

Effects of biodiversity on the functioning of trophic groups and ecosystems

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Over the past decade, accelerating rates of species extinction have prompted an increasing number of studies to reduce species diversity experimentally and examine how this alters the efficiency by which communities capture resources and convert those into biomass^{1,2}. So far, the generality of patterns and processes observed in individual studies have been the subjects of considerable debate^{3–7}. Here we present a formal meta-analysis of studies that have experimentally manipulated species diversity to examine how it affects the functioning of numerous trophic groups in multiple types of ecosystem. We show that the average effect of decreasing species richness is to decrease the abundance or biomass of the focal trophic group, leading to less complete depletion of resources used by that group. At the same time, analyses reveal that the standing stock of, and resource depletion by, the most species-rich polyculture tends to be no different from that of the single most productive species used in an experiment. Of the known mechanisms that might explain these trends, results are most consistent with what is called the ‘sampling effect’, which occurs when diverse communities are more likely to contain and become dominated by the most productive species. Whether this mechanism is widespread in natural communities is currently controversial. Patterns we report are remarkably consistent for four different trophic groups (producers, herbivores, detritivores and predators) and two major ecosystem types (aquatic and terrestrial). Collectively, our analyses suggest that the average species loss does indeed affect the functioning of a wide variety of organisms and ecosystems, but the magnitude of these effects is ultimately determined by the identity of species that are going extinct.

Whereas one of the most striking features of our planet is its great variety of life, one of the most pervasive environmental changes of our time is the global loss of this biological diversity^{8,9}. Considerable uncertainty exists about current rates of extinction, but estimates place it somewhere between two and three orders of magnitude higher than rates found in the fossil record^{10,11}. Biologists have long pondered the environmental effects of species extinction. Even so, it was not until the 1990s that research efforts began to formalize the hypothesis that species diversity might influence the fluxes of energy and matter that are fundamental to all ecological processes, including those that control the abundance, biomass and distribution of organisms. Seminal studies suggested that species loss does, in fact, decrease how productive communities are and how efficiently they capture and consume limited resources^{12–14}. But the interpretation of these studies provoked considerable debate^{3–7}, and subsequent work produced several counterexamples that questioned the generality of these biodiversity effects^{15–19}. As a result, it has been argued that the

consequences of biodiversity loss are likely to be idiosyncratic, differing quantitatively and qualitatively between trophic groups and ecosystems^{20–23}.

After more than a decade of research, a sufficient number of studies have now emerged to permit rigorous testing of whether there are indeed general effects of biodiversity on ecosystem functioning. Here we present a formal meta-analysis of 111 field, greenhouse and laboratory experiments that have manipulated the diversity of species for a wide variety of organisms and ecosystems (see Supplementary Information). We focused on experiments that varied the richness of three or more species in a given trophic group t and measured either of two response variables: the aggregate abundance or biomass of all species in t (referred to as ‘standing stock’) and/or the total amount of resources depleted by t from a known resource pool (see Methods). Data were summarized for four trophic groups: first, microalgal, macroalgal or herbaceous plants assimilating nutrients or water; second, protozoan or metazoan herbivores consuming live algal or herbaceous plant tissue; third, protozoan or metazoan predators consuming live prey; and fourth, bacterial, fungal or metazoan detritivores consuming dead organic matter. Diversity effects were quantified with two complementary metrics. First, for each experiment i , we calculated the proportional difference in the response variable y between the mean value of the most species-rich polyculture \bar{y} and the mean value of these same species grown in monoculture \bar{m} as the log response ratio $LR_m = \ln(y_{\bar{y}}/y_{\bar{m}})$. This unitless metric allows us to test whether there is a significant change in y with increasing richness when averaged across all species used in an experiment. We then calculated a complementary metric that quantifies the proportional difference between the mean value of the most species-rich polyculture and that of the taxon having the highest (lowest) mean value of y in monoculture \bar{m} , as $LR_{\bar{m}} = \ln(y_{\bar{y}}/y_{i\bar{m}})$, where $y_{i\bar{m}}$ is the highest (lowest) value when $LR_m > 0$ (< 0). Testing whether $LR_m > 0$ is analogous to tests for ‘transgressive’ overyielding, which are widely used to assess whether diverse polycultures are any more productive than the single most productive species²⁴.

Our analyses reveal quite general and consistent mean effects of species diversity on the aggregate abundance or biomass of species in a trophic group, with cascading effects on the resources used by that group. For LR_m , we found that species richness positively affected the standing stocks of all four trophic groups considered, increasing the abundance or biomass of plants, herbivores, predators and detritivores (Fig. 1a). Higher diversity within each group was also associated with more complete depletion of resources (Fig. 1b). Experimentally increasing plant, predator and detritivore diversity all led to greater decreases in nutrients/water, prey, and dead organic

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matter, respectively. There was a similar tendency for increasing herbivore diversity to decrease the amount of living plant matter ($P = 0.08$ for a mixed-model analysis of variance; see Methods). In total, 67 of 76 experiments recorded positive values of LR_m for standing stock (88%), and 54 of 70 recorded positive values for resource depletion (77%).

When LR_m was modelled as a function of trophic group, we found no significant difference in the average diversity effect size between the four trophic groups for either response variable (Table 1). Furthermore, we found no significant difference in the average diversity effect size between studies performed in aquatic and terrestrial ecosystems (Fig. 1c, d and Table 1). This degree of consistency is remarkable given that the experiments spanned a wide variety of life forms (bacteria, fungi, plants and animals) and many of Earth's major ecosystems (lakes, streams, oceanic coastal habitat, temperate grasslands and forests; see Supplementary Information). Although studies are certainly not invariable in their conclusions, our results suggest that variation among studies is not consistent with previously proposed differences between trophic levels or ecosystems^{19–22}.

One of the major controversies in biodiversity research concerns the fact that some species exert stronger control over ecological processes than others³. Thus, a primary question when interpreting the average effect of species diversity is whether a diverse polyculture performs any differently than the single 'best' species (that is, the species having the greatest influence over a process). Our analyses show that the standing stock of, and resource depletion by, the most diverse species polyculture is statistically indistinguishable from that of the single species that achieves the highest level of these response variables in monoculture. Specifically, LR_m did not differ from zero for any of the four trophic groups (Fig. 1a, b) or for either of the two ecosystems (Fig. 1c, d). These conclusions hold true even if we apply a liberal test, considering only studies in which $LR_m > 0$ ($P = 0.13$ for standing stock, 0.27 for resource depletion). Of the known mechanisms by which species diversity can affect ecosystem functioning, these results are most consistent with what is called the 'sampling effect' of biodiversity, in which communities comprising more species have a greater chance of being dominated by the most productive

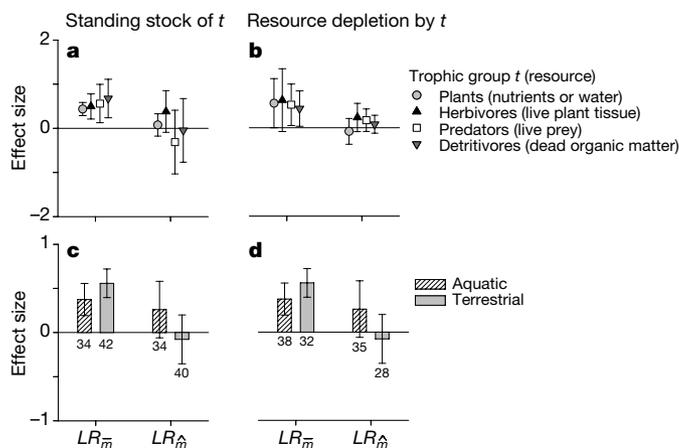


Figure 1 | Effects of species richness on the standing stock abundance or biomass of trophic group t , and the depletion of resources consumed by t . Data are means and 95% CI for two log response ratios that estimate the diversity 'effect size' from experiments. LR_m compares the mean value of the response variable y in a polyculture with the mean value of y for the same species in monoculture. $LR_m > 0$ indicates that more diverse polycultures achieve higher standing stock (a, c) and deplete resources more fully (b, d) than the average monoculture. LR_m compares the mean value of y in a polyculture with that of the species with the highest (for $LR_m > 0$) or lowest (for $LR_m < 0$) mean value of y in monoculture (see the text). $LR_m = 0$ indicates that polycultures perform no differently than monocultures of the most productive species. Results are divided between four trophic groups (a, b) and two ecosystem types (c, d).

taxa. Note, however, that confirmation of this mechanism requires data on the covariance between competitive dominance in polyculture and the performance of species in monoculture^{24,25}—data that are not generally reported. There has been much controversy about whether the sampling effect is best interpreted as a 'real' biological mechanism that operates in nature or as an artefact of experiments that use random draws of species to assemble experimental communities^{1,3,6}. Until this debate is resolved, the relevance of the sampling effect for predicting the functional consequences of extinction is open to debate.

Our use of log response ratios to quantify the effects of species diversity could be criticized on grounds that these ratios compare only two ends of a continuum (highest versus lowest diversity). Because the highest levels of diversity differ between experiments (range 3–72 species) and tend to be higher in studies of terrestrial organisms than in those of aquatic organisms ($t = 4.64$, $P < 0.01$; 12.2 ± 9.6 species for terrestrial studies, 5.4 ± 8.1 for aquatic studies (means \pm s.d.)), it is useful to ask how the general form of the diversity effect changes across levels of species richness. For 57 of 76 experiments that measured standing stock of a trophic group, and 51 of 70 experiments that measured resource depletion, species were manipulated at three or more levels of richness. This allowed us to fit data from each study to the Michaelis–Menten function $Y = Y_{\max}S/(K + S)$, where Y is the standing stock of, or resource depletion by, a trophic group standardized relative to the mean value of all monocultures y_m (that is, $Y = y_s/y_m$ where y_s is the value of y at richness level S). Y_{\max} is therefore the maximum proportion by which Y increases or decreases relative to the average one-species system, and K describes how quickly Y approaches Y_{\max} with increasing diversity. This function was an excellent fit to the data (median $R^2 = 0.84$), and better than several other models (see Methods). Thus, we used maximum-likelihood estimates of Y_{\max} and K to compare key features of the diversity–function curves across systems.

We found no significant differences in Y_{\max} or K between aquatic and terrestrial ecosystems (Fig. 2 and Table 1), which indicates that

Table 1 | Statistical comparison of diversity effect sizes

Variable	Among trophic groups		
	d.f.	F	Pr > F
LR_m			
Standing stock of t	76	0.43	0.73
Resource depletion by t	70	0.09	0.96
LR_h			
Standing stock of t	74	0.98	0.41
Resource depletion by t	63	0.86	0.47
Variable	Among ecosystems		
d.f.	F	Pr > F	
LR_m			
Standing stock of t	76	2.27	0.14
Resource depletion by t	70	0.13	0.72
LR_h			
Standing stock of t	74	3.24	0.08
Resource depletion by t	63	1.62	0.21
Standing stock of t			
Y_{\max}	55	1.93	0.17
K	55	2.74	0.10
Resource depletion by t			
Y_{\max}	50	1.73	0.19
K	50	1.09	0.30

Results for LR_m and LR_h are from separate mixed-model analyses of variance that compare how richness in trophic group t influences the standing stock abundance or biomass of t , and the depletion of resources consumed by t among trophic groups (plants, herbivores, predators and detritivores) or ecosystems (aquatic and terrestrial). LR_m is the log ratio comparing the mean value of the response variable y in a polyculture with the mean value of y for the same species in monoculture. LR_h is the log ratio comparing the mean value of y in a polyculture with that of the species having the highest (for $LR_m > 0$) or lowest (for $LR_m < 0$) mean value of y in monoculture (see the text). Results for Y_{\max} and K compare the maximum-likelihood parameter estimates for curves characterizing the diversity–function relationship (see Fig. 2) in aquatic and terrestrial ecosystems. All F values are non-significant, indicating that the effects of species richness on standing stocks and resource depletion do not differ between trophic groups or ecosystems.

the qualitative form of the diversity–function relationship is consistent across these habitat types (data were insufficient to make similar comparisons among trophic groups). With few exceptions, the curves were positive but decelerating, with values of Y_{\max} being greater than the null expectation of unity (that is, $y_S > y_m$, $t = 14.0$ and $t = 11.9$ for standing stock and resource depletion, respectively, both $P < 0.01$) and values of K being greater than 0 ($t = 6.7$ and $t = 5.5$ for standing stock and resource depletion, respectively, both $P < 0.01$). Asymptotic estimates of Y_{\max} suggest that the most diverse species polyculture would achieve 1.9-fold the standing stock of the average monoculture (95% confidence interval (CI) 1.6–2.2) and 1.8-fold the resource depletion (95% CI 1.5–2.1). Estimates of K indicate that half of the maximum value for both standing stock and resource depletion is achieved by the average species monoculture (mean for standing stock, 0.98 (95% CI 0.68–1.28); mean for resource depletion, 0.89 (95% CI 0.56–1.22)). However, the decelerating nature of these curves suggest that although a small number of species can maintain more than half the function, a disproportionately high number of species is required to maintain functions near maximal values.

Thus, our meta-analysis of 111 experiments conducted over more than a decade reveals two consistent results. First, as researchers have experimentally reduced the richness of species of a variety of organisms inhabiting numerous types of ecosystems, the average effect of diversity loss is to decrease the abundance or biomass of the focal trophic group, leading to less complete depletion of resources used by that group. Second, it is equally general that these average effects of species diversity on ecosystem functioning are best explained by the loss of the most productive species from a diverse community. There are at least two implications of these findings. First, from the perspective of basic research, our results present a new challenge to biologists. A fundamental tenet of biodiversity theory is that species must use resources in different ways to coexist stably^{26,27}. When

species do coexist by such niche differentiation, theory predicts that diverse polycultures will produce more biomass and capture a greater fraction of limited resources than even the ‘best’ species monoculture^{28,29}. The balance of evidence from experiments does not seem to support this, and understanding why there is a divergence between empirical and theoretical conclusions is one of the foremost challenges in this field. It may be that experiments have been performed at smaller spatial or shorter temporal scales than are the focus of theory, or that experiments do not meet equilibrium assumptions of theory. Second, our results re-emphasize a long-standing dilemma in the field of conservation biology—one that must soon be resolved. Biologists have long known that certain species exert much stronger control over ecological processes than others, but predicting which species these are in advance of extinction has proven difficult at best. A key challenge for future research is to detail more accurately how the traits that determine vulnerability to extinction are related to functional dominance in communities. Until that time, our finding that key aspects of ecosystem functioning decline consistently with the average species loss suggests that a precautionary approach to preserving as much biodiversity as possible is warranted.

METHODS

Selection of studies. We searched the literature for studies that experimentally manipulated the richness of three or more species in a given trophic group t and then measured a direct effect of richness on the standing stock of all species in t and/or the total depletion of resources by t . Standing stocks were calculated as the aggregate abundance or biomass of all organisms in t per unit area or volume. Depletion of resources was calculated as an instantaneous rate of consumption (for example, metabolic estimates of consumption of organic matter by bacteria or fungi), the difference between a known initial and a measured final resource concentration (for example, the depletion of soil nitrogen by plants), or the difference between treatments and zero-species controls (for example, the capture of prey by predators). Because our focus was on how richness affects ecosystem functioning at a given moment, we did not include studies focusing on community stability (that is, how diversity affects temporal variation in a dependent variable or invasibility). In all, we reviewed 184 papers, amassing data from digitized figures or tables or by acquiring original data from the authors of 58 studies reporting results from 111 experiments that met our criteria (see Supplementary Information).

Analyses of the diversity ‘effect size’. We used two log response ratios to quantify the diversity effect size in each experiment (see the text for the equations). LR_m was used to characterize the mean effect of diversity, testing whether the average of all replicates from the highest diversity treatment was different from the average response of these same species when grown in monocultures. In contrast, $LR_{\bar{m}}$ was used to test whether the average response of the highest diversity treatment was any different from that of the species having the highest (if $LR_m > 0$) or lowest (if $LR_m < 0$) value in monoculture. Two or more replicates of each monoculture were run for 59 of 63 experiments that measured resource depletion (94%), and 62 of 74 experiments measuring standing stock (84%). For these, we used the average value of replicates in our calculation of LR_m . For the small remainder of studies that had only $N = 1$ replicate for each monoculture, we used the point estimate.

Log ratios are the most widely used metrics in meta-analyses for two reasons: first, they estimate a proportional difference between treatments that can be readily compared between studies, and second, they have sampling properties that are known to be normal and that are robust to bias from small sample sizes³⁰. Mixed-model analyses of variance were used to test whether log response ratios differed from zero and to compare the mean values of these response ratios between trophic groups and ecosystem types. The general statistical model was $y_i = \mu + \tau_i + b_i + \varepsilon_i$, where y_i is LR_m or $LR_{\bar{m}}$ for each response variable, τ_i is a fixed categorical effect (trophic group or ecosystem type), b_i is the random effect associated with experiment i (with errors that are distributed normally and independently, $N[0, \sigma_b^2]$), and ε_i is the residual error. An important decision in meta-analyses is whether to standardize effect sizes by the variance of an experiment, giving greater weight to studies with higher ‘certainty’. We performed analyses with and without weighting, and these led to identical conclusions. Here we present unweighted results because these allow the more realistic, but also more variable, field studies to have the same influence on our conclusions as greenhouse and laboratory studies that tend to have higher replication and smaller variance.

Curve fitting. To characterize the general form of diversity–function relationships, we fit data from each study to three nonlinear functions that have

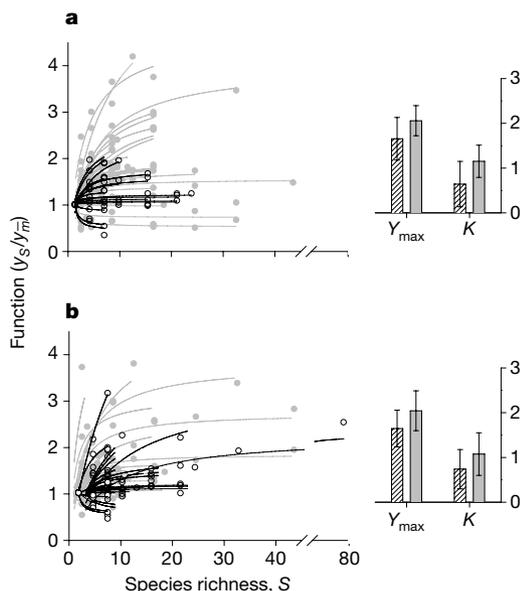


Figure 2 | The general form of the diversity–function relationship. Effects of species richness on the standing stock abundance or biomass of trophic group t (a), and the depletion of resources consumed by t (b). Each curve corresponds to data from a single study fitted to $Y = Y_{\max}S/(K + S)$, where Y is the proportional change in the dependent variable with increasing richness S , Y_{\max} is the asymptotic estimate of Y , and K is the value of S at which $Y = Y_{\max}/2$. Sample sizes are 18 and 27 aquatic (black circles and lines), and 37 and 23 terrestrial studies (grey circles and lines) in a and b, respectively. Insets show the mean and 95% CI for the maximum-likelihood parameter estimates (hatched, aquatic; grey, terrestrial).

previously been used in the literature (log, power and hyperbolic). The Michaelis–Menten version of the hyperbolic function was the best-fitting model for the majority of studies (44% compared with 35% for power and 21% for log functions), and had the highest explanatory power (mean $R^2 = 0.71$, median 0.84). However, all three functions led to identical conclusions. For data fitted to the power function $\log(y) = m\log(S) + b$, m was positive (function increases with diversity, 95% CI 0.15–0.32 for standing stock and 0.11–0.29 for resource depletion) and did not differ between aquatic and terrestrial studies ($P > 0.26$ for both). For the log function $Y = b + m\log(S)$, m was positive (95% CI 0.25–0.66 for standing stock and 0.20–0.49 for resource depletion) and did not differ between aquatic and terrestrial studies ($P > 0.25$ for both).

Received 8 July; accepted 5 September 2006.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

Acknowledgements We thank S. Gaines, H. Hillebrand, M. Huston, J. Hille Ris-Lambers, J. Levine, J. Melack, B. Starzomski, D. Tilman and D. Wardle for comments that improved this manuscript. This work was supported by grants from the US National Science Foundation and is a product of the BioMERGE diversity-synthesis network.

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