
190 illustrated in this manuscript.

### 191 *Meta-analysis*

192 Standardized path coefficients from the SEMs were used as effect size estimates in the meta-analysis  
193 with the sample variance adjusted by the sample size. To calculate the overall effect size for each path,  
194 we fitted multivariate mixed effects models accounting for differences between study types (field study  
195 or experiment) and ecosystem types (terrestrial, freshwater, marine) using the *metafor* package [29] in  
196 R (R version 3.1.1., R core development team, 2015). While calculating the summary effect, the effect  
197 sizes from each study were weighted by the inverse of the study variance. Models were fitted using  
198 restricted maximum likelihood estimation and the Q-test was used to test for residual heterogeneity. As  
199 the effects significantly differed between study and ecosystem types, we reanalyzed the data separately  
200 for each group, which reduced heterogeneity considerably.

## 201 **Results**

### 202 *Impact of resource availability on diversity and productivity*

203 Overall resource availability directly increased realized productivity (standardized coefficient ( $\gamma$ ) = 0.15)  
204 and diversity (richness,  $\gamma$  = 0.04; evenness  $\gamma$  = 0.05) (Fig. 2). However, these effects were highly variable  
205 between the studies. In field observational studies, effects of resource availability on producer biomass  
206 (realized productivity) and diversity varied depending on the ecosystem type (Fig. 3 and 4). In forests,  
207 resource availability increased both species richness ( $\gamma$  = 0.15) and evenness ( $\gamma$  = 0.12), but it should be  
208 stressed that this result is due to a single study (GAM01). In grasslands and saltmarshes, resource  
209 availability increased realized productivity ( $\gamma$  = 0.11), but had no effect on richness or evenness. In  
210 freshwater ecosystems, higher resource availability led to higher realized productivity ( $\gamma$  = 0.44) and



211 higher species richness ( $\gamma = 0.16$ ). Surprisingly, negative effects of resource availability on biomass  
212 production ( $\gamma = -0.06$ ) and richness ( $\gamma = -0.14$ ) were observed for marine ecosystems. In experiments,  
213 resource availability affected neither richness nor evenness, but had a strong positive impact on realized  
214 productivity in freshwater experiments ( $\gamma = 0.61$ ). Evenness was not affected by changing resource  
215 supply in freshwater or in marine systems, and this pattern was consistent among studies (see  
216 Supplementary Material). We found significantly positive effects of resource availability on evenness in  
217 four of 69 studies included in the meta-analysis. The only significantly negative effect of resource  
218 availability on evenness was found in a long-term study on phytoplankton in the western English  
219 Channel (Western Channel Observatory, station L4;  $\gamma = -0.19$ ,  $p = 0.012$ ).

#### 220 *Impact of resource imbalance on diversity and productivity*

221 In general, resource imbalance had no effect on diversity and had a marginal positive effect on the  
222 realized productivity (Fig. 2). The positive effects on realized productivity and species richness were  
223 primarily found in marine ecosystems (Fig. 3), driven by five long-term (11 years) studies on coastal  
224 phytoplankton off the coast of the Netherlands. In freshwater ecosystems, resource imbalance had a  
225 weak negative effect on species richness ( $\gamma = -0.05$ ), but in some studies (e.g. eutrophic lakes in the  
226 United States, HILL04) resource imbalance increased richness (Fig. S3, Supplementary Material).  
227 Resource imbalance did not affect productivity in marine or freshwater experiments or in terrestrial  
228 ecosystems.

#### 229 *Interactions between richness and productivity*

230 Overall, richness and realized productivity positively covaried ( $\gamma = 0.18$ ) (Fig. 2a). However, separating  
231 study types (field observational study or experiment) highlighted that the significant effects were found  
232 only in field studies. The strongest relationship between richness and biomass production was observed  
233 in marine ecosystems (Fig. 3). The only field study showing a significantly negative effect of richness on  
234 productivity ( $\gamma = -0.18$ ,  $p = 0.038$ ) was a study on plants in saltmarshes (TREIBSEL, Fig. S5, Supplementary  
235 Material). In general, no relationship between richness and realized productivity was found in grasslands  
236 and saltmarshes.

#### 237 *Interactions between evenness and productivity*

238 As predicted, we found an overall negative relationship between evenness and realized productivity ( $\gamma =$   
239  $-0.10$ ) in aquatic and terrestrial studies (Fig. 2b). The strongest relationship was observed in freshwater

240 (field studies:  $\gamma = -0.42$ ; experiments:  $\gamma = -0.38$ ) and in marine experiments ( $\gamma = -0.42$ ). In contrast,  
241 productivity increased with evenness in forests ( $\gamma = 0.16$ ,  $p < 0.001$ ).

242

## 243 **Discussion**

244 Across ecosystems and study types the realized productivity of autotrophs was largely influenced by the  
245 availability of resources. In observational studies, these effects were either direct or mediated by  
246 changes in the number of species, confirming previous findings that higher species richness leads to  
247 higher efficiency in resource use and in consequence to higher biomass production [4,14,15,25].  
248 However, neither resource availability nor imbalance significantly affected evenness, which suggests  
249 that the dominance structure of autotrophs is primarily driven by factors other than resources, such as  
250 trophic interactions or external forces such as warming, drought, salinity or changes in pH. Such effects  
251 on evenness have been previously reported in the literature. For example, a meta-analysis across  
252 ecosystems showed that herbivory enhances producer evenness [25]. Comparably, greater evenness  
253 with lower soil moisture was observed in experimental plant communities [30].

254 Surprisingly, in marine ecosystems, biomass and the number of phytoplankton species decreased with  
255 higher resource supply, but increased in response to resource imbalance. These results were largely  
256 driven by studies on pelagic ecosystems off the coast of the Netherlands. These coastal waters are  
257 generally turbid systems with high proportion of dissolved organic nutrients [31]. Consequently,  
258 available nitrogen and phosphorus might be primarily incorporated by heterotrophic microbes and not  
259 by phytoplankton. Including availability of light as one of the limiting resources for phytoplankton  
260 growth in turbid waters could change the shape of examined relationships. Contrasting results for  
261 phytoplankton at the station L4 in the western English Channel (resource availability  $\rightarrow$  richness,  $\gamma =$   
262  $0.31$ ,  $p < 0.001$ ; resource availability  $\rightarrow$  realized productivity,  $\gamma = 0.28$ ,  $p < 0.001$ ; non-significant  
263 relationships with resource imbalance), which contained information on light availability (Table S1,  
264 Supplementary Material), support this interpretation. Station L4 is seasonally stratified and also  
265 characterized by lower turbidity than stations along the coast of the Netherlands [32]. These results  
266 highlight the importance of light availability for autotrophic growth in ecosystems where nutrients are  
267 replete and suggest that interpretation of the resource supply-productivity relationships in plants,  
268 particularly in aquatic systems, might be misleading if the influence of light is not considered [33].

269 In aquatic experimental studies and unmanipulated grasslands, we found significant relationships  
270 between resource availability and realized productivity, but no significant effect of resource availability  
271 or imbalances on diversity. These results are broadly consistent with previous meta-analyses, for  
272 example Elser et al. [34] demonstrated that across ecosystems, productivity generally increases with  
273 nutrient supply. Although experimental nutrient supply in many ecosystems tends to lead to loss of  
274 plant evenness or richness [25], the diversity of unmanipulated grasslands likely arises from many  
275 interacting processes (e.g. resource supply, trophic interactions, invasion, etc.), across a broad range of  
276 observed soil resources. Thus, in the absence of significantly elevated nutrients, our results  
277 demonstrate that grassland diversity is not tightly coupled to soil nutrients. Further, the richness  
278 gradients in the aquatic experimental studies might not represent biodiversity of natural communities,  
279 thus constraining the responsiveness of diversity to the experimental manipulations [35]. Aquatic  
280 communities in experimental studies may suffer from bottle (enclosure) effects, thereby preventing the  
281 growth of some species while favoring others, particularly with nutrient amendments. Also, strong  
282 nutrient recycling in closed experimental systems might lead to overestimation of the effects related to  
283 enhanced resource supply. In some experiments included in our analysis (Table S1, Supplementary  
284 Material), nutrients were added to the system, often in higher proportions and at different ratios than in  
285 natural environment. Other environmental drivers such as turbidity and grazing effects are altered in  
286 experiments compared with natural systems [35].

287 As expected, we found an overall positive effect of species richness on realized productivity of  
288 autotrophs in the field. The only field study showing a negative response of biomass production to  
289 increasing species richness was a study on plants in saltmarshes (TREIBSEL, Supplementary Material),  
290 where salinity and water regime rather than nutrients were the main drivers of diversity and biomass  
291 [36–39]. The limited ability of our model to explain variation in richness and realized productivity in  
292 saltmarshes (only 8% for richness and 4% for realized productivity) seems to confirm that we did not  
293 quantify the key factors influencing this system. Our simplistic model typically explained a large  
294 proportion of variation in biomass production, but only small amounts of variation in diversity (Table  
295 S1), emphasizing the importance of other factors such as disturbance [40] and trophic interactions for  
296 shaping community structure.

297 The overall negative relationship between evenness and biomass production confirms our hypothesis  
298 that most communities are dominated by a few highly productive species; reducing the dominance by  
299 these species decreases the realized productivity. Biomass production increased with evenness only in

300 forests, which is consistent with results from a global meta-analysis exploring drivers of diversity-  
301 productivity relationships in forests [41]. Higher heterogeneity of functional traits (e.g. shade tolerance,  
302 root traits) in more even forest communities might significantly increase complementarity in resource  
303 use and consequently productivity [41]. However, our model explained only 10% of the variance in total  
304 tree biomass, which again suggests that the measured resources were not the main drivers of the  
305 system in this study. Environmental changes such as management for preferred species [42], stand age  
306 [43] or differences in soil moisture [44] could be potentially more important factors for shaping tree  
307 distribution and biomass.

308 In general, our analysis emphasizes the importance of diversity for primary productivity of natural  
309 ecosystems. The role of diversity remains largely unappreciated in experimental aquatic studies,  
310 probably because the levels of diversity are limited in these experiments and the effects of  
311 manipulations are often stronger than in the natural environment. Moreover, we Based on the field  
312 observational studies, we can partly support  $H_1$  i.e. that resource availability increases producer biomass  
313 and diversity. Resource availability had a positive effect on biomass and richness, but did not affect  
314 evenness except in forests. Interestingly, the direct effect of resource supply on productivity ( $\gamma = 0.15$  in  
315 the SEM with richness;  $\gamma = 0.07$  in the SEM with evenness) was overall stronger than the indirect effect  
316 mediated by diversity (for richness:  $\gamma = 0.04 \cdot 0.18 = 0.01$ ; for evenness:  $\gamma = -0.10 \cdot 0.05 = -0.01$ ),  
317 suggesting that the role of diversity for biomass production across ecosystems is rather weak when  
318 compared to the direct effect of resources on realized productivity, consistent with other such studies  
319 [15,16].

320 Resource imbalance only reduced diversity in the freshwater field studies (Fig. 2). As this effect was  
321 marginal ( $\gamma = -0.05$ ) and did not appear in other types of ecosystems, we reject  $H_2$ . The surprisingly weak  
322 effects of resource imbalance on diversity and realized productivity can appear as a result of a narrow  
323 range of  $b$  caused by limited number of resources included in our analysis (mostly N and P). This should  
324 be further explored using data from studies with contrasting resource ratios and naturally occurring  
325 diversity gradients. In long-term studies, seasonality in resource supply can also play a role in limiting  
326 the absolute range of resource imbalance. Comparing the results among seasons could bring a new  
327 insight into the framework proposed by Cardinale et al. [15] and explored in this article.

328 As hypothesized, biomass production generally increased with the number of species ( $H_3$ ) but was  
329 reduced in more even communities ( $H_4$ ). However, a positive impact of evenness on biomass was found  
330 in forests, suggesting overyielding in this type of ecosystem.

331 In spite of the power of SEM and meta-analytical approaches, our interface has some limitations. First,  
332 our measures of resource availability and imbalance are based on equal supply of resources, ignoring  
333 physiological requirements of the organisms and their stoichiometric plasticity. However, a major  
334 advantage of this measure is that it combines multiple resources despite of their type, units and ranges.  
335 Second, the number of resources included in our analysis is rather low and conclusions might be  
336 misleading if the most limiting resource (e.g. light for aquatic communities) is omitted, as discussed  
337 above. Finally, we incorporated only the effects of resources, because the lack of consistent data for  
338 other potentially important environmental factors would not allow for comparison of effects across  
339 ecosystems. However, the multivariate approach which we used [15] integrates the effects of potential  
340 productivity (total resource supply) on diversity and the effects of diversity on realized productivity,  
341 advancing mechanistic understanding of these relationships. For the first time, this approach has been  
342 applied to datasets spanning a wide variety of ecosystems, elucidating similarities and differences in the  
343 response among ecosystem types.

344 Although our simple model did not account for all potentially influential drivers of diversity-productivity  
345 relationships (e.g. consumers, disturbance), our meta-analysis demonstrates that in the natural  
346 environment richness significantly affects realized productivity independent of the ecosystem type,  
347 although the absolute effect on biomass was weak. However, we found no evidence that evenness is  
348 directly related to changes in resource supply suggesting that trophic interactions (e.g. herbivory) likely  
349 play a key role in shaping the dominance structure of the producer community. We expect that this  
350 meta-analysis will stimulate further studies evaluating the importance of evenness for ecosystem  
351 functioning.

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373

374 **Data accessibility**

375 TBA

376 **Authors' contributions**

377 H.H., A.L., S.A.J.D., E.D., W.S.H., C.A.K., H.O.V, E.S., M.S., J.U. and D.B.W. contributed to the design of the  
378 study. All authors contributed to data interpretation and manuscript editing. A.L. performed data  
379 analyses and wrote the first draft of the manuscript.

380 **Competing interests**

381 We have no competing interests.

382

383 **References**

- 384 1. Cardinale, B. J., Matulich, K. L., Hooper, D. U., Byrnes, J. E., Duffy, E., Gamfeldt, L., Balvanera, P.,  
385 O'Connor, M. I. & Gonzalez, A. 2011 The functional role of producer diversity in ecosystems. *Am.*  
386 *J. Bot.* **98**, 572–92. (doi:10.3732/ajb.1000364)  
387
- 388 2. Cardinale, B. J., Srivastava, D. S., Duffy, J. E., Wright, J. P., Downing, A. L., Sankaran, M. & Jouseau,  
389 C. 2006 Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* **443**,  
390 989–92. (doi:10.1038/nature05202)  
391
- 392 3. Gamfeldt, L., Lefcheck, J. S., Byrnes, J. E. K., Cardinale, B. J., Duffy, J. E. & Griffin, J. N. 2015 Marine  
393 biodiversity and ecosystem functioning: what's known and what's next? *Oikos* **124**, 252–265.  
394 (doi:10.1111/oik.01549)  
395
- 396 4. Ptacnik, R., Solimini, A. G., Andersen, T., Tamminen, T., Brettum, P., Lepistö, L., Willén, E. &  
397 Rekolainen, S. 2008 Diversity predicts stability and resource use efficiency in natural  
398 phytoplankton communities. *Proc. Natl. Acad. Sci. U. S. A.* **105**, 5134–8.  
399 (doi:10.1073/pnas.0708328105)  
400
- 401 5. Hillebrand, H. & Lehmpfuhl, V. 2011 Resource Stoichiometry and Consumers Control the  
402 Biodiversity-Productivity Relationship in Pelagic Metacommunities. *Am. Nat.* **178**, 171–181.  
403 (doi:10.1086/660831)  
404
- 405 6. Fox, J. W. 2005 Interpreting the selection effect of biodiversity on ecosystem function. *Ecol. Lett.*  
406 **8**, 846–856. (doi:10.1111/j.1461-0248.2005.00795.x)  
407
- 408 7. Adler, P. B. et al. 2011 Productivity is a poor predictor of plant species richness. *Science* **333**,  
409 1750–3. (doi:10.1126/science.1204498)  
410
- 411 8. Fraser, L. H. et al. 2015 Worldwide evidence of a unimodal relationship between productivity and  
412 plant species richness. *Science*. **349**, 302–305. (doi:10.1126/science.aab3916)  
413
- 414 9. Grace, J. B., Adler, P. B., Stanley Harpole, W., Borer, E. T. & Seabloom, E. W. 2014 Causal  
415 networks clarify productivity-richness interrelations, bivariate plots do not. *Funct. Ecol.* **28**, 787–  
416 798. (doi:10.1111/1365-2435.12269)  
417
- 418 10. Grime, J. P. 1973 Competition and Diversity in Herbaceous Vegetation (reply). *Nature* **244**, 311–  
419 311. (doi:10.1038/244311a0)  
420
- 421 11. Mittelbach, G. G., Steiner, C. F., Scheiner, S. M., Gross, K. L., Reynolds, H. L., Waide, R. B., Willig,

- 422 M. R., Dodson, S. I. & Gough, L. 2001 What is the observed relationship between species richness  
423 and productivity? *Ecology* **82**, 2381–2396. (doi:10.1890/0012-9658)  
424
- 425 12. Whittaker, R. J. 2010 Meta-analyses and mega-mistakes: calling time on meta-analysis of the  
426 species richness–productivity relationship. *Ecology* **91**, 2522–2533. (doi:10.1890/08-0968.1)  
427
- 428 13. Gross, K. & Cardinale, B. J. 2007 Does species richness drive community production or vice versa?  
429 Reconciling historical and contemporary paradigms in competitive communities. *Am. Nat.* **170**,  
430 207–20. (doi:10.1086/518950)  
431
- 432 14. Cardinale, B. J., Bennett, D. M., Nelson, C. E. & Gross, K. 2009 Does productivity drive diversity or  
433 vice versa? A test of the multivariate productivity–diversity hypothesis in streams. *Ecology* **90**,  
434 1227–1241. (doi:10.1890/08-1038.1)  
435
- 436 15. Cardinale, B. J., Hillebrand, H., Harpole, W. S., Gross, K. & Ptacnik, R. 2009 Separating the  
437 influence of resource ‘availability’ from resource ‘imbalance’ on productivity-diversity  
438 relationships. *Ecol. Lett.* **12**, 475–487. (doi:10.1111/j.1461-0248.2009.01317.x)  
439
- 440 16. Grace, J. B. et al. *in press* Integrative modeling reveals mechanisms linking productivity and plant  
441 species richness. *Nature*  
442
- 443 17. Hautier, Y., Niklaus, P. A. & Hector, A. 2009 Competition for Light Causes Plant Biodiversity Loss  
444 After Eutrophication. *Science*. **324**, 636–638. (doi:10.1126/science.1169640)  
445
- 446 18. Hillebrand, H., Cowles, J. M., Lewandowska, A., Van de Waal, D. B. & Plum, C. 2014 Think ratio! A  
447 stoichiometric view on biodiversity–ecosystem functioning research. *Basic Appl. Ecol.* **15**, 465–  
448 474. (doi:10.1016/j.baae.2014.06.003)  
449
- 450 19. Tilman, D., Kilham, S. S. & Kilham, P. 1982 Phytoplankton Community Ecology: The Role of  
451 Limiting Nutrients. *Annu. Rev. Ecol. Syst.* **13**, 349–372.  
452 (doi:10.1146/annurev.es.13.110182.002025)  
453
- 454 20. Hillebrand, H., Bennett, D. M. & Cadotte, M. W. 2008 Consequences of dominance: a review of  
455 evenness effects on local and regional ecosystem processes. *Ecology* **89**, 1510–1520.  
456 (doi:10.1890/07-1053.1)  
457
- 458 21. Norberg, J., Swaney, D. & Dushoff, J. 2001 Phenotypic diversity and ecosystem functioning in  
459 changing environments: A theoretical framework. *Proc. Natl. Acad. Sci. U. S. A.* **98**, 11376–11381.  
460
- 461 22. Matthiessen, B., Mielke, E. & Sommer, U. 2010 Dispersal decreases diversity in heterogeneous



- 462 metacommunities by enhancing regional competition. *Ecology* **91**, 2022–2033. (doi:10.1890/09-  
463 1395.1)  
464
- 465 23. Lewandowska, A. M., Breithaupt, P., Hillebrand, H., Hoppe, H.-G., Jürgens, K. & Sommer, U. 2012  
466 Responses of primary productivity to increased temperature and phytoplankton diversity. *J. Sea*  
467 *Res.* **72**, 87–93. (doi:10.1016/j.seares.2011.10.003)  
468
- 469 24. Mulder, C. P. H., Bazeley-White, E., Dimitrakopoulos, P. G., Hector, a., Scherer-Lorenzen, M. &  
470 Schmid, B. 2004 Species evenness and productivity in experimental plant communities. *Oikos*  
471 **107**, 50–63. (doi:10.1111/j.0030-1299.2004.13110.x)  
472
- 473 25. Hillebrand, H. et al. 2007 Consumer versus resource control of producer diversity depends on  
474 ecosystem type and producer community structure. *Proc. Natl. Acad. Sci. U. S. A.* **104**, 10904–9.  
475 (doi:10.1073/pnas.0701918104)  
476
- 477 26. Grace, J. B. et al. 2007 Does species diversity limit productivity in natural grassland communities?  
478 *Ecol. Lett.* **10**, 680–9. (doi:10.1111/j.1461-0248.2007.01058.x)  
479
- 480 27. Pielou, E. C. 1966 The measurement of diversity in different types of biological collections. *J.*  
481 *Theor. Biol.* **13**, 131–144. (doi:10.1016/0022-5193(66)90013-0)  
482
- 483 28. Rosseel, Y. 2012 lavaan: An R package for structural equation modeling. *J. Stat. Softw.*  
484
- 485 29. Viechtbauer, W. 2010 metafor: Meta-Analysis Package for R. *R Packag. version*  
486
- 487 30. Engel, E. C., Weltzin, J. F., Norby, R. J. & Classen, A. T. 2009 Responses of an old-field plant  
488 community to interacting factors of elevated [CO<sub>2</sub>], warming, and soil moisture. *J. Plant Ecol.* **2**,  
489 1–11. (doi:10.1093/jpe/rtn026)  
490
- 491 31. Van Engeland, T., Soetaert, K., Knuijt, A., Laane, R. W. P. M. & Middelburg, J. J. 2010 Estuarine ,  
492 Coastal and Shelf Science Dissolved organic nitrogen dynamics in the North Sea : A time series  
493 analysis ( 1995 e 2005 ). *Estuar. Coast. Shelf Sci.* **89**, 31–42. (doi:10.1016/j.ecss.2010.05.009)  
494
- 495 32. Tilstone, G. H. et al. 2012 Remote Sensing of Environment Variability in speci fi c-absorption  
496 properties and their use in a semi-analytical ocean colour algorithm for MERIS in North Sea and  
497 Western English Channel Coastal Waters. *Remote Sens. Environ.* **118**, 320–338.  
498 (doi:10.1016/j.rse.2011.11.019)  
499
- 500 33. Brauer, V. S., Stomp, M. & Huisman, J. 2012 The Nutrient-Load Hypothesis : Patterns of Resource  
501 Limitation and Community Structure Driven by Competition for Nutrients and Light. *am* **179**,

- 502 721–740. (doi:10.1086/665650)  
503
- 504 34. Elser, J. J. et al. 2007 Global analysis of nitrogen and phosphorus limitation of primary producers  
505 in freshwater, marine and terrestrial ecosystems. *Ecol. Lett.* **10**, 1135–1142.  
506
- 507 35. Brose, U. & Hillebrand, H. *this issue* Biodiversity and ecosystem functioning in dynamic  
508 landscapes. *Phil. Trans. R. Soc. B*  
509
- 510 36. Gough, L., Grace, J. B. & Taylor, K. L. 1994 The relationship between species richness and  
511 community biomass : the importance of environmental variables. *Oikos* **70**, 271–279.  
512 (doi:10.2307/3545638)  
513
- 514 37. Minden, V., Andratschke, S., Spalke, J., Timmermann, H. & Kleyer, M. 2012 Plant trait–  
515 environment relationships in salt marshes: Deviations from predictions by ecological concepts.  
516 *Perspect. Plant Ecol. Evol. Syst.* **14**, 183–192. (doi:10.1016/j.ppees.2012.01.002)  
517
- 518 38. Minden, V. & Kleyer, M. 2015 Ecosystem multifunctionality of coastal marshes is determined by  
519 key plant traits. *J. Veg. Sci.* **26**, 651–662. (doi:10.1111/jvs.12276)  
520
- 521 39. Waide, R. B., Willig, M. R., Steiner, C. F., Mittelbach, G., Gough, L., Dodson, S. I., Juday, G. P. &  
522 Parmenter, R. 1999 The Relationship Between Productivity and Species Richness. *Annu. Rev. Ecol.*  
523 *Syst.* **30**, 257–300. (doi:10.1146/annurev.ecolsys.30.1.257)  
524
- 525 40. Minden, V., Scherber, C., Cebrian Piqueras, M., Trinogga, J., Trenkamp, A., Mantilla-Contreras, J.,  
526 Lienin, P. & Kleyer, M. *this issue* Consistent drivers of plant biodiversity across managed  
527 ecosystems. *Phil. Trans. R. Soc. B*  
528
- 529 41. Zhang, Y., Chen, H. Y. H. & Reich, P. B. 2012 Forest productivity increases with evenness, species  
530 richness and trait variation: a global meta-analysis. *J. Ecol.* **100**, 742–749. (doi:10.1111/j.1365-  
531 2745.2011.01944.x)  
532
- 533 42. Fedrowitz, K. et al. 2014 Can retention forestry help conserve biodiversity? A meta-analysis. *J.*  
534 *Appl. Ecol.* **51**, 1669–1679. (doi:10.1111/1365-2664.12289)  
535
- 536 43. Gamfeldt, L. et al. 2013 Higher levels of multiple ecosystem services are found in forests with  
537 more tree species. *Nat. Commun.* **4**, 1340.  
538
- 539 44. Condit, R., Engelbrecht, B. M. J., Pino, D., Pérez, R. & Turner, B. L. 2013 Species distributions in  
540 response to individual soil nutrients and seasonal drought across a community of tropical trees.  
541 *Proc. Natl. Acad. Sci. U. S. A.* **110**, 5064–8. (doi:10.1073/pnas.1218042110)  
542

## Tables

Table 1. The number of studies included in the meta-analysis on the role of richness (S) and evenness (J) in resource use and biomass production of autotrophs. More details on the studies can be found in the Supplementary Material (Table S1).

<b>Study type</b>	<b>Ecosystem type</b>	<b>Habitat</b>	<b>S</b>	<b>J</b>
Field observational	Terrestrial	Grassland	41	40
		Forest	1	1
		Saltmarsh	2	0
	Freshwater	Lake	10	8
		Pond	2	0
		Rock pools	1	1
	Marine	Coastal waters	9	9
		Brackish waters	3	3
Experimental	Freshwater	Mesocosm	3	1
		Microcosm	1	1
	Marine	Mesocosm	4	4
		Microcosm	1	1
<b>Total</b>			<b>78</b>	<b>69</b>

## Figure legend

Figure 1. **(A)** Geometry used to estimate resource availability  $a$  and imbalance  $b$ . For simplicity, we present the concept for only two resources (R1 and R2).  $k$  number of resources can be included by adding more dimensions.  $y$  is the 1:1 reference vector and  $r$  is the resource vector. **(B)** Conceptual diagram illustrating causal relationships between resource availability  $a$  and imbalance  $b$ , diversity and community biomass. For more detail see description in text.

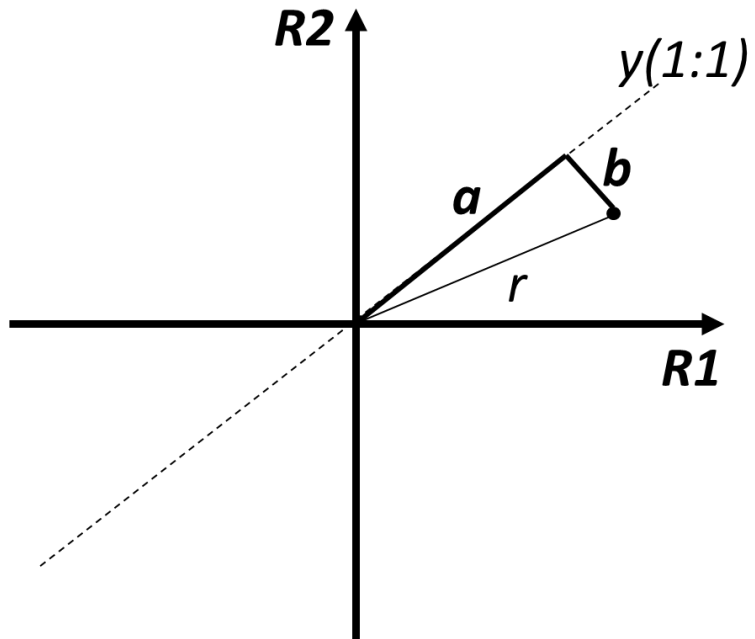
Figure 2. Summary of meta-analysis results for the structural equation model (SEM) with richness **(A)** and evenness **(B)** over all studies. Shown are effect sizes as standardized path coefficients.  $n$  is the number of studies. Blue and red paths are positive and negative relationships, respectively and grey paths are non-significant relationships.

Figure 3. Summary of meta-analysis results for the structural equation model (SEM) with richness over all studies. Shown are effect sizes as standardized path coefficients.  $n$  is the number of studies. Blue and red paths are positive and negative relationships, respectively and grey paths are non-significant relationships.

Figure 4. Summary of meta-analysis results for the SEM with evenness (for more detail see Table S2). Shown are effect sizes as standardized path coefficients.  $n$  is the number of studies. Blue and red paths are positive and negative relationships, respectively and grey paths are non-significant relationships.

Figure 1.

(A)



(B)

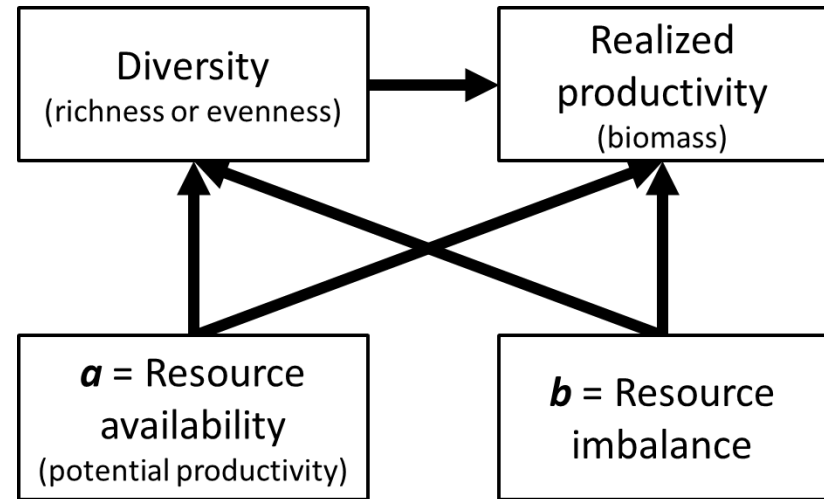
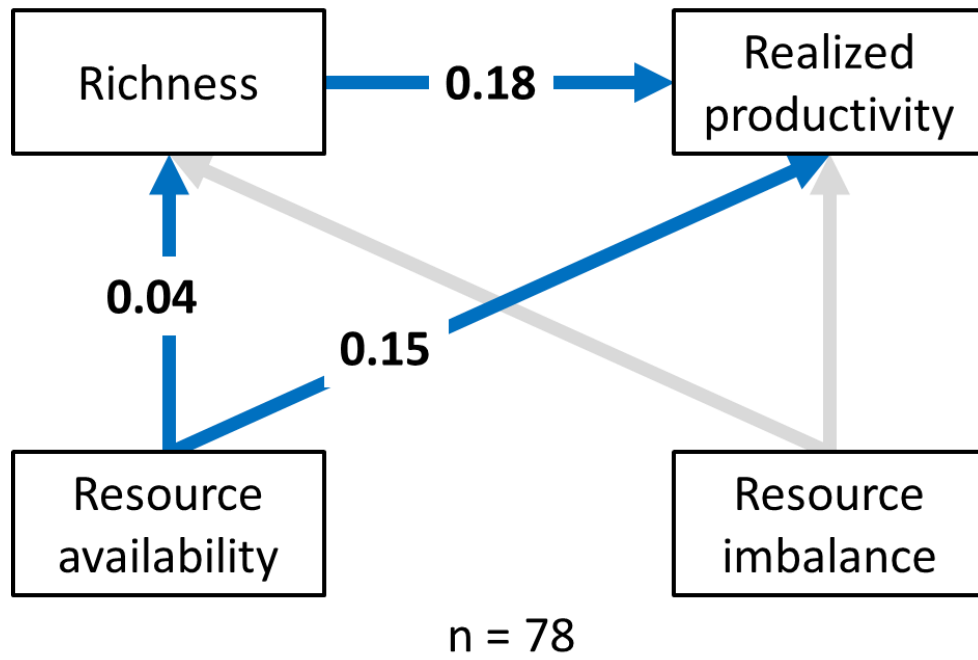


Figure 2.

(A)



(B)

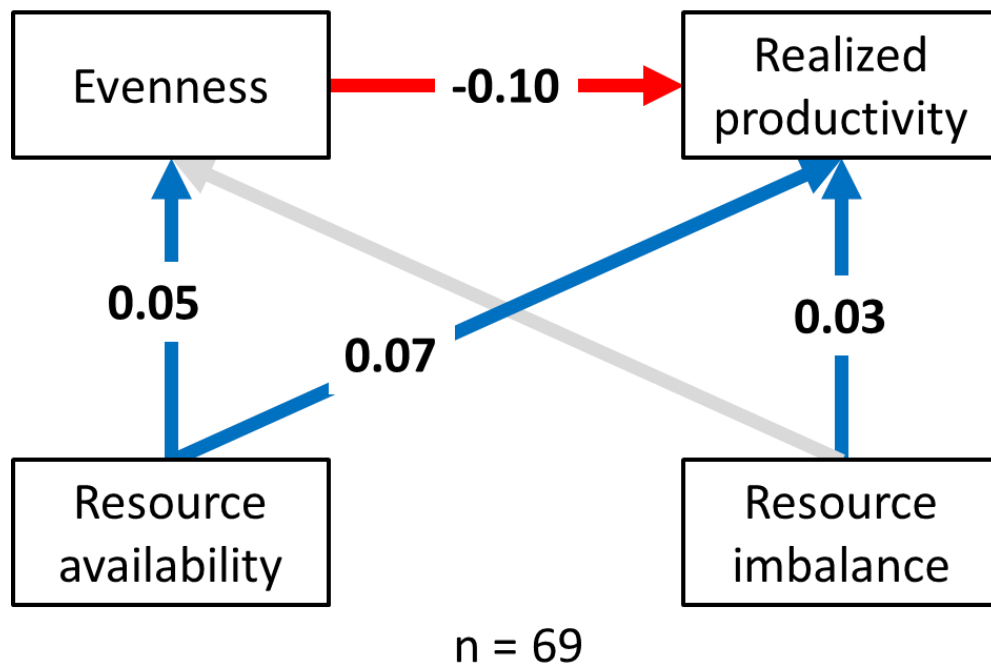


Figure 3

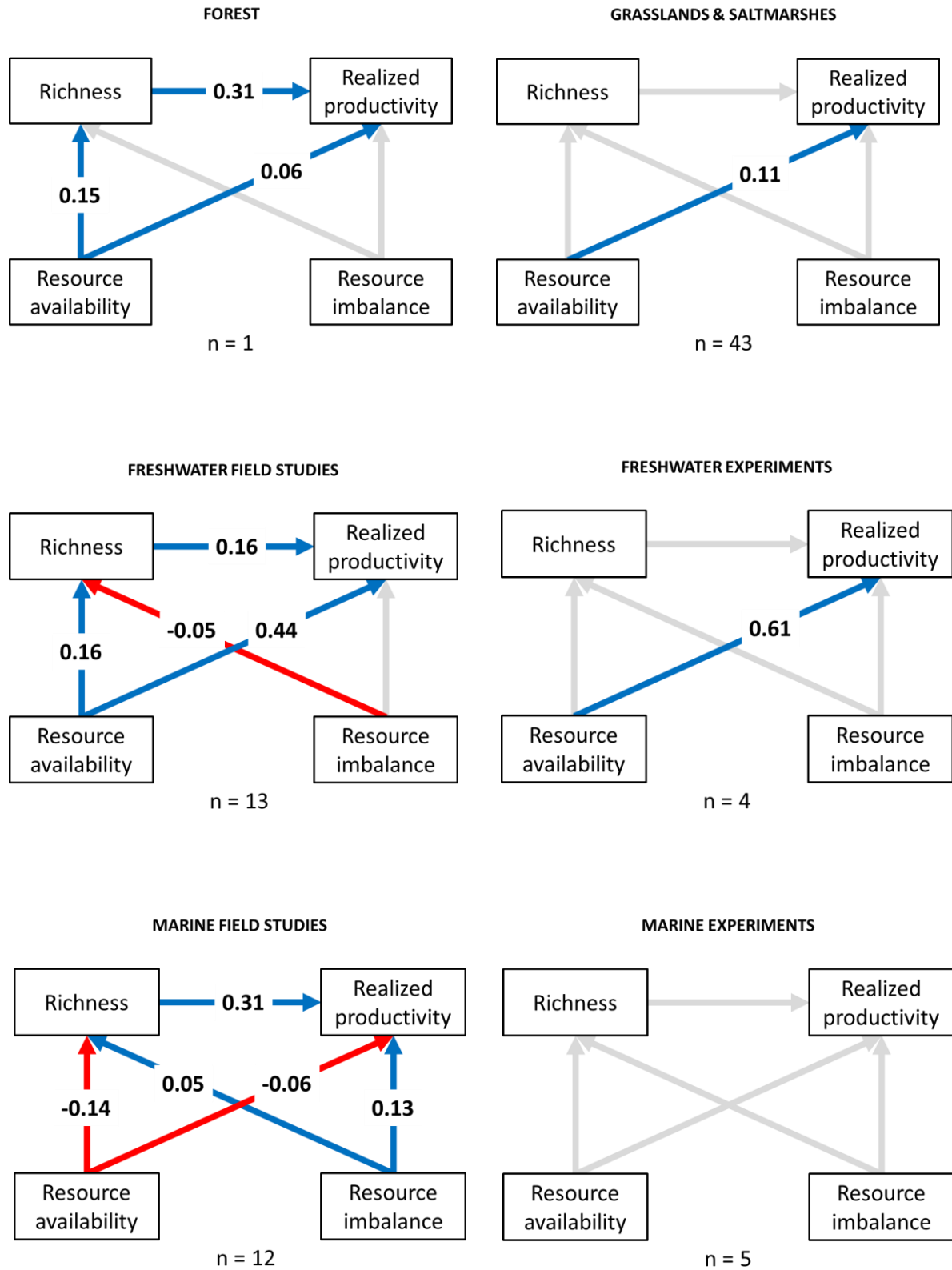


Figure 4.

