Research

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The influence of balanced and imbalanced resource supply on biodiversity–functioning relationship across ecosystems

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Numerous studies show that increasing species richness leads to higher ecosystem productivity. This effect is often attributed to more efficient

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

1. Introduction

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

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

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

Concerning (ii), the evidence that biodiversity not only responds to potential productivity but also influences realized productivity [13,14] negates the relevance of simple bivariate analyses, although they are still commonly used in ecology [8,9]. Instead, multivariate frameworks with resource availability (potential productivity), biodiversity and realized productivity as causally connected components promise greater mechanistic insights regarding biodiversity–productivity relationships. Cardinale et al. [15] developed a structural equation model (SEM) to illustrate a multivariate approach, in which availability of multiple resources is decomposed into two independent components: overall resource availability and the degree of imbalance among these resources. Their suggested framework was tested with a single freshwater phytoplankton dataset, which—as predicted—found increased species richness and biomass with higher resource availability, reduced richness and productivity with increasing resource imbalance, and greater biomass with increasing richness.

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

In this study, we present the first general test of the multivariate framework proposed by Cardinale et al. [15] across ecosystems (marine, freshwater and terrestrial) and approaches (field observational studies and experiments). We combined SEM with meta-analysis, using the analytical framework proposed by Cardinale et al. [15] for each single study and derived the standardized path coefficients as effect sizes for the meta-analysis [26]. In addition to the effects of richness on resource use, we also analysed effects of evenness within the same framework across systems. Our study, which merges the theory of ecological stoichiometry (ES) with the framework of biodiversity–ecosystem functioning (BEF), aims to increase

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 electronic supplementary material (table S1).

study type	ecosystem type	habitat	S	J
field observational				
	terrestrial			
		grassland	41	40
		forest	1	1
		salt marsh	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
total			78	69

the mechanistic understanding of how resource use transfers into primary production.

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

2. Methods

(a) Data sources

We assembled 78 datasets comprising terrestrial, freshwater and marine studies that included information on available resources and producer diversity. This database contains data from published experimental and field observational studies across a broad range of habitats and geographical regions (table 1), amended by the authors' own data. All studies provided the number of species (richness) and 69 studies provided evenness, as Pielou's index [27]. We did not consider experimental studies that manipulated species richness or composition as this could bias our model results, but we included experiments that manipulated resource supply (electronic supplementary material, table S1). To be included in the analysis, studies needed to contain information on total biomass of producers (realized productivity), producer diversity

(at least richness) and supply of at least two resources. From 78 datasets, 46 contained information on the supply of three or more resources, mostly nitrogen, phosphorus and potassium (electronic supplementary material, table S1). Depending on the producer community, realized productivity was measured as concentration of chlorophyll a, biovolume, above-ground plant biomass or total carbon content of the plant tissue. The measurements of resources included photosynthetically active radiation and concentrations of total nitrogen, phosphorus, potassium and other elements in water or soil. The total amount of each element was estimated as the sum of organic and inorganic bioavailable fractions. Electronic supplementary material, table S1 contains information on the resources and the biomass measurement for each study.

(b) Structural equation model

To quantify resource availability and imbalance, we followed the geometrical approach of Cardinale *et al.* [15]. To compare resources, we rescaled resource measurements within each study to have a mean of zero and standard deviation of one. Thus, changes on the multidimensional coordinate system (figure 1) are in units of standard deviation from the mean value of all sampling points within each study. We then defined a reference vector y, where the change in standard deviation of one resource corresponds to the equal change in all other resources on the multi-dimensional coordinate system (figure 1). For two resources, vector y represents the 1 : 1 proportion. No specific stoichiometric requirements (e.g. Redfield ratio of $N : P = 16 : 1$) are considered.

The total amount of resources (resource availability, a) was calculated after Cardinale *et al.* [15] as

$$a = \frac{\sum_{i=1}^{k} r_i y_i}{\|y\|}, \tag{2.1}$$

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

$$\|r\| = \sqrt{\sum_{i=1}^{k} (r_i)^2}. \tag{2.2}$$

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

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

$$b = \begin{cases} \arccos\left(\dfrac{a}{\|r\|}\right) & a \geq 0 \\ 180° - \arccos\left(\dfrac{a}{\|r\|}\right) & a < 0 \end{cases} \tag{2.3}$$

To quantify the direct and indirect effects of resource availability and imbalance on realized productivity, we followed the set of causal relationships proposed by Cardinale *et al.* [15]. In this model, resource availability and imbalance each have a direct as well as indirect impact (mediated through diversity) on the realized productivity. The model was evaluated separately for each study in our dataset using species number (richness) or Pielou's evenness as diversity variables. Model fitting was performed using maximum-likelihood estimation with robust standard errors in the lavaan package [28] of R statistical software (R version 3.1.1., R core development team, 2015). Prior to fitting the model, we tested bivariate relationships between variables to check for nonlinear relationships. Because we found no significant nonlinearities, no polynomial terms were included in the models. For time series, we first fitted
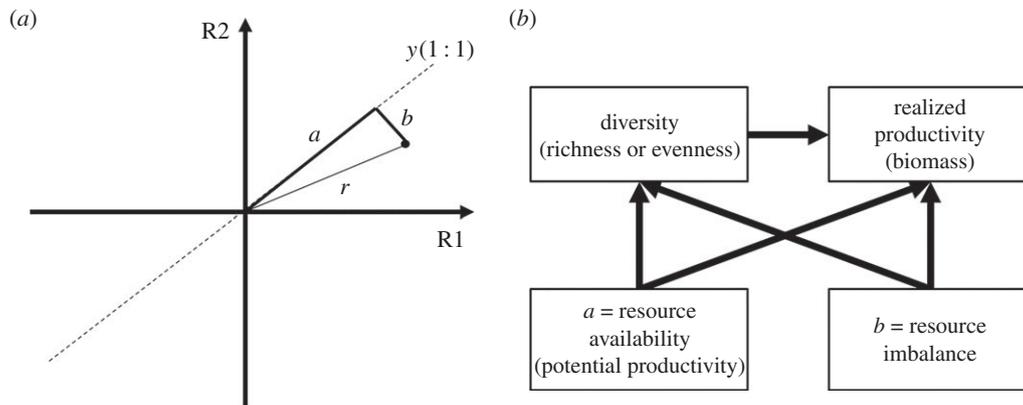
Figure 1. (a) Geometry used to estimate resource availability a and imbalance b. For the sake of simplicity, we present the concept for only two resources (R1 and R2). k number of resources can be included by adding more dimensions. y is the 1 : 1 reference vector and r is the resource vector. (b) Conceptual diagram illustrating causal relationships between resource availability a and imbalance b, diversity, and community biomass. For more detail, see description in text.

autoregressive models to the data and used lagged values in SEM. The relative importance of paths was compared using Fisher's z-transformed standardized coefficients (γ). A chi-square test was used to quantify the overall fit of the model. To enable comparison of all the studies in the meta-analysis, no attempt was made to select a best fitting model. Only the models which were not statistically different from our theoretical model ($p(\chi^2) > 0.05$) were used in the meta-analysis and are illustrated in this manuscript.
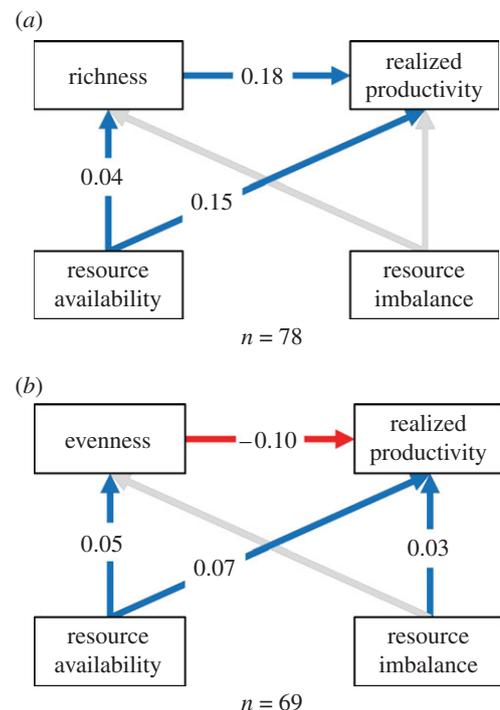
(c) Meta-analysis

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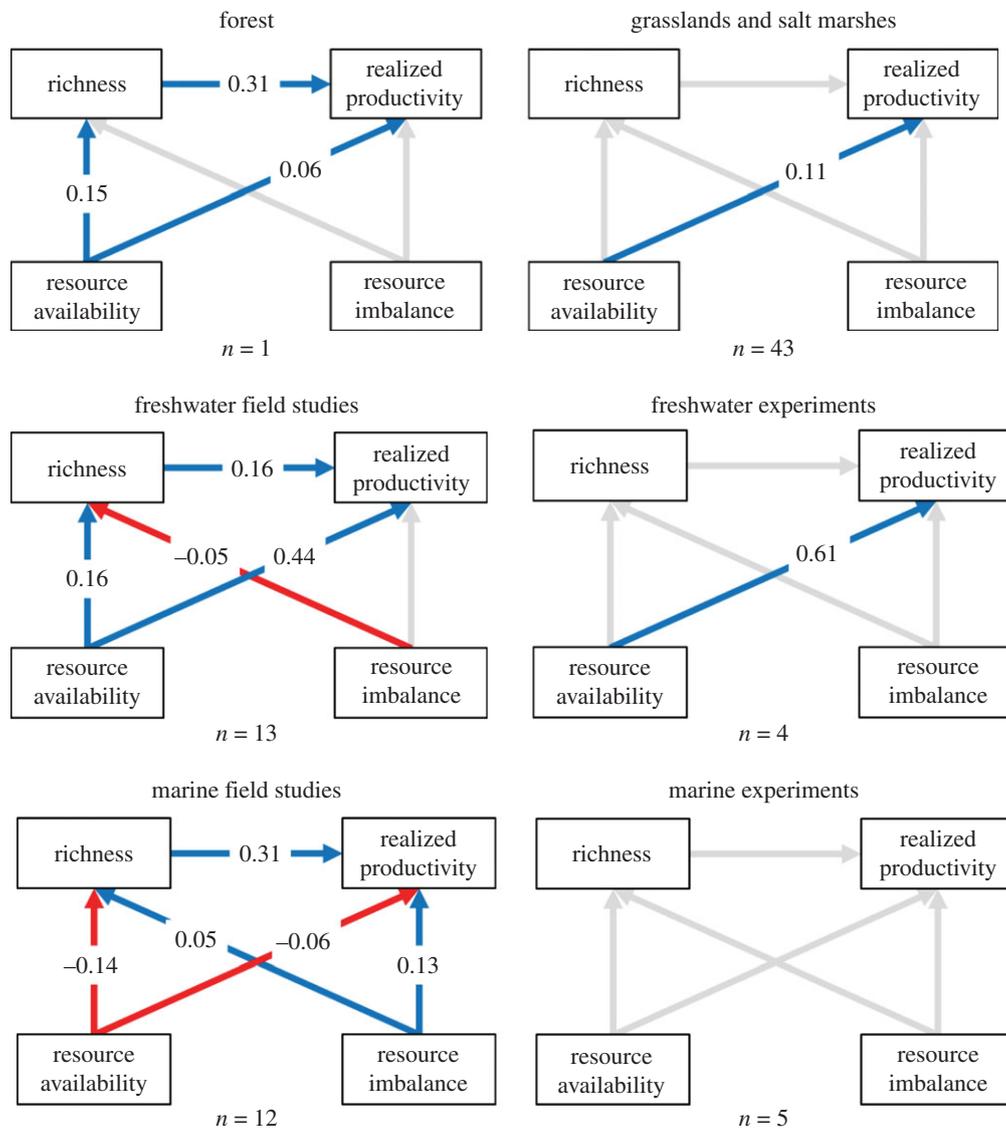
3. Results

(a) Impact of resource availability on diversity and productivity

Overall resource availability directly increased realized productivity (standardized coefficient (γ) = 0.15) and diversity (richness, $\gamma = 0.04$; evenness $\gamma = 0.05$; figure 2). However, these effects were highly variable between the studies. In field observational studies, effects of resource availability on producer biomass (realized productivity) and diversity varied depending on the ecosystem type (figures 3 and 4). In forests, resource availability increased both species richness ($\gamma = 0.15$) and evenness ($\gamma = 0.12$), but it should be stressed that this result is due to a single study (GAM01). In grasslands and salt marshes, resource availability increased realized productivity ($\gamma = 0.11$), but had no effect on richness or evenness. In freshwater ecosystems, higher resource availability led to higher realized productivity ($\gamma = 0.44$) and higher species richness ($\gamma = 0.16$). Surprisingly,

Figure 2. Summary of meta-analysis results for the SEM with richness (a) and evenness (b) over all studies. Effect sizes are shown 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. (Online version in colour.)

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

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Figure 3. Summary of meta-analysis results for the 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. (Online version in colour.)

(b) Impact of resource imbalance on diversity and productivity

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

(c) Interactions between richness and productivity

Overall, richness and realized productivity positively covaried ($\gamma = 0.18$) (figure 2a). However, separating study types (field observational study or experiment) highlighted that the significant effects were found only in field studies. The strongest relationship between richness and biomass production was observed in marine ecosystems (figure 3). The only field study showing a significantly negative effect of richness on productivity ($\gamma = -0.18$, $p = 0.038$) was a study on plants in salt marshes (TREIBSEL, electronic supplementary material, figure S5). In general, no relationship between richness and realized productivity was found in grasslands and salt marshes.

(d) Interactions between evenness and productivity

As predicted, we found an overall negative relationship between evenness and realized productivity ($\gamma = -0.10$) in aquatic and terrestrial studies (figure 2b). The strongest relationship was observed in freshwater (field studies: $\gamma = -0.42$; experiments: $\gamma = -0.38$) and in marine experiments ($\gamma = -0.42$). In contrast, productivity increased with evenness in forests ($\gamma = 0.16$, $p < 0.001$).

4. Discussion

Across ecosystems and study types, the realized productivity of autotrophs was largely influenced by the availability of resources. In observational studies, these effects were either
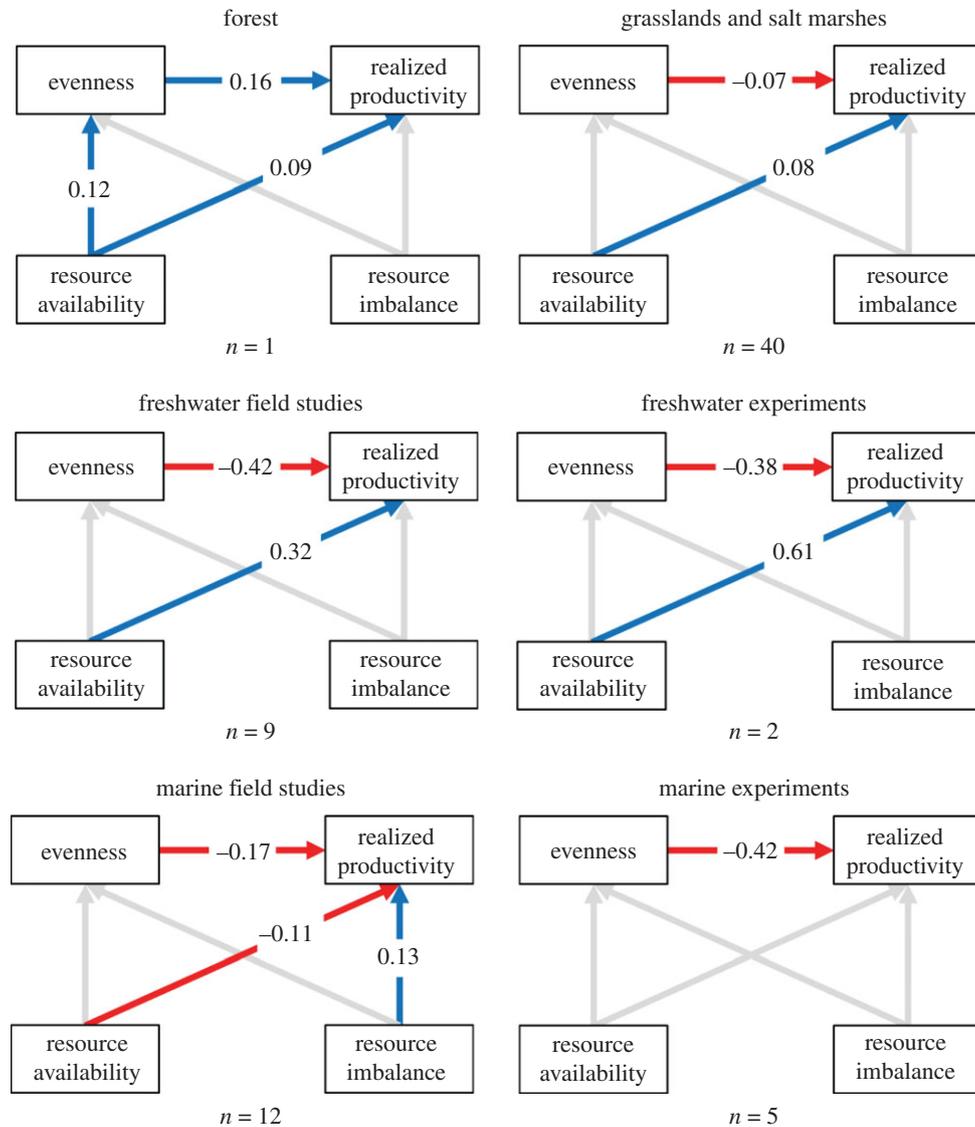
Figure 4. Summary of meta-analysis results for the SEM with evenness (for more detail, see electronic supplementary material, table S2). Shown are effect sizes as standardized path coefficients. n is the number of studies. Blue and red paths are positive and negative relationships, respectively and grey paths are non-significant relationships. (Online version in colour.)

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

Surprisingly, in marine ecosystems, biomass and the number of phytoplankton species decreased with higher resource supply, but increased in response to resource imbalance. These results were largely driven by studies on pelagic ecosystems off the coast of the Netherlands. These coastal waters are generally turbid systems with high proportion of dissolved organic nutrients [31]. Consequently, available nitrogen and phosphorus might be primarily incorporated by heterotrophic microbes and

not by phytoplankton. Including availability of light as one of the limiting resources for phytoplankton growth in turbid waters could change the shape of examined relationships. Contrasting results for phytoplankton at the station L4 in the western English Channel (resource availability → richness, $\gamma = 0.31$, $p < 0.001$; resource availability → realized productivity, $\gamma = 0.28$, $p < 0.001$; non-significant relationships with resource imbalance), which contained information on light availability (electronic supplementary material, table S1), support this interpretation. Station L4 is seasonally stratified and also characterized by lower turbidity than stations along the coast of the Netherlands [32]. These results highlight the importance of light availability for autotrophic growth in ecosystems where nutrients are replete, and suggest that interpretation of the resource supply–productivity relationships in plants, particularly in aquatic systems, might be misleading if the influence of light is not considered [33].

In aquatic experimental studies and unmanipulated grasslands, we found significant relationships between resource availability and realized productivity, but no significant effect of resource availability or imbalances on diversity. These results are broadly consistent with previous meta-analyses; for

example, Elser *et al.* [34] demonstrated that across ecosystems, productivity generally increases with nutrient supply. Although experimental nutrient supply in many ecosystems tends to lead to loss of plant evenness or richness [25], the diversity of unmanipulated grasslands probably arises from many interacting processes (e.g. resource supply, trophic interactions, invasion, etc.) across a broad range of observed soil resources. Thus, in the absence of significantly elevated nutrients, our results demonstrate that grassland diversity is not tightly coupled to soil nutrients. Further, the richness gradients in the aquatic experimental studies might not represent biodiversity of natural communities, thus constraining the responsiveness of diversity to the experimental manipulations [35]. Aquatic communities in experimental studies may suffer from bottle (enclosure) effects, thereby preventing the growth of some species while favouring others, particularly with nutrient amendments. In addition, strong nutrient recycling in closed experimental systems might lead to overestimation of the effects related to enhanced resource supply. In some experiments included in our analysis (electronic supplementary material, table S1), nutrients were added to the system, often in higher proportions and at different ratios than in the natural environment. Other environmental drivers such as turbidity and grazing effects are altered in experiments compared with natural systems [35].

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

The overall negative relationship between evenness and biomass production confirms our hypothesis that most communities are dominated by a few highly productive species; reducing the dominance by these species decreases the realized productivity. Biomass production increased with evenness only in forests, which is consistent with results from a global meta-analysis exploring drivers of diversity–productivity relationships in forests [41]. Higher heterogeneity of functional traits (e.g. shade tolerance, root traits) in more even forest communities might significantly increase complementarity in resource use and consequently productivity [41]. However, our model explained only 10% of the variance in total tree biomass, which again suggests that the measured resources were not the main drivers of the system in this study. Environmental changes such as management for preferred species [42], stand age [43] or differences in soil moisture [44] could be potentially more important factors for shaping tree distribution and biomass.

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

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

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

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

Although our simple model did not account for all potentially influential drivers of diversity–productivity relationships (e.g. consumers, disturbance), our meta-analysis demonstrates that in the natural environment richness significantly affects realized productivity independent of the ecosystem type, although the absolute effect on biomass was weak. However, we found no evidence that evenness is directly related to changes in resource

supply, suggesting that trophic interactions (e.g. herbivory) probably play a key role in shaping the dominance structure of the producer community. We expect that this meta-analysis will stimulate further studies evaluating the importance of evenness for ecosystem functioning.

References

1. Cardinale BJ, Matulich KL, Hooper DU, Byrnes JE, Duffy E, Gamfeldt L, Balvanera P, O'Connor MI, Gonzalez A. 2011 The functional role of producer diversity in ecosystems. Am. J. Bot. 98, 572–592. (doi:10.3732/ajb.1000364)

2. Cardinale BJ, Srivastava DS, Duffy JE, Wright JP, Downing AL, Sankaran M, Jouseau C. 2006 Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature 443, 989–992. (doi:10.1038/nature05202)

3. Gamfeldt L, Lefcheck JS, Byrnes JEK, Cardinale BJ, Duffy JE, Griffin JN. 2015 Marine biodiversity and ecosystem functioning: what's known and what's next? Oikos 124, 252–265. (doi:10.1111/oik.01549)

4. Ptacnik R, Solimini AG, Andersen T, Tamminen T, Brettum P, Lepistö L, Willén E, Rekolainen S. 2008 Diversity predicts stability and resource use efficiency in natural phytoplankton communities. Proc. Natl Acad. Sci. USA 105, 5134–5138. (doi:10.1073/pnas.0708328105)

5. Hillebrand H, Lehmpfuhl V. 2011 Resource stoichiometry and consumers control the biodiversity–productivity relationship in pelagic metacommunities. Am. Nat. 178, 171–181. (doi:10.1086/660831)

6. Fox JW. 2005 Interpreting the 'selection effect' of biodiversity on ecosystem function. Ecol. Lett. 8, 846–856. (doi:10.1111/j.1461-0248.2005.00795.x)

7. Adler PB et al. 2011 Productivity is a poor predictor of plant species richness. Science 333, 1750–1753. (doi:10.1126/science.1204498)

8. Fraser LH et al. 2015 Worldwide evidence of a unimodal relationship between productivity and plant species richness. Science 349, 302–305. (doi:10.1126/science.aab3916)

9. Grace JB, Adler PB, Stanley Harpole W, Borer ET, Seabloom EW. 2014 Causal networks clarify productivity–richness interrelations, bivariate plots do not. Funct. Ecol. 28, 787–798. (doi:10.1111/1365-2435.12269)

10. Grime JP. 1973 Competition and diversity in herbaceous vegetation (reply). Nature 244, 311. (doi:10.1038/244311a0)

11. Mittelbach GG, Steiner CF, Scheiner SM, Gross KL, Reynolds HL, Waide RB, Willig MR, Dodson SI, Gough L. 2001 What is the observed relationship between species richness and productivity? Ecology 82, 2381–2396. (doi:10.1890/0012-9658(2001)082[2381:WITORB]2.0.CO;2)

12. Whittaker RJ. 2010 Meta-analyses and mega-mistakes: calling time on meta-analysis of the species richness–productivity relationship. Ecology 91, 2522–2533. (doi:10.1890/08-0968.1)

13. Gross K, Cardinale BJ. 2007 Does species richness drive community production or vice versa? Reconciling historical and contemporary paradigms in competitive communities. Am. Nat. 170, 207–220. (doi:10.1086/518950)

14. Cardinale BJ, Bennett DM, Nelson CE, Gross K. 2009 Does productivity drive diversity or vice versa? A test of the multivariate productivity–diversity hypothesis in streams. Ecology 90, 1227–1241. (doi:10.1890/08-1038.1)

15. Cardinale BJ, Hillebrand H, Harpole WS, Gross K, Ptacnik R. 2009 Separating the influence of resource 'availability' from resource 'imbalance' on productivity–diversity relationships. Ecol. Lett. 12, 475–487. (doi:10.1111/j.1461-0248.2009.01317.x)

16. Grace JB et al. 2016 Integrative modelling reveals mechanisms linking productivity and plant species richness. Nature 529, 390–393. (doi:10.1038/nature16524)

17. Hautier Y, Niklaus PA, Hector A. 2009 Competition for light causes plant biodiversity loss after eutrophication. Science 324, 636–638. (doi:10.1126/science.1169640)

18. Hillebrand H, Cowles JM, Lewandowska A, Van de Waal DB, Plum C. 2014 Think ratio! A stoichiometric view on biodiversity–ecosystem functioning research. Basic Appl. Ecol. 15, 465–474. (doi:10.1016/j.baae.2014.06.003)

19. Tilman D, Kilham SS, Kilham P. 1982 Phytoplankton community ecology: the role of limiting nutrients. Annu. Rev. Ecol. Syst. 13, 349–372. (doi:10.1146/annurev.es.13.110182.002025)

20. Hillebrand H, Bennett DM, Cadotte MW. 2008 Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. Ecology 89, 1510–1520. (doi:10.1890/07-1053.1)

21. Norberg J, Swaney D, Dushoff J, Lin J, Casagrandi R, Levin S. 2001 Phenotypic diversity and ecosystem functioning in changing environments: a theoretical framework. Proc. Natl Acad. Sci. USA 98, 11 376–11 381. (doi:10.1073/pnas.171315998)

22. Matthiessen B, Mielke E, Sommer U. 2010 Dispersal decreases diversity in heterogeneous metacommunities by enhancing regional competition. Ecology 91, 2022–2033. (doi:10.1890/09-1395.1)

23. Lewandowska AM, Breithaupt P, Hillebrand H, Hoppe H-G, Jürgens K, Sommer U. 2012 Responses of primary productivity to increased temperature and phytoplankton diversity. J. Sea Res. 72, 87–93. (doi:10.1016/j.seares.2011.10.003)

24. Mulder CPH, Bazeley-White E, Dimitrakopoulos PG, Hector A, Scherer-Lorenzen M, Schmid B. 2004 Species evenness and productivity in experimental plant communities. Oikos 107, 50–63. (doi:10.1111/j.0030-1299.2004.13110.x)

25. Hillebrand H *et al.* 2007 Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. *Proc. Natl Acad. Sci. USA* **104**, 10 904–10 909. (doi:10.1073/pnas.0701918104)

26. Grace JB *et al.* 2007 Does species diversity limit productivity in natural grassland communities? *Ecol. Lett.* **10**, 680–689. (doi:10.1111/j.1461-0248.2007.01058.x)

27. Pielou EC. 1966 The measurement of diversity in different types of biological collections. *J. Theor. Biol.* **13**, 131–144. (doi:10.1016/0022-5193(66)90013-0)

28. Rosseel Y. 2012 lavaan: an R package for structural equation modeling. *J. Stat. Softw.* **48**, 1–36. (doi:10.18637/jss.v048.i02)

29. Viechtbauer W. 2010 Conducting meta-analyses in R with the metafor package. *J. Stat. Softw.* **36**, 1–48. (doi:10.18637/jss.v036.i03)

30. Engel EC, Weltzin JF, Norby RJ, Classen AT. 2009 Responses of an old-field plant community to interacting factors of elevated [CO_2], warming, and soil moisture. *J. Plant Ecol.* **2**, 1–11. (doi:10.1093/jpe/rtn026)

31. Van Engeland T, Soetaert K, Knuijt A, Laane RWPM, Middelburg JJ. 2010 Estuarine, coastal and shelf science dissolved organic nitrogen dynamics in the North Sea: a time series analysis (1995–2005). *Estuar. Coast. Shelf Sci.* **89**, 31–42. (doi:10.1016/j.ecss.2010.05.009)

32. Tilstone GH *et al.* 2012 Variability in specific-absorption properties and their use in a semi-analytical ocean colour algorithm for MERIS in North Sea and Western English Channel Coastal Waters. *Remote Sens. Environ.* **118**, 320–338. (doi:10.1016/j.rse.2011.11.019)

33. Brauer VS, Stomp M, Huisman J. 2012 The nutrient-load hypothesis: patterns of resource limitation and community structure driven by competition for nutrients and light. *Am. Nat.* **179**, 721–740. (doi:10.1086/665650)

34. Elser JJ *et al.* 2007 Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecol. Lett.* **10**, 1135–1142. (doi:10.1111/j.1461-0248.2007.01113.x)

35. Brose U, Hillebrand H. 2016 Biodiversity and ecosystem functioning in dynamic landscapes. *Phil. Trans. R. Soc. B* **371**, 20150267. (doi:10.1098/rstb.2015.0267)

36. Gough L, Grace JB, Taylor KL. 1994 The relationship between species richness and community biomass: the importance of environmental variables. *Oikos* **70**, 271–279. (doi:10.2307/3545638)

37. Minden V, Andratschke S, Spalke J, Timmermann H, Kleyer M. 2012 Plant trait–environment relationships in salt marshes: deviations from predictions by ecological concepts. *Perspect. Plant Ecol. Evol. Syst.* **14**, 183–192. (doi:10.1016/j.ppees.2012.01.002)

38. Minden V, Kleyer M. 2015 Ecosystem multifunctionality of coastal marshes is determined by key plant traits. *J. Veg. Sci.* **26**, 651–662. (doi:10.1111/jvs.12276)

39. Waide RB, Willig MR, Steiner CF, Mittelbach G, Gough L, Dodson SI, Juday GP, Parmenter R. 1999 The relationship between productivity and species richness. *Annu. Rev. Ecol. Syst.* **30**, 257–300. (doi:10.1146/annurev.ecolsys.30.1.257)

40. Minden V, Scherber C, Cebrián Piqueras MA, Trinogga J, Trenkamp A, Mantilla-Contreras J, Lienin P, Kleyer M. 2016 Consistent drivers of plant biodiversity across managed ecosystems. *Phil. Trans. R. Soc. B* **371**, 20150284. (doi:10.1098/rstb.2015.0284)

41. Zhang Y, Chen HYH, Reich PB. 2012 Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. *J. Ecol.* **100**, 742–749. (doi:10.1111/j.1365-2745.2011.01944.x)

42. Fedrowitz K *et al.* 2014 Can retention forestry help conserve biodiversity? A meta-analysis. *J. Appl. Ecol.* **51**, 1669–1679. (doi:10.1111/1365-2664.12289)

43. Gamfeldt L *et al.* 2013 Higher levels of multiple ecosystem services are found in forests with more tree species. *Nat. Commun.* **4**, 1340. (doi:10.1038/ncomms2328)

44. Condit R, Engelbrecht BMJ, Pino D, Pérez R, Turner BL. 2013 Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees. *Proc. Natl Acad. Sci. USA* **110**, 5064–5068. (doi:10.1073/pnas.1218042110)

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