LETTER

A global synthesis reveals biodiversity loss as a major driver of ecosystem change

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Evidence is mounting that extinctions are altering key processes important to the productivity and sustainability of Earth's ecosystems[1–4]. Further species loss will accelerate change in ecosystem processes[5–8], but it is unclear how these effects compare to the direct effects of other forms of environmental change that are both driving diversity loss and altering ecosystem function. Here we use a suite of meta-analyses of published data to show that the effects of species loss on productivity and decomposition—two processes important in all ecosystems—are of comparable magnitude to the effects of many other global environmental changes. In experiments, intermediate levels of species loss (21–40%) reduced plant production by 5–10%, comparable to previously documented effects of ultraviolet radiation and climate warming. Higher levels of extinction (41–60%) had effects rivalling those of ozone, acidification, elevated CO_2 and nutrient pollution. At intermediate levels, species loss generally had equal or greater effects on decomposition than did elevated CO_2 and nitrogen addition. The identity of species lost also had a large effect on changes in productivity and decomposition, generating a wide range of plausible outcomes for extinction. Despite the need for more studies on interactive effects of diversity loss and environmental changes, our analyses clearly show that the ecosystem consequences of local species loss are as quantitatively significant as the direct effects of several global change stressors that have mobilized major international concern and remediation efforts[9].

A variety of global changes are driving rates of species extinction that greatly outpace background rates in the fossil record[10,11]. If these trends continue, projections suggest that within 240 years Earth may face the sixth mass extinction[12]. Such projections have prompted hundreds of experiments examining how different components of biodiversity affect ecosystem processes that sustain the provisioning of goods and services to society. Syntheses of these experiments have made it clear that plant biodiversity loss will reduce plant production and alter decomposition[5,6]. However, it is uncertain how the sizes of these effects compare with the direct effects of other types of environmental change, such as changing atmospheric composition, climate warming and nutrient pollution, that also threaten ecosystem functioning[13–15]. This uncertainty has generated wide-ranging speculation about how strongly biodiversity loss might affect humanity[16,17].

Here we report the results of a large data synthesis in which we compared the effects of species loss against other drivers of environmental change. We focus on primary production and decomposition because these major biological processes influence carbon storage and other ecosystem services, and illustrate the breadth of sensitivity of ecosystem processes to changes in species richness[2,6,18]. We took two approaches in our analyses. First, we statistically summarized existing meta-analyses that have estimated the mean effect size of experimental manipulations of a variety of environmental changes on primary production (biomass production by plants) and decomposition (mass loss of plant litter) in a variety of ecosystems around the world (Tables 1 and 2). We compared these environmental effect sizes to the estimated effects of species loss derived from a database we constructed using 192 peer-reviewed publications on experiments that manipulated species richness and examined the effects on ecosystem processes (see Methods). This approach allows comparison among a wide range of environmental changes, but has the limitation that it evaluates the effects of environmental and diversity changes measured by different researchers using different organisms and ecosystems. To complement our summary of meta-analyses, we also summarized the results of 16 experiments that simultaneously manipulated plant species richness in factorial combination with some other environmental change (elevated CO_2, nutrient pollution, etc). Although a far smaller data set, analysis of factorial experiments allowed two additional comparisons: (1) effect sizes of diversity loss versus other environmental changes, within experiments focusing on identical ecosystems; and (2) effect sizes of diversity loss under current versus projected environmental conditions. We assessed a breadth of projections of local species loss because estimates vary widely for magnitudes of global species extinctions (Supplementary Table 1). Similarly, species losses at local scales most relevant to biodiversity and ecosystem functioning (BEF) experiments and ecosystem services (m^2 to watersheds) probably do not bear a one-to-one relationship with global extinctions (complete loss of a species from the planet) and may respond nonlinearly to multiple environmental changes[10,19,20].

Our analyses suggest that biodiversity loss in the 21st century could rank among the major drivers of ecosystem change. Experiments to date have shown that effects of plant species richness on biomass production are nonlinear and saturating (Fig. 1). Our analysis suggests that in areas where local species loss this century falls within the lower range of projections (1–20%), negligible effects on biomass production will result, and changes in species richness will rank low relative to the effects projected for other environmental changes (Fig. 1 and Table 1). Where actual losses fall within intermediate projections (21–40%), however, species loss is expected to reduce biomass production by 5–10% below the most diverse mixtures (based on exponentiation of log response ratios (LRR): $e^{-0.05} = 0.951$, $e^{-0.107} = 0.898$). This effect is comparable in magnitude to the effects of ultraviolet radiation and climate warming on plant production (Fig. 1 and Table 1).

Where losses fall within higher projections of extinction (41–60%), the effects of species loss rank with those of many other drivers of environmental change, such as warming, ozone and acidification (Fig. 1). The mid-point of this range, fifty per cent species loss, is a benchmark at the upper end of 21st century projections of global extinctions, but is a common estimate at the local scale in heavily-affected

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Table 1 | Effects of species richness and environmental changes on primary productivity for the broad meta-analysis and factorial diversity crossed with environment experiments.

Factor	Broad meta-analysis				Factorial experiments			
	N_S, N_{obs}	LRR	LCI	UCI	N_S, N_{obs}	LRR	LCI	UCI
Primary producer diversity								
50% loss	60, 145	−0.144	−0.175	−0.112	10, 15	−0.168	0.104	−0.439
Avg. mono.	73, 299	−0.332	−0.378	−0.285	16, 30	−0.458	−0.259	−0.658
Best mono.	62, 241	0.159	0.116	0.203	13, 29	−0.136	0.067	−0.338
Other factors								
Acidif.	1, 12	−0.186	−0.342	−0.020				
+Ca	1, 31	0.351	−0.105	0.820	1, 1	0.256	−0.781	1.293
+CO$_2$	6, 3076	**0.217**	**0.207**	**0.227**	3, 5	0.070	−0.400	0.539
Drought	1, 20	−0.616	−0.892	−0.342	3, 5	0.215	−0.255	0.686
+N	6, 2895	**0.310**	**0.192**	**0.428**	+N-med 3, 13	0.155	−0.155	0.466
					+N-high 2, 21	0.434	0.165	0.703
+N +CO$_2$	1, 252	**0.694**	**0.622**	**0.766**				
+N +P	1, 941	**0.964**	**0.894**	**1.034**	5, 8	0.586	0.215	0.958
+Ozone	4, 2162	**−0.149**	**−0.161**	**−0.137**				
+P	2, 766	**0.239**	**0.175**	**0.302**	1, 1	1.216	0.177	2.254
Plant inv.	1, 144	**0.514**	**0.447**	**0.581**				
+Ultraviolet	2, 432	**−0.082**	**−0.107**	**−0.057**				
Warming	1, 1064	0.116	0.078	0.154	1, 1	−0.529	−1.568	0.510

N_S, total number of studies—references listed in Supplementary Table 2, except for diversity effects for the broad meta-analysis which come from the database on biodiversity and ecosystem functioning (BEF) experiments[6]; N_{obs}, total number of observations across all meta-analyses or experiments; LRR, log response ratio; LCI, lower 95% confidence interval; UCI, upper 95% confidence interval. Bold values indicate bootstrapped mean LRRs and confidence intervals in the broad meta-analysis (see Supplementary Fig. 2). Treatment factors: 50% loss; Avg. mono., average monoculture; Best mono., best monoculture (see Methods for calculation of LRRs). In all of these, negative values indicate that species loss causes a decline in productivity rates. Acidif., acidification; Ca, calcium; CO$_2$, carbon dioxide; N, nitrogen (for terrestrial N addition, 'low' rates were $\leq 3\,\mathrm{g\,m^{-2}}$ (no such factorial experiments), medium (med.) were > 3 and $\leq 15\,\mathrm{g\,m^{-2}}$, and high were $> 15\,\mathrm{g\,m^{-2}}$); P, phosphorus; Plant inv., plant invasion.

landscapes that have experienced $>90\%$ habitat loss[21]. A 50% species loss is expected to reduce biomass production by an average of 13% ($e^{-0.144}$; Table 1), an effect consistent across terrestrial, freshwater and marine ecosystems (Supplementary Fig. 1). For comparison, elevated CO_2 experiments have produced greater overall magnitudes of changes in biomass ($+24\%$). This average, however, combines studies performed in diverse natural systems as well as in agricultural monocultures. Experiments performed in multi-species communities have shown the effects of CO_2 on production of $+12$–13% (ref. [22], Supplementary Fig. 2, Tot$_{multi}$ under Elevated CO_2)—on par with projected effects of 50% species loss. Similarly, the average effect of nitrogen (N) on plant biomass production depended on N addition rates. Rates of N addition similar to intensive agricultural fertilization had effects on production ($+54\%$ for factorial experiments) that were greater than those of intermediate or high levels of species loss. However, the magnitude of effects of high species loss on production was comparable to those of intermediate ($+17\%$; Table 1) or low (rare in terrestrial experiments, Supplementary Fig. 3)[23] rates of N addition. Thus, the magnitude of the effects of high species loss on production also seems to be comparable to those of increased nitrogen deposition, a well-recognized environmental problem[24,25].

To rival the environmental changes that have had the greatest documented effect on primary production (for example, heavy nutrient pollution, invasive species, drought), species loss would need to exceed that of prior mass extinctions ($\geq75\%$ species loss). This scenario is unlikely to be realized globally in the coming century, but could occur for some types of organisms (for example, vertebrates) within 240–540 years if current rates of extinction continue[12]. It may also occur for a variety of organisms at local scales where human activities heavily affect land use. If such a scenario were realized for plants, biomass production in natural systems would be expected to decline by an average of one third, exceeding the effects of all other environmental changes except invasive species, drought and interactions among multiple pollutants (N, P, CO_2) applied in combination (Fig. 1). However, uncertainty around the effects of extinction grows large as the fraction of species loss increases, in part because the identity and biological traits of surviving species have an increasingly large effect on biomass production. The importance of species identity is most apparent from examining extreme cases where experiments reduce diverse communities to single species. Whereas the average effect of reducing diversity to a monoculture is a 28% loss in production, the distribution ranged from -68% to $+62\%$ of production compared to the most diverse mixture. Similarly, if one can conserve the most productive monocultures, these outperformed the most diverse mixtures by an average 17%, but ranged from -40% to $+132\%$ (Table 1; Supplementary Discussion, Productivity section). These values span the range of plausible effects for nearly all other environmental changes, and underscore the large variation in possible outcomes of extinction that can result from functional differences among species and ecosystems[4].

Table 2 | Effects of species richness and environmental changes on decomposition from the broad meta-analysis.

| Factor	N_S, N_{obs}	LRR	LCI	UCI	Response variable
Litter diversity					
50% loss	24, 39	0.023	−0.062	0.108	Mixed
Avg. mono.	31, 67	0.034	−0.130	0.199	Mixed
Best mono.	21, 39	0.266	0.153	0.378	Mixed
Consumer diversity					
50% loss	22, 52	−0.074	−0.155	0.008	Mixed
Avg. mono.	22, 55	−0.235	−0.359	−0.111	Mixed
Best mono.	19, 49	−0.056	−0.190	0.077	Mixed
Other factors					
+CO$_2$	1, 101	−0.020	−0.041	0.010	Mass loss
Eutrophication	1, 6	0.250	−0.180	0.660	Microbial breakdown rate
Plant inv.	2, 62	**0.729**	**0.677**	**0.782**	Decomposition rate, microbial breakdown rate
Acidification	1, 5	−0.830	−1.600	−0.520	Microbial breakdown rate
+N	2, 520	**−0.023**	**−0.046**	**0.000**	Decomposition rate, mass loss

Abbreviations as in Table 1. Response variable, biomass types and response variables used to calculate LRR value. Mixed: microbial respiration rate, decomposition rate, mass loss rate, feeding rate. Bold values indicate bootstrapped mean LRRs and confidence intervals.
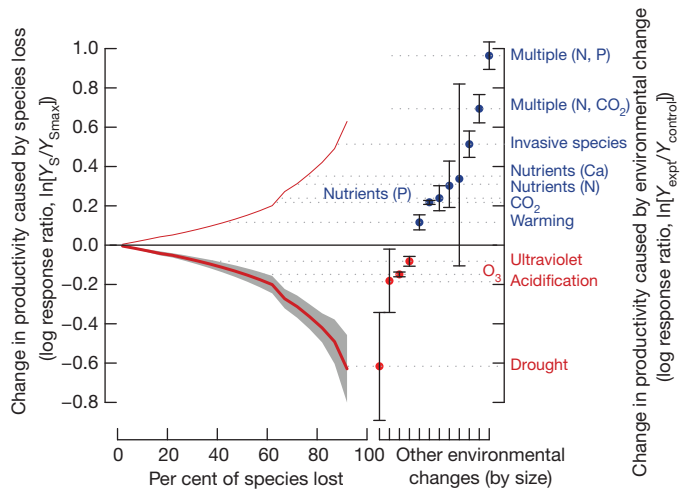
Figure 1 | Changes in primary production as a function of per cent local species loss. Effects of species loss on primary production from 62 studies (379 observations). Thick red line, lower productivity as species richness decreases; grey bands and black error bars, 95% confidence intervals. The thin red line shows the inverse of the thick red line to allow comparison of effect magnitudes with environmental changes with positive effects. Dotted grey lines show the mean effect of each environmental change for comparison with the effect of richness. Right axis, effects of other environmental changes. Blue is for increases and red for decreases in productivity (Table 1 and Supplementary Table 2).

Analysis of experiments that manipulated species richness in factorial combination with other environmental changes generally reinforced our conclusions from the broader meta-analysis (Table 1; Supplementary Discussion, Productivity section). Within intermediate projections of species loss (21–40%), the effects of species loss on plant biomass production equalled or exceeded the effects of elevated CO_2, and rivalled the effect of drought (Table 1 and Supplementary Fig. 4). Interactions between species loss and environmental changes are important for understanding net effects on ecosystem processes, because both will often occur simultaneously (environmental changes rank among the major drivers of species loss[13,26,27]). We compared the effects of species loss (average monoculture metric) under experimental conditions with the effects of species loss under control environmental conditions to investigate potential interactions between these drivers of ecosystem processes (Supplementary Figs 5 and 6). The available evidence indicates that diversity effects were independent of many environmental changes (interactions were not detectably different from zero). The exception was N addition, which led to smaller average effects of diversity under elevated than control conditions ($P = 0.043$, when weighted by n; Supplementary Fig. 5). However, the scarcity of studies meant we found three or fewer experiments for any change other than fertilization. Clearly, this is a critical topic for future research.

Both environmental changes and species loss had smaller effects on decomposition than on production. However, the effects of consumer species loss on decomposition were comparable to the effects of some major forms of environmental change. Loss of litter consumer richness reduced decomposition rates by ~8% for mid-ranges of projected extinction, giving rise to effects that were comparable in magnitude to elevated CO_2 (-2%) and nitrogen pollution (-2%), although smaller than the effects of multiple nutrient addition in aquatic systems, acidification and plant invasion (Fig. 2 and Table 2). The effects of consumer loss were more pronounced and consistent in freshwater, where the majority of experiments have taken place[6], than in terrestrial ecosystems (-12% versus -7%, respectively, for a 50% loss scenario, Supplementary Fig. 1). In contrast to the effects of consumer species loss, loss of litter diversity did not alter average rates of decomposition (Fig. 2 and Table 2; Supplementary Discussion, Decomposition section). Because species loss reduced primary productivity more than
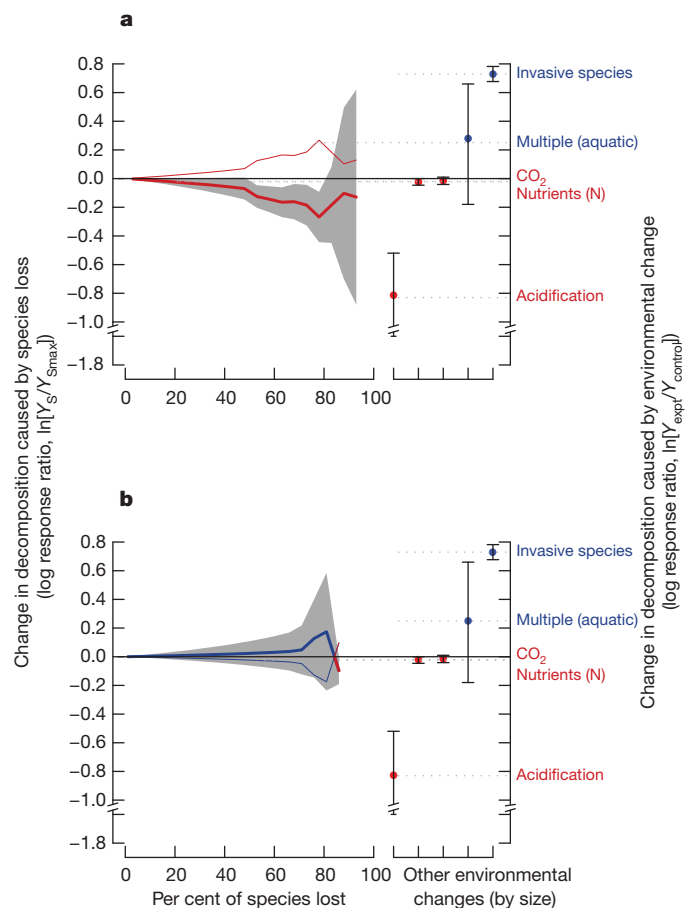
Figure 2 | Changes in decomposition as a function of per cent local species loss. a, Effects of detrital consumer diversity on decomposition from 19 studies (54 observations). **b**, Effects of plant litter diversity on decomposition from 22 studies (60 observations). Thick red lines, slower decomposition rates as species richness decreases; thick blue lines, higher decomposition rate as species richness decreases; grey bands and black error bars, 95% confidence intervals. Thin coloured lines, dotted grey lines, axes and colour coding as in Fig. 1. See also Table 2 and Supplementary Table 3.

decomposition, future species loss could limit the capacity for carbon uptake and storage in the biosphere[18].

In summary, we have shown that species loss ranks among the major drivers of primary production and decomposition—key processes involved in the carbon cycle and the provisioning of many ecosystem services[11,18]. Refining these estimates for key ecosystem services will require a better understanding of how realistic extinction scenarios interact with other forms of environmental change in influencing multiple ecosystem processes[4,16,26]. Even so, the range of effects caused by species loss spanned the range of plausible outcomes for nearly all other drivers of environmental change. And the average effects of local extinction were comparable in magnitude to numerous other global change stressors that have already mobilized major international concern and remediation efforts. As such, our study provides a quantitative basis for integrating consequences of species loss into assessments to be conducted by the Intergovernmental Science Policy Platform for Biodiversity and Ecosystem Services[28].

METHODS SUMMARY

To quantify how species loss affects primary production and decomposition, we used the database of ref. 6 that summarized 192 studies (574 experiments) through 2009 that manipulated species richness and measured the effects on ecosystem processes. We extracted experiments describing (1) how species richness of primary producers influenced producer biomass and (2) how primary producer or consumer richness affected decomposition of litter. We then calculated two log response

ratios (LRRs) for each experiment: $\ln(Y_{Avemono}/Y_{Smax})$ and $\ln(Y_{Bestmono}/Y_{Smax})$ where Y_{Smax} was production or decomposition in the most diverse mixture in an experiment, $Y_{Avemono}$ is the average value of the monocultures, and $Y_{Bestmono}$ is the value in the most productive or fastest decomposing monoculture (for considerations, see Methods and Supplementary Discussion[29]). When possible, we also fit data from each study to a power function $\ln(Y_S/Y_{Smax}) = a + b \times \ln(S)$. Parameter estimates were used to produce the nonlinear species loss curves in Figs 1, 2 and Supplementary Fig. 4, and the 50% loss scenario in Tables 1 and 2.

To gather data on how other forms of environmental change affect production and decomposition, we searched the ISI Web of Science for published meta-analyses (see Methods). From each paper or publicly available data set[23], we extracted response ratios ($RR = Y_{expt}/Y_{control}$, where Y_{expt} is the response variable in the experimental treatment), number of studies, and estimates of variance (Data Thief III, Version 1.5). We calculated the overall mean LRR and 95% confidence interval for each treatment via bootstrapping using skew normal distributions[30].

We also identified 16 factorial experiments to directly compare productivity LRRs for diversity to other forms of environmental change in the same experiment. Where manipulations either reduced or enhanced resources, we changed the sign of the LRRs to allow comparison to the broader meta-analysis. We analysed LRRs using mixed models in SYSTAT v.12, with environmental change as a fixed effect and study as a random effect.

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

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

Author Contributions All authors contributed to the design of the study, data interpretation and manuscript editing; B.J.C. and K.L.M. developed the database of biodiversity and ecosystem functioning experiments; D.U.H., E.C.A., J.E.K.B., B.J.C. and K.L.M. collected additional data and performed statistical analyses. E.C.A., J.E.K.B., B.J.C., B.A.H. and D.U.H. drafted the figures and D.U.H. wrote the initial draft.

Author Information The biodiversity and ecosystem functioning database is deposited with the National Center for Ecological Analysis and Synthesis (http://knb.ecoinformatics.org/knb/metacat/nceas.984/nceas). Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of this article at www.nature.com/nature. Correspondence and requests for materials should be addressed to D.U.H. (hooper@biol.wwu.edu).

METHODS

Biodiversity and ecosystem functioning database. To quantify the effects of species loss on biomass production and decomposition, we used the data set of ref. 6. This data set summarizes 192 peer-reviewed papers published through 2009 reporting results from 574 experiments that manipulated species richness and measured the effects on various ecosystem processes. We extracted the subset of experiments that examined (1) how species richness of primary producers influenced producer biomass accumulation and (2) how richness of producer litter, or richness of litter consumers, affected decomposition rates (Tables 1 and 2). For multi-year studies, we used only data from the last year as this was least likely to be influenced by transient responses. For each experiment, we calculated two log response ratios (LRRs): $\ln(Y_{Avemono}/Y_{Smax})$ and $\ln(Y_{Bestmono}/Y_{Smax})$ where Y_{Smax} was production or decomposition in the most diverse mixture in an experiment, $Y_{Avemono}$ is the average value of the monocultures, and $Y_{Bestmono}$ is the value in the most productive or fastest decomposing monoculture. Both LRRs quantify the net effect of species loss going from the most to least diverse communities, but differ in their assumptions about the sequence of extinction. For productivity only, best monoculture values were restricted to communities where increasing plant diversity increased production (that is, where the average monoculture LRR was positive)[6]. Statistical issues may bias the effects of best monocultures[29]; because this topic is controversial, however, we use the best monoculture metric primarily to illustrate the range of potential process responses, particularly in heavily managed ecosystems.

Log ratios like those described above are frequently used to summarize diversity effect sizes[6], in part because they can be calculated for most experiments. However, these metrics represent extreme scenarios of local diversity loss that are not likely to be realized in many natural communities. Therefore, we also ran a more comprehensive analysis on the subset of experiments that included at least three levels of species richness. For these experiments, we fit the mean value of the response at each level of richness S to the power function: $\ln(Y_S/Y_{Smax}) = a + b \times \ln(S)$. Prior meta-analyses lend much stronger support to saturating models of diversity effects (for example, Michaelis–Menten or power functions) compared to linear or exponential fits[6]. We used the power function here because it gave a good fit and provided a balance between simplicity and generality (mean $R^2 = 0.71$ for productivity and 0.30 for decomposition, compared to mean $R^2 = 0.73$ and 0.29 for Michaelis–Menten). After obtaining parameter estimates for each experiment, we calculated the effect of species loss on production and decomposition across all levels of per cent loss that we could interpolate within an individual experiment. We calculated the log response ratio $\ln(Y_S/Y_{Smax})$ at 5% increments of species loss, where Y_S is the value at S species ($<S_{max}$). The distribution of log ratios was estimated by bootstrapping, and means and 95% confidence intervals were plotted in Fig. 1. The 50% loss scenario in Tables 1 and 2 came from these estimates.

Meta-analysis comparison. To quantify how other forms of environmental change have an effect on production and decomposition, we collated data published in past syntheses and data analyses. These studies typically manipulated abiotic conditions consistent with accepted scenarios of environmental change for the factors at hand (for example, doubling of atmospheric CO_2, ref. 9; Supplementary Fig. 2).

Productivity: we searched ISI Web of Science for meta-analyses that examined the effects of global change factors on biomass production (search terms: [product* AND meta-analysis] OR [biomass AND meta-analysis]). Because more recent meta-analyses often have extensive reference overlap with earlier meta-analyses of the same environmental effect, we only used meta-analyses published after 2005 to maximize independence across studies. We found 18 meta-analyses summarizing 67 LRRs showing how various aspects of environmental change influence primary production in marine, freshwater and terrestrial ecosystems (Supplementary Table 2). LRRs were calculated as ln(mean treatment biomass/ mean control biomass). From each meta-analysis, we extracted the LRR, number of observations, and the associated error measurement from text, tables or digitized figures (Data Thief III, Version 1.5), or calculated them directly where data were freely available[23].

We found LRR values for 12 forms of environmental change: acidification, calcium (Ca) additions, elevated CO_2, drought, plant invasion, nitrogen (N) additions, phosphorous (P) additions, N + P additions, N additions + elevated CO_2, elevated ozone, elevated ultraviolet radiation, and warming (Table 1 and Supplementary Table 2). If a treatment was represented by only one LRR value, then the reported LRR and associated confidence intervals were used in our analysis (Table 1). If a treatment was represented by more than one LRR value, we calculated the overall mean LRR and confidence interval for each treatment via bootstrapping from skew normal distributions[30]. Distributions were resampled 10,000 times to generate an overall mean and lower/upper confidence interval using the 'fGarch' package of R version 2.12.2. Bootstrapped means and

confidence intervals are compared with the means and confidence intervals from the original data sources in Supplementary Fig. 2.

Decomposition: to limit reference overlap, we searched for decomposition meta-analyses published after 2000, using the search terms [decomp* AND meta-analysis] in the ISI Web of Science. We found five meta-analyses, resulting in seven LRRs of a treatment effect on decomposition in freshwater and/or terrestrial ecosystems (Table 2 and Supplementary Table 3). LRR values were available for five different treatments: acidification, elevated CO_2, plant invasion, N additions and eutrophication (multiple nutrient additions in aquatic ecosystems). We extracted data and calculated mean LRR and associated confidence intervals as described above for productivity.

Environment crossed with species richness manipulations. We complemented our summary of meta-analyses with a more focused analysis that compared the effects of species richness to the effects of other forms of environmental change when both were manipulated simultaneously in the same experiment. To do this, we extracted records from the ref. 6 database for experiments that manipulated species richness and some component of environmental change in factorial combination. We only had sufficient data to assess effects of diversity and environmental manipulations on biomass production (16 studies, Supplementary Table 2): +calcium[31], +CO_2 (refs 32–34), water availability ("drought")[35–37], nitrogen addition[31,32,38], phosphorus addition[39], multiple nutrient addition[40–44], and warming[45]. In our statistical analyses, we also included effects of light manipulation[46], although the explicit link to global environmental change is less clear for this factor, so it is not shown in figures. For each study, we calculated the suite of diversity LRRs previously described, as well as the effect of the environmental manipulations at maximum species richness (Table 1). For experiments where manipulations either reduced or enhanced resources (for example, nutrient or water availability), we changed the sign of the LRRs appropriately so that magnitudes of effects could be compared on a scale similar to environmental changes assessed in the broader meta-analysis. We analysed LRRs using mixed models in SYSTAT v.12 (SYSTAT, Inc.) with environmental change as a fixed effect and study as a random effect. We compared equally weighted results to analyses where we weighted LRRs by sample size $(n_1 \times n_2)/(n_1 + n_2)$; results were qualitatively similar, unless otherwise noted.

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