

Biodiversity effects in the wild are common and as strong as key drivers of productivity

J. Emmett Duffy¹, Casey M. Godwin² & Bradley J. Cardinale²

More than 500 controlled experiments have collectively suggested that biodiversity loss reduces ecosystem productivity and stability^{1–3}. Yet the importance of biodiversity in sustaining the world's ecosystems remains controversial^{4–8}, largely because of the lack of validation in nature, where strong abiotic forcing and complex interactions are assumed to swamp biodiversity effects^{6–9}. Here we test this assumption by analysing 133 estimates reported in 67 field studies that statistically separated the effects of biodiversity on biomass production from those of abiotic forcing. Contrary to the prevailing opinion of the previous two decades that biodiversity would have rare or weak effects in nature, we show that biomass production increases with species richness in a wide range of wild taxa and ecosystems. In fact, after controlling for environmental covariates, increases in biomass with biodiversity are stronger in nature than has previously been documented in experiments and comparable to or stronger than the effects of other well-known drivers of productivity, including climate and nutrient availability. These results are consistent with the collective experimental evidence that species richness increases community biomass production, and suggest that the role of biodiversity in maintaining productive ecosystems should figure prominently in global change science and policy.

Human well-being depends strongly on the interacting web of living species, so much so that we take this for granted³. Food, fuel, clean water, oxygen, disease control and other services essential for human life are products of biological processes performed by the variety of living organisms that inhabit natural and managed ecosystems. Yet it was not until the 1990s that accelerating declines in wild species sparked a concerted effort to answer the question: how do changes in biological diversity affect the way ecosystems function and the goods and services they provide to humanity? A surge of research stimulated by this question took environmental science in a different direction¹⁰, generating new models and more than 500 experiments showing how genetic, species and functional diversity influences the functioning of ecosystems^{1–3}. Meta-analyses of this work have now demonstrated that experimental systems with multiple species are on average 50% more efficient and productive than single-component species, and are better at delivering many essential goods and services^{2,3}.

Like any transformative idea, the notion that biodiversity drives ecosystem functioning was controversial. Critics argued that early experiments did not adequately control for confounding variables^{4–6}, which led to improved designs and analyses in subsequent research^{3,11–13}. Even with these improvements, some experts remained concerned that experiments are too small in scale, too short in duration and too unrealistic in conditions to be meaningful in the real world^{6–9}. Sceptics suggested that, although biodiversity affects ecosystem processes in simplified experiments, similar effects are unlikely to occur in nature, or will be weak compared to the well-documented abiotic control of ecosystem productivity and stability^{5–9}. Resolving these issues has been hampered by inadequate understanding of how biodiversity

affects functioning of 'real-world' ecosystems. Such understanding requires analysis of field communities varying in both diversity and environment to statistically isolate the effects of biodiversity from those of other environmental drivers^{14,15}.

Here we present a synthesis of 133 estimates reported in 67 empirical studies that measured biodiversity and the functioning of natural ecosystems at 623,464 sampling locations around the world (Fig. 1). These studies then used recent analytical advances to quantify the effects of species or functional diversity on ecosystem functioning after statistically controlling for environmental covariates (see Methods). We focus on community biomass and production as ecosystem functions, because these are the response variables most frequently measured in past experiments, and they are fundamentally important for nearly all ecosystem goods and services. Our data synthesis addressed three questions: First, are the effects of biodiversity on biomass production detectable in natural systems and, if so, are they consistent with predictions from experiments and corresponding theory? Second, are the effects of biodiversity in natural systems comparable in magnitude to those estimated in small-scale, controlled experiments? Finally, how do the effects of biodiversity compare to effects of other major environmental drivers of ecosystem biomass production?

First, our study shows that higher biodiversity is commonly associated with higher biomass production in natural ecosystems and that the positive association is more, not less, likely to be statistically significant when environmental covariates are controlled for (Fig. 2a). This finding runs counter to a common criticism of field studies linking biodiversity to productivity, which is that correlations between species richness and community biomass might arise spuriously as side effects of environmental conditions that simultaneously enhance both diversity and productivity⁵. If this covariate hypothesis were true, apparent biodiversity effects should weaken or disappear when environmental drivers are accounted for; yet our analysis shows the opposite. Among studies that did not account for covariates, 69% detected a significant relationship between biodiversity and ecosystem functioning (Fig. 2a, black bars), whereas this proportion increased to 82% when environmental covariates were statistically controlled (Fig. 2a, grey bars). Note, however, that only a fraction of individual studies estimated biodiversity effects both before and after accounting for covariates, and some reported multiple estimates (for example, multiple response variables). Both of these issues lead to unequal sample sizes in Fig. 2a and potential non-independence of data. To account for non-independence, we ran 10,000 randomizations that selected a single estimate from each study and recalculated the proportions of studies showing significant diversity effects with and without accounting for covariates. This resampling test confirmed that a significantly higher proportion of diversity effects were detected after accounting for covariates ($P=0.04$, Supplementary Fig. 1).

Second, we found that in 75% of studies the relationship between richness and biomass production was positive when controlling for covariates, with most increasing monotonically (Fig. 2b and inset).

¹Tennenbaum Marine Observatories Network, Smithsonian Institution, 647 Contees Wharf Road, Edgewater, Maryland 21037, USA. ²School for Environment and Sustainability, University of Michigan, 440 Church Street, Ann Arbor, Michigan 48109, USA.

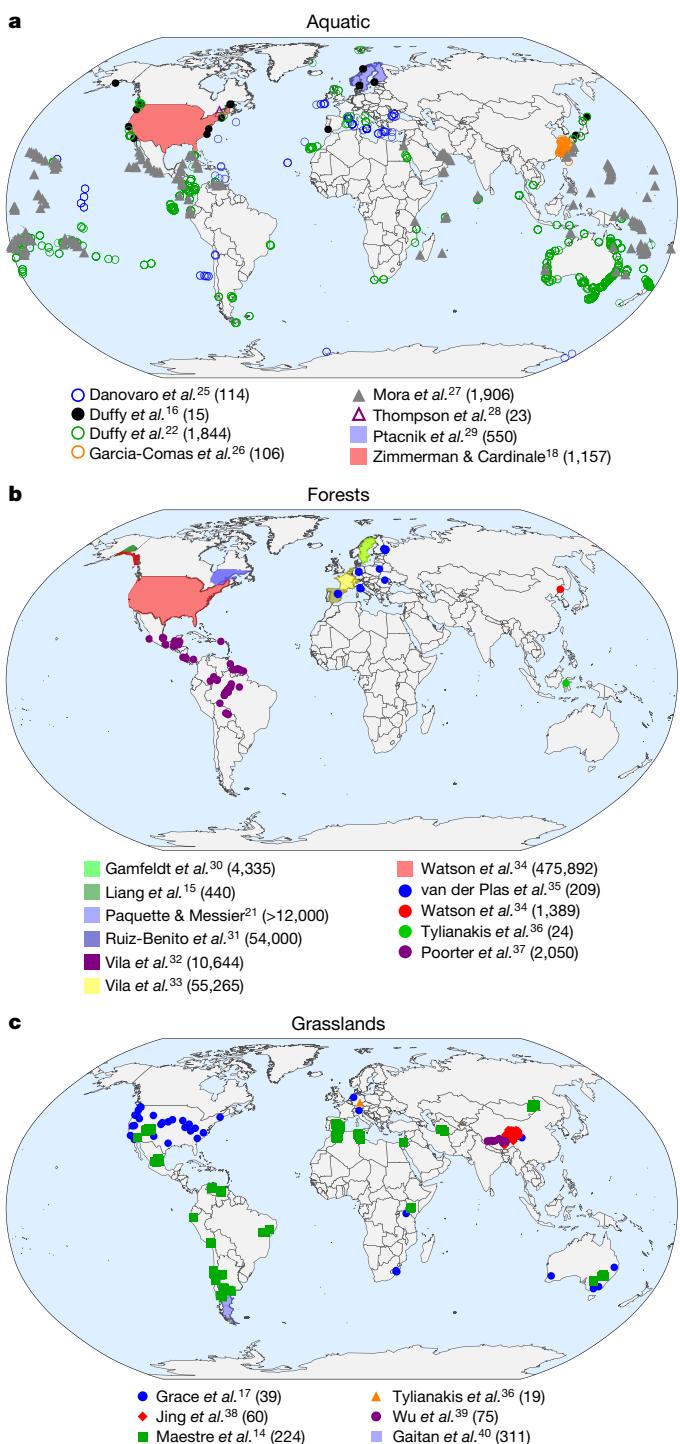


Figure 1 | Distribution of observational field studies used in our analysis. **a–c**, Studies focused on algal and consumer diversity in freshwater and marine ecosystems (**a**), tree diversity in forests (**b**) or herbaceous plant diversity in grasslands (**c**). These three categories encompass 63 out of 67 studies analysed. The number in parentheses after each study is the number of sites that the study included. The studies^{25–40} are listed in Supplementary Table 1 and are shown as symbols for individual or closely neighbouring sites, and as shaded regions where numerous sites are located within a limited geographic area.

These results match a priori predictions of ecological theory as well as the results of most experiments. Again using a resampling approach, the proportion of studies showing positive effects of diversity was significantly higher among studies that controlled for environmental covariates (Fig. 2b and Supplementary Fig. 2, bootstrapped $P=0.02$,

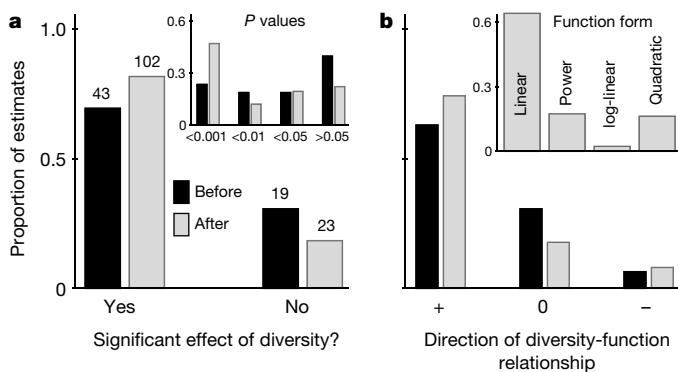


Figure 2 | Biodiversity effects on community biomass production are widespread in nature, and more robust when covariates are accounted for. **a**, Proportions of field studies in which the effect of diversity on biomass was significant ($P<0.05$) before (black) and after (grey) accounting for environmental covariates. Inset, distribution of studies by P value. Numbers above bars denote the number of studies in each category. **b**, Proportions of studies with positive, neutral or negative diversity effect when covariates were not (black) and were (grey) accounted for. Inset, proportions of studies with different forms of the richness–productivity relationship.

whereas non-significant effects were fewer ($P=0.03$) and negative effects remained unchanged ($P=0.33$). Therefore, not only do observational studies qualitatively mirror the results of past biodiversity experiments, but the agreement between observations and experiments also increases after environmental covariates are accounted for.

Finally, we analysed the strength of biodiversity effects on biomass production in nature. The effects of species richness on biomass production have often been analysed differently in experiments and meta-analyses (log ratios of response in high compared to low richness treatments) versus field observations (regressions across a range of richness), complicating efforts to compare them directly. However, we were able to extract comparable measurements of biodiversity effect sizes from a subset of experiments and observational field studies for four specific cases: (1) effects of algal richness on production of phytoplankton biomass; (2) effects of herbaceous plant richness on grassland biomass; (3) effects of forest tree species richness on tree production; and (4) effects of invertebrate herbivore richness on algal biomass in marine eelgrass systems. Biodiversity effects in natural ecosystems proved stronger than those documented in controlled experiments for all four comparisons (Fig. 3 and Extended Data Figs 1, 2). In part, this result was driven by the broader range of diversity considered in observational studies compared with experiments (blue circles, Fig. 3). However, even after we restricted the observational data to match the levels of species richness used in experiments, observational studies (blue diamonds) continued to show stronger effects of biodiversity than did experiments (Fig. 3).

Given that natural ecosystems commonly show stronger associations of biodiversity with biomass production than those documented in experiments, we investigated how important biodiversity is compared to abiotic drivers of global change. We were able to identify 28 observational field studies reporting 65 estimates in which authors simultaneously quantified statistical effects of biodiversity and climatic variables (usually temperature) on biomass or productivity, and 10 studies with 22 estimates that simultaneously quantified effects of biodiversity and nutrient availability (usually nitrogen). When studies statistically separated their effects, biodiversity ranked higher in effect size than climate variables in 51% of field estimates, and higher than nutrient-related variables in 64% of estimates (Fig. 4). These results remained robust after accounting for non-independence of data (resampling test, Supplementary Fig. 3). Because the observational studies spanned different latitudinal and longitudinal ranges, the range of abiotic covariates is not directly comparable among all studies. However, we note that several studies that were conducted at continental to global

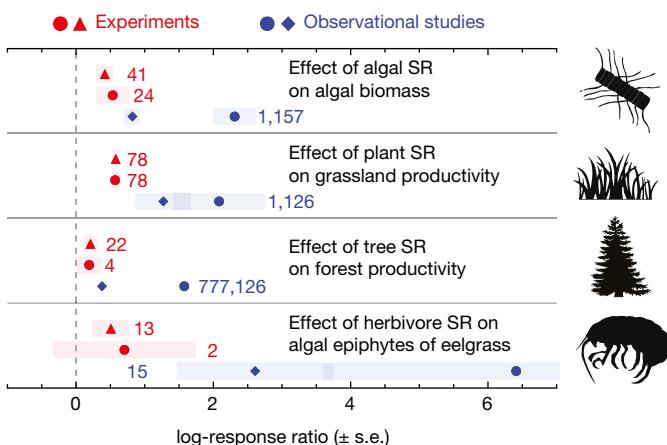


Figure 3 | Comparison of diversity effects on biomass production in observational versus experimental studies. Mean effect sizes are from experiments (red) and observational studies after accounting for covariates (blue). Observational estimates are calculated from the full dataset (circles) and over the narrower range of species richness (SR) used in experiments (diamonds). Triangles show log-response ratios calculated directly from experiments with ≥ 2 levels of species richness (without fitting a power function), whereas red circles show log response ratios calculated from the fitted power function. Numbers of experiments or sites included are shown. Horizontal bands denote standard errors. Extended Data Figs 1 and 2 show direct estimates of β and illustrate derivation of estimates, respectively.

scales nevertheless found effects of biodiversity comparable to or stronger than those of climate^{16–19}.

Because of the long history of scepticism that species diversity affects productivity of natural ecosystems, the strength and consistency of results presented here were unanticipated. In every case we found the opposite of long-standing views expressed in the ecological literature^{4–6,8,9}. Ecosystems with high species richness commonly had higher biomass and productivity in observational field data from a wide range of taxa and ecosystems, including grassland plants, trees, lake phytoplankton and zooplankton, and marine fishes. Observed positive associations of biodiversity with production in nature were stronger when covariates were accounted for, stronger than biodiversity effects documented in controlled experiments, and comparable to or stronger than associations with climate and nutrient availability, which are arguably two of the strongest abiotic drivers of ecosystem structure and functioning, as well as major global change drivers. Our results also corroborate findings of a recent synthesis of experimental data reporting that biodiversity effects are comparable in magnitude to major drivers of global change²⁰, and extend related conclusions based on observational data from forests¹⁵ and dryland plants¹⁴ to a broad range of ecosystems.

For more than two decades, arguments have persisted about whether species diversity causally affects ecosystem functioning or merely responds to environmental forcing, such as variation in climate and resources that control ecosystem fertility. This debate fostered further arguments about whether biodiversity effects that have been documented in experiments also occur in nature and, if so, whether they are important or trivial. These questions have remained unresolved, in part because isolating causality without the gold standard of manipulative experiments is notoriously difficult in systems with complex, interacting and often nonlinear forcing¹⁷. All studies included in our synthesis used statistical approaches designed specifically to isolate effects of diversity after controlling for the effects of confounding environmental covariates^{17,21,22}. Moreover, all studies included here involved diversity gradients that were established by natural community assembly processes, refuting the long-standing argument^{6,8,9} that diversity effects on productivity are artefacts of the random species combinations used in experiments. As is true of all analyses based on

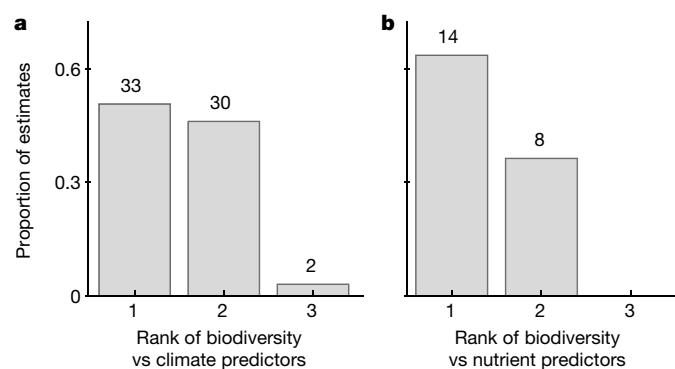


Figure 4 | Biodiversity effects on biomass production are comparable to or greater than those of climate and plant resources. **a, b,** The proportion of studies where biodiversity (species richness or functional diversity) ranked first, second or third in importance relative to climate-related variables (a) or plant nutrients (b) as predictors of biomass or productivity in general linear models of observational field data. Relative importance rank was estimated from standardized effect sizes (see Methods). Numbers above bars show the number of studies in each category.

non-experimental data, we cannot definitively exclude the possibility that the studies we reviewed missed some important environmental variable(s) that increases diversity and production in parallel, thereby generating a spurious (non-causal) correlation between them. But we consider it unlikely that a generation of field ecologists has failed to consider the major drivers of biomass production in the ecosystems they study and know well. A more realistic limitation of our synthesis is that, with very few exceptions (for example, ref. 17), available studies have not addressed the potential for feedbacks among species richness, biomass and environmental drivers, such as resources. Such feedbacks might generate more complex associations between diversity and productivity, and evaluating how they operate in nature is a frontier for future research.

In summary, the accumulated weight of evidence, including the consistency of findings across taxa and systems, the match of results to predictions of theory, and the consistency of results with those of hundreds of experiments, collectively supports the conclusion that biodiversity has a major role in sustaining the productivity of Earth's ecosystems. Integration of this perspective into global change policy is increasingly urgent as Earth faces widespread and potentially irreversible losses and invasions of species, which are already changing ecosystems^{23,24}.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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Supplementary Information is available in the online version of the paper.

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Author Contributions J.E.D. conceived the idea, developed it with B.J.C., and drafted the paper with conceptual and editorial input from all authors. All authors collated the data and contributed to the analyses. C.M.G. drafted the figures.

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METHODS

Data collection. We assembled all the published empirical studies that we could find that used field observational data to quantify the effect of biodiversity on community biomass or productivity while statistically accounting for one or more environmental covariates. To locate these studies, we used an online search of the ISI Web of Science database using the keyword sequence: *diversity AND ecosystem* AND (function* OR service* OR multifunctionality). This search returned 20,820 papers published on or before 31 December 2016 (our cut-off for this study). We read through the titles and/or abstracts of each paper to identify studies that met three criteria for inclusion. (1) The study used some measurement of biodiversity (for example, taxonomic richness, Shannon diversity, phylogenetic diversity, and so on) as a causal variable to predict biomass or production. Studies that considered biodiversity only as a response variable, for example, responding to variation in climate or resources, but where biodiversity was not tested as a potential cause of biomass production, were not included in this synthesis. (2) The study used observational data collected in an un-manipulated (not experimental) ecosystem. (3) The study statistically controlled for the influence of environmental covariates to isolate and quantify the unique contribution of biodiversity. When the same or substantially overlapping datasets had been analysed and reported in more than one paper (for example, refs 17,41), we used the most recent paper. The final dataset used in our study included 25 papers that reported results of 67 independent studies (for example, those performed at different locations, that is, sites, surveys or plots) with a total of 133 estimates (for example, studies often quantified multiple metrics of biodiversity and/or response variables). This full dataset, along with explanations of studies that were not included, is given in Supplementary Table 1. In addition to these observational studies, which form the basis of our primary analyses, we also provide the 154 additional experimental studies used to compare effect sizes (Fig. 3 and Extended Data Fig. 1).

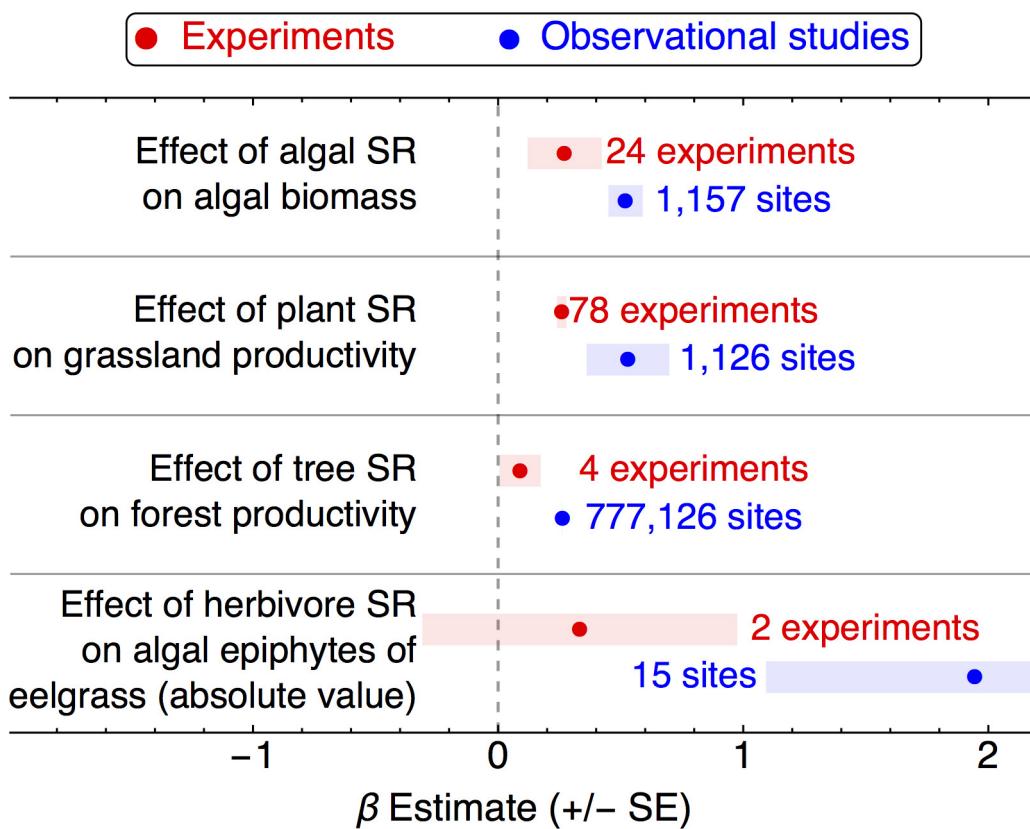
For those studies that included climate-related and/or nutrient-related predictors in modelling biomass or productivity, and that reported these effects in comparable (standardized) units, we compared the relative importance of these predictors with the effects of biodiversity. Depending on the study, relative effect sizes were based on standardized partial regression coefficients, values of the Akaike Information Criterion reported in a comparison of alternative models, the proportion of variation explained by each predictor in a boosted regression tree¹⁹ or a relative importance index defined as the 'sum of the Akaike weights of all models that included the predictor of interest, taking into account the number of models in which each predictor appears'¹⁴. The dataset used in our analyses is provided in Supplementary Table 1.

Data analysis. Several studies identified in our initial search used model selection to screen out less influential environmental variables before the main analysis, biasing the intended comparison of biodiversity versus abiotic drivers. Other studies included as predictors the abundance of particular dominant species, which are components of biodiversity and thus tend to reduce the influence of richness as a separate predictor and to generally confound the separation of biodiversity from environmental influences. For these reasons, our analyses focused on the subset of studies that allowed a cleaner comparison of species-richness effects against those of climate and plant nutrients, for which there are accepted theoretical arguments and empirical evidence for influence on biomass and productivity.

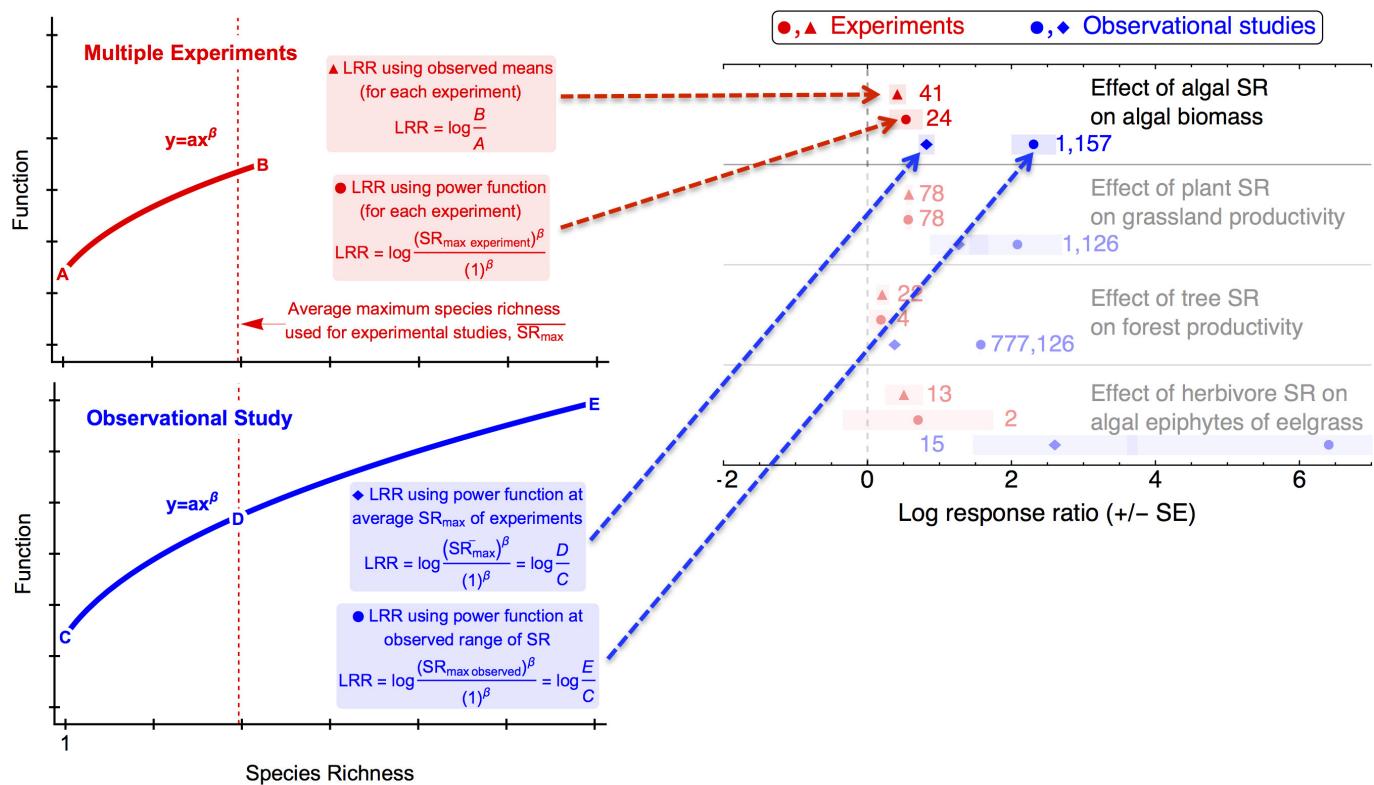
To compare the magnitude of effect sizes in comparable experiments and field observational datasets, we located four collections of studies for which both sufficient experimental and observational data were available. These focused on pelagic freshwater algae¹⁸, grassland plants¹⁷, forest trees¹⁵, and eelgrass herbivores and epiphytic algae¹⁶. Most experiments reported effect size as the log ratio of response in the highest-richness treatment over the mean response in the single-species treatments. To obtain a comparable metric from the observational studies, we computed the log-response ratio by evaluating β in the power function $y = ax^\beta$ where x is species richness and y is biomass or production (using unstandardized estimates), for the highest and lowest level of species richness observed in the survey and for a monoculture (see Extended Data Fig. 2 for a complete explanation). Because the range of species richness observed in the observational studies exceeded that of the experiments, we also computed the log-response ratio for each observational study using the maximum species richness used in the corresponding experiments. To control for non-independence of data from the same experimental study, we estimated the mean effect size and the associated standard error using a mixed model in which study was incorporated as a random effect. When all of the estimates were from independent experiments, we calculated the mean and standard error without incorporating a random effect. The observational studies used for this comparison are listed in Supplementary Table 1. Note that the study in ref. 15 was the largest forest study with estimates of β for a power function, and was therefore included in Fig. 3. It was not included in other analyses (Figs 1, 2, 4), because of overlap with other forest studies.

Data availability. The authors declare that the data supporting the findings of this study are available in Supplementary Table 1.

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Extended Data Figure 1 | Comparison of diversity effect sizes on biomass production in observational versus experimental studies, using directly comparable analyses. Symbols show mean effect sizes as β in the power function $y = ax^\beta$ where x is species richness (SR) and y is biomass or production. Horizontal bands denote the standard error of the parameter estimate.



Extended Data Figure 2 | Schematic diagram explaining how log-response ratios (LRR) were calculated for experimental (red) and observational studies (blue). The top diagram illustrates the calculation for a single experiment; these calculations were then repeated for multiple

experiments and summarized in Fig. 3. The bottom diagram illustrates the calculation for a single observational study. Horizontal bands denote the standard error of the mean log response ratio.

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