




Assessing the roles of nitrogen, biomass, and niche dimensionality as drivers of species loss in grassland communities

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Eutrophication is a major driver of species loss in plant communities worldwide. However, the underlying mechanisms of this phenomenon are controversial. Previous studies have raised three main explanations: 1) High levels of soil resources increase standing biomass, thereby intensifying competitive interactions (the “biomass-driven competition hypothesis”). 2) High levels of soil resources reduce the potential for resource-based niche partitioning (the “niche dimension hypothesis”). 3) Increasing soil nitrogen causes stress by changing the abiotic or biotic conditions (the “nitrogen detriment hypothesis”). Despite several syntheses of resource addition experiments, so far, no study has tested all of the hypotheses together. This is a major shortcoming, since the mechanisms underlying the three hypotheses are not independent. Here, we conduct a simultaneous test of the three hypotheses by integrating data from 630 resource addition experiments located in 99 sites worldwide. Our results provide strong support for the nitrogen detriment hypothesis, weaker support for the biomass-driven competition hypothesis, and negligible support for the niche dimension hypothesis. The results further show that the indirect effect of nitrogen through its effect on biomass is minor compared to its direct effect and is much larger than that of all other resources (phosphorus, potassium, and water). Thus, we conclude that nitrogen-specific mechanisms are more important than biomass or niche dimensionality as drivers of species loss under high levels of soil resources. This conclusion is highly relevant for future attempts to reduce biodiversity loss caused by global eutrophication.

fertilization | meta-analysis | nutrient enrichment | productivity | species diversity

A decline in species richness with increasing resource availability is a universal pattern in plant communities (1–3). This pattern is particularly common in herbaceous plant communities and has been documented in hundreds of experiments worldwide (3–10). The recognition that anthropogenic eutrophication is a major threat to global diversity (11, 12) has accelerated research of the extent and implications of this phenomenon (13, 14). Nevertheless, the mechanisms by which high levels of resources cause a decline in species richness are not fully understood (15–21).

Early attempts to explain the decrease of richness under high levels of soil resources have attributed this pattern to an increase in biomass, leading to intensified interspecific competition (22, 23). According to this hypothesis (hereafter, the “biomass-driven competition hypothesis”), high levels of soil resources provide a competitive advantage for fast-growing and large species, excluding smaller and slow-growing species from the community (22–25). It has also been proposed (23) and demonstrated (26) that such competitive exclusion is primarily related to competition for light. Recent work attributes the pattern to the asymmetric nature of this competition [i.e., tall plants shade shorter ones but not the opposite (27)]. However, other works suggest that root competition may also contribute to species loss under high resource levels (15).

Another hypothesis that has gained support in the last decade has its roots in niche theory (28, 29). This hypothesis, known as the “niche dimension hypothesis” (30), is based on the idea that species coexistence requires niche partitioning via differences in resource requirements (29). According to this hypothesis, limiting resources function as “niche axes.” Thus, high levels of soil resources reduce the number of limiting resources, thereby reducing the number of species that can coexist in the community (30). The strongest support for this hypothesis comes from a global-scale experiment (8) where the same experimental protocol was applied in all sites. This initiative is the most extensive experimental effort ever undertaken to evaluate diversity responses to resource addition (45 sites from five continents) and is unique in its factorial design: All communities in all sites received all possible combinations of nitrogen, phosphorus, and potassium (i.e., N, P, K, NP, NK, PK, and NPK). This factorial design allowed

Significance

Nutrient enrichment of natural ecosystems is a primary characteristic of the Anthropocene and a known cause of biodiversity loss, particularly in grasslands. In a global meta-analysis of 630 resource addition experiments, we conduct a simultaneous test of the three most prominent explanations of this phenomenon. Our results conclusively indicate that nitrogen is the leading cause of species loss. This result is important because of the increase in nitrogen deposition and the frequent use of nitrogen-based fertilizers worldwide. Our findings provide global-scale, experimental evidence that minimizing nitrogen inputs to ecological systems may help to conserve the diversity of grassland ecosystems.

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the authors to test the effect of the number of added resources on species richness. Consistent with their expectations, species loss in fertilized plots was strongly and positively related to the number of added resources. Similar results were found in other studies (30–32) and were interpreted as support for the niche dimension hypothesis (although see ref. 20).

A third hypothesis suggests that the decline in species richness under high levels of soil resources is specifically related to nitrogen (hereafter, N). High levels of N may reduce plant performance by several mechanisms, including ammonium toxicity (33), acidification (34), changes in soil microbiome (35), and increased susceptibility to various stress agents (13, 14). This “nitrogen detriment hypothesis” is supported by studies showing that N addition has a stronger negative effect on species richness than other soil resources (refs. 4, 9, and 36, although see ref. 18).

In the last few decades, numerous studies, including a large number of meta-analyses, have investigated the drivers of species loss under high levels of resource availability (2, 3, 6–10, 37). However, each of these studies has focused on particular resources or mechanisms, and no study has attempted to test the three hypotheses simultaneously. This is a significant shortcoming because the mechanisms underlying the three hypotheses are not independent. Such a lack of independence increases the likelihood of confounding effects and may result in biased conclusions concerning the effects of the underlying mechanisms.

Here, we test the three hypotheses together using an extensive dataset collected from 630 different resource addition experiments in 99 different sites worldwide (Fig. 1 and *SI Appendix, Table S1*). Our analysis was designed to explicitly test distinct predictions derived from the above hypotheses. The first, derived from the biomass-driven competition hypothesis, is a negative effect of biomass on species richness. The second, derived from the niche dimension hypothesis, is a negative effect of the number of added resources on species richness. The third, derived from the nitrogen detriment hypothesis, is a negative effect of the presence of N on species richness (with all other resources having much weaker effects).

As emphasized above, the three hypotheses are not mutually exclusive, and more than a single mechanism might be involved in causing richness decline in response to resource addition. Thus, rather than considering the three hypotheses as alternatives, we aimed to evaluate the degree to which each hypothesis receives support from previously published experiments. To this end, we analyzed the data in two steps. First, we tested each hypothesis separately in order to verify that the patterns obtained from our dataset are consistent with those obtained in previous studies when testing each hypothesis by itself. Then, in a second step, we tested the three hypotheses simultaneously using two complementary approaches: multiple regression models and structural equation models. These approaches allowed us to quantitatively compare the effects of the three previously proposed drivers of species loss (biomass, number of resources, and presence of N) based on their predictive power and effect size and compare their direct vs. indirect effects on species richness.

Results

The first prediction, a decrease of species richness at high biomass levels, was supported by the data. However, a quadratic model provided a better fit to the data, indicating that the effect of biomass on richness was unimodal rather than negative

(Fig. 2A and *SI Appendix, Fig. S1* and Table S2). The quadratic model showed a corrected Akaike Information Criterion value that was lower by 33 units than that of the linear model (evidence ratio of 17×10^6). We, therefore, incorporated the quadratic term of biomass in all further models that included biomass as a predictor variable.

The second prediction, a negative effect of the number of added resources on species richness, was supported by the data (Fig. 2B). The effect was highly significant when tested using a linear mixed-effects model with the number of added resources as a linear predictor (as done in previous studies) (blue line in Fig. 2B; *SI Appendix, Table S3*). A corresponding model relaxing the assumption of linearity, in which the number of added resources was incorporated using dummy variables, indicated that the effects of one resource, two resources, and three resources were highly significant (red error bars in Fig. 2B; *SI Appendix, Table S4*). Moreover, the mean values of richness corresponding to the addition of zero, one, two, and three resources fell almost precisely on the linear regression line (Fig. 2B), confirming the linear response. Treatments including all four resources were removed from the latter analysis due to inadequate sample size ($n = 3$).

The third prediction, a negative effect of the presence of N on species richness, was also supported by the data (Fig. 2C and *SI Appendix, Table S3*). Moreover, this N-specific model showed a much better fit to the data (in terms of the model's corrected Akaike information criterion [AICc] value) than the other two models (evidence ratio of 7×10^{12} compared to the biomass model and 3×10^9 compared to the number of added resources model; *SI Appendix, Table S3*). The results further demonstrate that treatments including N ($N = 1$ in Fig. 2C) had lower richness than both control treatments and treatments without N (Fig. 2C). Similar results were obtained for a larger dataset, including an additional 374 records for which biomass data were unavailable (*SI Appendix, Fig. S2*).

Thus, all hypotheses were supported by our global dataset. To evaluate the relative importance of the drivers of species loss proposed by the three hypotheses, we incorporated the effects of the three factors in a single, mixed-effects model, with biomass (including its quadratic term), number of added resources, and N as fixed effects. The results of this integrated model indicated that biomass and N had statistically significant negative effects on richness, while the number of resources had a negligible and statistically insignificant effect (Table 1). Moreover, removing the number of added resources as a predictor from the model improved its AICc score by about seven units (evidence ratio of 39; Table 1). Conversely, omitting either biomass or N from the model resulted in a lower predictive power (Table 1). Thus, based on information theoretic criteria, the model providing the best fit to the data was one combining the effects of biomass (including its quadratic term) and N (Table 1).

One limitation of the integrated mixed-effects model is that it does not explicitly account for indirect relationships between model variables. Specifically, both N and the number of added resources are expected to influence richness indirectly through their effects on biomass. A common approach for modeling the combined direct and indirect effects in a single framework is structural equation modeling (SEM) (38). However, this approach is usually limited to linear relationships (38). We, therefore, incorporated a composite variable into the model. This composite variable describes the overall effect of biomass on species richness as the sum of its linear and quadratic terms (39) (Fig. 3). In essence, this approach reduces the

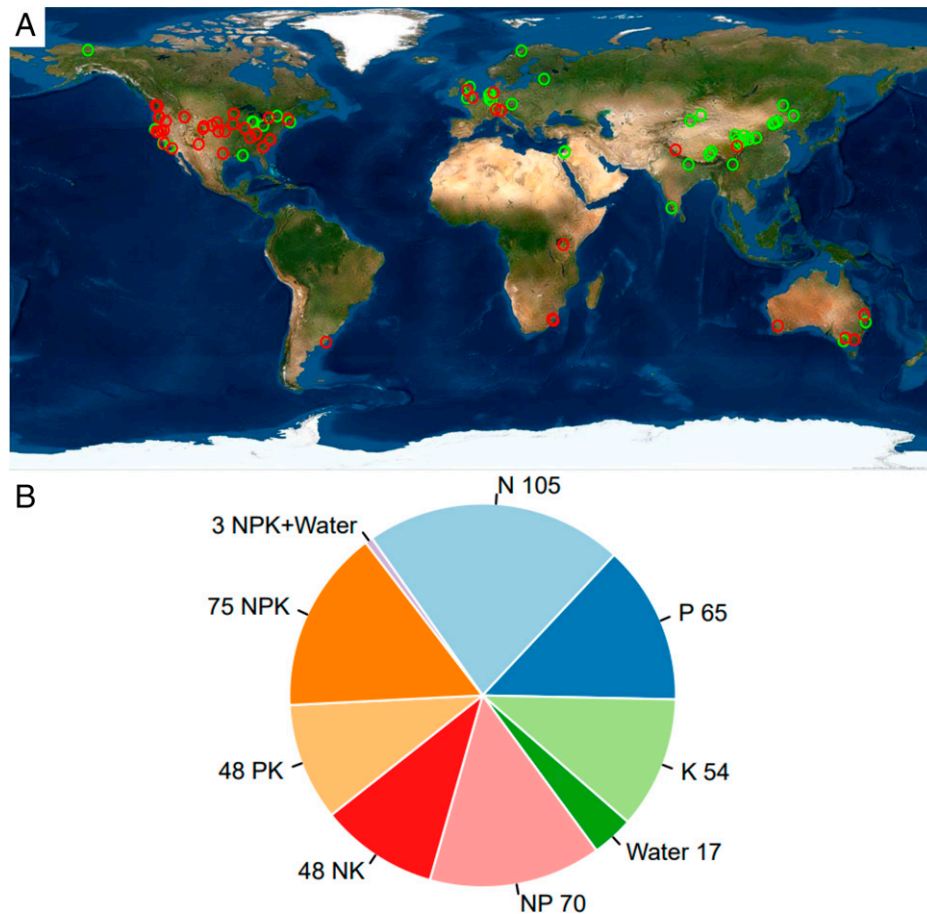


Fig. 1. General characteristics of the data included in our meta-analysis. (A) Geographical distribution of the sites included in the meta-analysis [red, sites of the nutrient network included in Harpole et al.'s study (8); green, other sites]. (B) The experimental treatments included in the meta-analysis and their prevalence in the dataset.

dimensionality of the biomass effect on richness from two dimensions (the linear and quadratic components) into a single variable that captures the combined effects of the original two dimensions on species richness. This synthetic (“composite”) variable is then incorporated within the SEM framework as a linear term, thereby allowing us to quantify the effects of biomass, number of added resources, and N on species richness while accounting for the direct and indirect effects of N and the number of added resources through their effects on biomass [by multiplying the relevant coefficients (38)]. It should be noted, however, that the composite variable is not interchangeable with biomass in this model (e.g., the standardized coefficient for the effect of the composite variable on species richness is not equivalent to the effect of biomass on richness).

The results (Fig. 3 and *SI Appendix, Table S5*) revealed two important patterns. First, the direct effect of N on species richness was much larger than the direct effect of the number of added resources. The latter effect was also insignificant, as in the integrated mixed-effects model. Second, the direct effect of N on species richness was much larger than its indirect effect through the composite variable representing biomass (-0.1197 vs. -0.0150 , respectively). Thus, N had both direct and indirect effects on richness, with the direct effect being much larger than the indirect one. This conclusion was also supported by an alternative SEM formulation in which the effect of biomass was introduced to the model in terms of its effect size (the log-response ratio; *SI Appendix, Fig. S3*). However, while this SEM formulation has the advantage that it does not require a

composite variable, it ignores the unimodal nature of the biomass–richness relationship and should therefore be interpreted with caution.

A final analysis was performed to test the effects of all combinations of resources for which we had data (N, P, K, water, NP, NK, PK, NPK, and NPK with water) on both standing biomass and species richness. The results of the biomass model indicated that only two treatments had statistically significant effects on biomass: N and P (Fig. 4A and *SI Appendix, Table S6*). Thus, both N and P had the potential to reduce richness through their indirect effects on biomass (as predicted by the biomass-driven competition hypothesis). However, a corresponding model with species richness as the response variable showed that only N had a statistically significant effect (blue bars in Fig. 4B; *SI Appendix, Table S7*). Thus, although P enrichment increases biomass according to our dataset, this increase is not translated into a decrease in richness. Finally, we found that adding biomass as a predictor to the all-resources model (red bars in Fig. 4B; *SI Appendix, Table S7*) had a negligible effect on the results. This result provides further support that the indirect effect of N on species richness through its effect on biomass was negligible relative to its direct effect.

Overall, our results can be summarized into three major findings: 1) Among the three previously proposed explanations for the negative effect of resource addition on species richness, the nitrogen detriment hypothesis receives the strongest support from published experiments. 2) Although both N and P (and the number of added resources) increase biomass, N is the

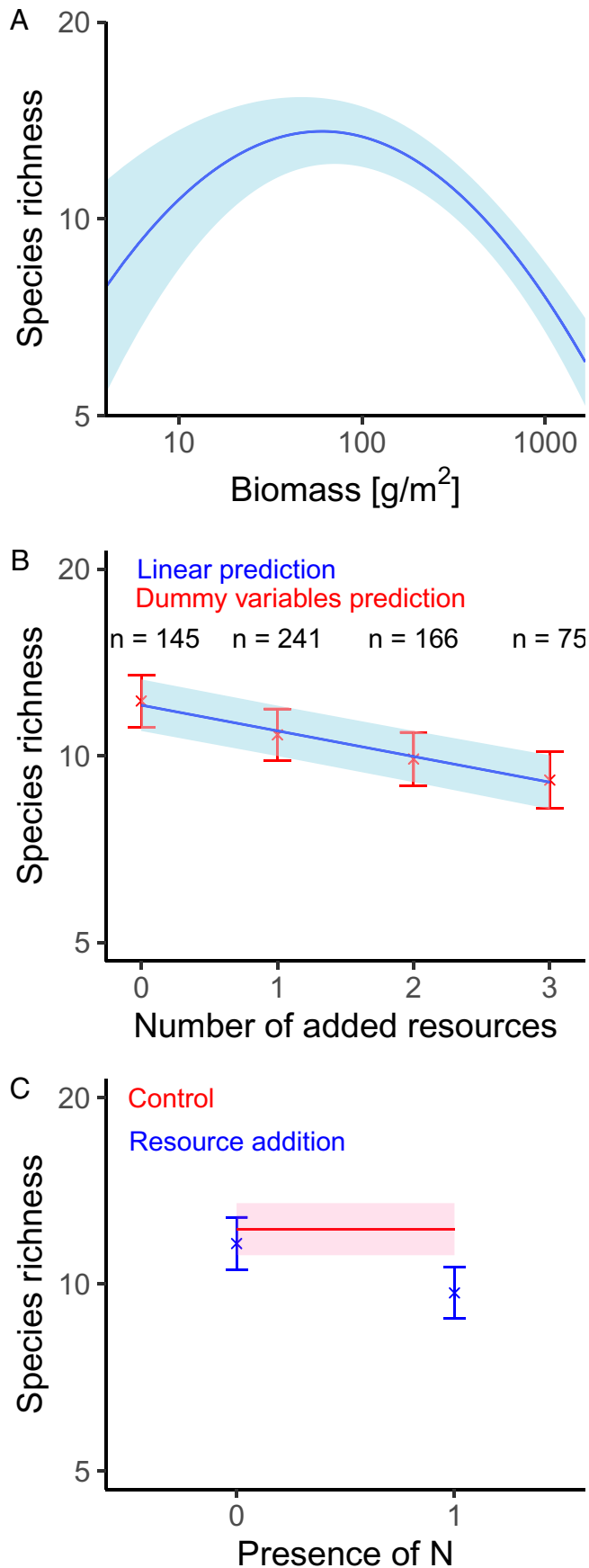


Fig. 2. Predicted species richness (mean \pm 95% CI) as a function of (A) standing biomass, (B) the number of added resources, and (C) the presence of nitrogen. (A) Prediction is based on a mixed-effects linear model with the linear and quadratic terms of biomass as fixed effects (conditional $R^2 = 0.888$, marginal $R^2 = 0.073$). (B) Blue, prediction of a mixed-effects linear

primary driver of species loss in this global-scale dataset. 3) The direct effect of N on richness is much larger than its indirect effect through biomass.

Discussion

We performed a global meta-analysis to test three major hypotheses regarding the decrease of species richness under high levels of soil resources: The biomass-driven competition hypothesis, the niche dimension hypothesis, and the nitrogen detriment hypothesis. The nitrogen detriment hypothesis gained the strongest support, the biomass-driven competition hypothesis gained intermediate support, and the niche dimension hypothesis has gained meager support in our analyses. Although these results do not refute the role of the biomass-driven competition hypothesis or the niche dimension hypothesis in specific systems, they suggest that, on a global scale, the primary mechanism of species loss following resource addition is specifically related to the presence of N. In the following sections, we discuss the interpretation and implications of these results in view of each hypothesis, as well as the limitations and implications of this study.

The Biomass-Driven Competition Hypothesis. The biomass-driven competition hypothesis asserts that the mechanism underlying species loss under high levels of soil resources is an increase in biomass which increases the likelihood of competitive exclusion (22–25). This hypothesis is supported by experimental studies (1, 3, 8, 9, 14). It has often been proposed to explain the decreasing phase of the unimodal biomass–richness relationships observed in many natural communities (2, 40).

In this meta-analysis, we limited our analysis to experimental studies and found that the effect of biomass on species richness was unimodal (Fig. 2A and *SI Appendix, Table S2*). This was somewhat surprising, as the prevalent pattern emerging from previous experimental studies is a monotonic decline in richness with increasing biomass. A common explanation for the disparity between experimental studies showing mostly negative relationships and natural gradients often showing a unimodal relationship is that many experimental studies are conducted at systems representing the decreasing phase of the unimodal biomass–richness relationship. Our results are consistent with this hypothesis, showing that, once a sufficiently broad biomass gradient is examined (and controlling for differences between sites), the pattern emerging from experimental studies is also unimodal.

Nevertheless, the biomass-driven competition hypothesis (22) gained only modest support in our analysis. While the total effect of N addition on species richness in our dataset was a reduction of $\sim 20\%$ (Fig. 4B), only $\sim 2\%$ was mediated by an increase in standing biomass (as indicated by the difference between the effects of N in models with and without biomass; Fig. 4B).

model with the number of resources treated as a continuous variable (conditional $R^2 = 0.879$, marginal $R^2 = 0.024$); red, predictions of a mixed-effects model with the number of resources treated as dummy variables (conditional $R^2 = 0.880$, marginal $R^2 = 0.025$). Data for four added resources are not shown due to small sample size. (C) Predictions are based on a mixed-effects model with three levels of resource addition treatments: control (red, no addition), treatments that do not include nitrogen (blue, N = 0), and treatments that include nitrogen (blue, N = 1, conditional $R^2 = 0.889$, marginal $R^2 = 0.031$). Biomass and richness are in logarithmic scale. See *SI Appendix, Table S3* for statistical details.

Table 1. Results of mixed-effects models testing the effects of various combinations of biomass (B), number of added resources (NAR), and nitrogen (N), on log-transformed species richness

Predictors of species richness	Estimates			
	All	NAR + N	B + N	B + NAR
Intercept	0.67 *** (0.41 to 0.94)	1.09 *** (1.04 to 1.13)	0.65 *** (0.39 to 0.92)	0.68 *** (0.41 to 0.96)
Biomass	0.43 *** (0.21 to 0.66)		0.46 *** (0.24 to 0.69)	0.46 *** (0.23 to 0.70)
Biomass ²	-0.11 *** (-0.16 to -0.06)		-0.12 *** (-0.17 to -0.07)	-0.12 *** (-0.17 to -0.07)
Number of added resources	-0.01 (-0.02 to 0.00)	-0.02 ** (-0.03 to -0.01)		-0.03 *** (-0.04 to -0.02)
N presence	-0.06 *** (-0.08 to -0.05)	-0.07 *** (-0.09 to -0.05)	-0.07 *** (-0.09 to -0.06)	
Random effects				
σ^2	0.01	0.01	0.01	0.01
τ_{00}	0.06	0.06	0.06	0.06
ICC	0.89	0.89	0.89	0.88
<i>n</i>	141	141	141	141
Observations	630	630	630	630
Marginal R^2 /conditional R^2	0.048/0.895	0.032/0.891	0.050/0.895	0.049/0.888
AICc	-802.804	-798.651	-810.138	-766.253

*** $P < 0.01$, **** $P < 0.001$; σ^2 , residual (within-cluster) variance; τ_{00} , between-cluster variance; ICC, intraclass correlation coefficient; *n*, number of clusters; AICc, corrected AIC.

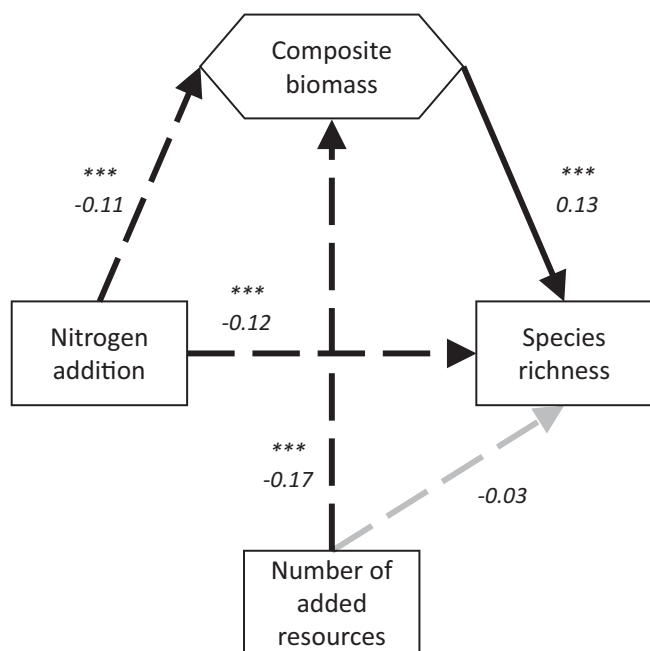


Fig. 3. Results of a structural equation model testing the three hypotheses together (the biomass-driven competition hypothesis, the niche dimension hypothesis, and the nitrogen detriment hypothesis). The model includes two equations; one with composite biomass as the response variable (conditional $R^2 = 0.83$, marginal $R^2 = 0.07$); another with species richness as the response variable (conditional $R^2 = 0.9$, marginal $R^2 = 0.05$). The observed variables are represented in rectangles. The hexagon indicates a composite variable (biomass-predicted species richness, including the linear and quadratic terms of biomass). Arrows show structural relationships (solid arrows indicate a positive effect, while dashed arrows indicate a negative effect). Black arrows represent significant ($P < 0.05$) relationships, and the gray arrow represents the nonsignificant relationship. Numbers near arrows are standardized coefficients obtained by local estimation. *** $P < 0.001$. The model was tested against nested unsaturated models and was found to be the best according to the AICc. See *SI Appendix, Table S5* for details. Note that interpretation of arrows related to the composite variable within SEM differs from other types of variables (see details in *Methods*).

The Niche Dimension Hypothesis. The niche dimension hypothesis posits that limiting resources function as niche axes. According to this hypothesis, resource addition reduces the number of niche axes (i.e., the “dimensionality” of the niche space), thereby reducing the number of species that can coexist in the community (30). The most common prediction derived from this hypothesis is that increasing the number of added resources in resource addition experiments should decrease species richness (8, 31, 32, 41). Patterns consistent with this prediction have been observed in several previous experiments (as well as in our analysis; Fig. 2B) and were interpreted as a support for the niche dimension hypothesis (8, 31, 32, 41). However, this interpretation suffers from two limitations. First, previous studies show that increasing the number of added resources also increases aboveground biomass (20, 21). The more acute problem is that the total number of added resources is inherently correlated with the likelihood that any particular resource would be included in the set of added resources. For example, a balanced design of a factorial experiment including all combinations of N, P, and K (e.g., refs. 8, 31, 32, and 41) should include N addition in a third of the plots representing the single-resource treatment, two-thirds of the plots representing the two-resource treatment, and all plots of the three-resource treatment. This inherent correlation is expected to produce a negative response of mean richness to the number of added resources even if N is the only resource that reduces richness. This problem is well recognized in the statistical literature and is usually referred to as the problem of “multiple versions of a treatment” (42). As far as we know, none of the previous tests of the niche dimension hypothesis has considered this inherent confounding effect.

This study controlled for these confounding effects using two alternative modeling approaches: a mixed-effects model and a structural equation model. The latter approach explicitly accounts for possible indirect effects of the number of added resources and N on species richness through their effects on biomass. Our results indicate that, for both models, the effect

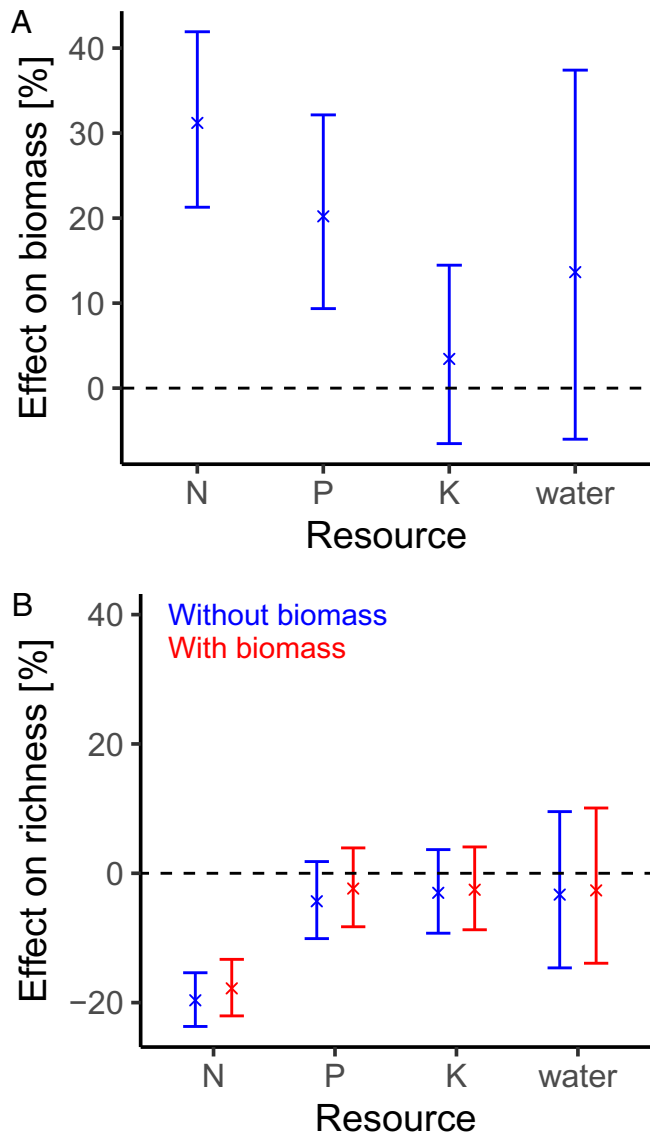


Fig. 4. Effects of the four resources examined in our analysis (N, P, K, and water) on (A) standing biomass and (B) species richness. Data shown are estimates of the predicted effects on (A) biomass and (B) richness, as estimated by mixed-effects models including all resources and their combinations (NP, NK, PK, NPK, and NPK with water) as fixed effects, without (blue) and with (red) biomass as a predictor in the model. Interactions are not shown, since they were statistically insignificant. For ease of interpretation, the estimated effects (mean \pm 95% CI) of each resource were transformed into percentage gain/loss of (A) biomass and (B) richness relative to the control (the dashed lines). See *SI Appendix, Table S6* for details of the biomass model, and see *SI Appendix, Table S7* for the richness model.

of the number of added resources on species richness was insignificant (Fig. 3, Table 1, and *SI Appendix, Fig. S4* and Table S5). This result contrasts the strong negative effect obtained in a simple model that ignores such confounding effects (Fig. 2B). Moreover, removing the number of added resources from the mixed-effects model increased the predictive power of the model (based on the AICc criterion; Table 1). These results seriously question previous studies interpreting the decrease in richness with an increasing number of added resources as evidence for the niche dimension hypothesis (8, 30–32).

The Nitrogen Detriment Hypothesis. Of all resource combination treatments included in our analysis (N, P, K, water, NP, NK, PK, NPK, and NPK with water; Fig. 1B), N had the largest and most significant effect on species richness (*SI Appendix,*

Table S7). This pattern did not change when standing biomass was incorporated as an additional predictor in the model (*SI Appendix, Table S7*). Further analyses in which each resource was characterized by its amount (in grams per square meter per year or millimeters per year) provided similar results (*SI Appendix, Table S7*). This highly consistent finding aligns with previous meta-analyses indicating that N addition is the primary driver of richness decline in resource addition experiments (refs. 3, 4, 7, 9, and 36, although see ref. 18).

In principle, N addition could reduce species richness through its effect on biomass or through N-specific mechanisms not related to biomass (the essence of the nitrogen detriment hypothesis). There are two indications in our analysis for dominance of the latter hypothesis. First, in the SEM analysis, the standardized coefficient of the direct path from N to species richness was roughly an order of magnitude larger than that of the indirect path through biomass (-0.1197 vs. -0.0150 , respectively). Second, a mixed-effects model incorporating the effects of all combinations of resources on species richness, with and without biomass, indicated that the total effect of N (direct + indirect) was larger by only 2% than its direct effect (a reduction of species richness by 20% vs. 18%, respectively; Fig. 4B). These results support our conclusion that the decline in richness under high levels of nutrients is related to N-specific effects.

In fact, more than three decades ago, Goldberg and Miller (43) proposed that the reduction in species richness following N enrichment might be related to resource-specific effects rather than an indirect effect through biomass. These authors compared the effects of adding water and N (as well as other nutrients) on both biomass and species richness. They found that water addition had a greater effect on biomass than N addition, but only N addition caused a decline in species richness. Based on these findings, they concluded that the decline in richness in their experiment was not related to an effect of N through biomass. They suggested, instead, that a differential phenology of limitation by different resources was the mechanism responsible for the change in richness. While their explanation cannot be tested with our dataset, our global-scale results are consistent with their experimental findings.

Several mechanisms can drive a “direct” negative effect of N on species richness. Besides direct toxicity of ammonia (33), N addition often causes soil acidification (13, 14, 34, 44–47). The acidification of the soil subsequently leads to lower availability of nutrients (13). Soil acidification also has adverse long-term effects, such as increased litter accumulation and concentrations of toxic metals (13). Experiments comparing the effects of N addition with and without soil buffering (using lime) have shown that the effect of N addition on species richness is much smaller once soil acidification is prevented (34). Consistent with these results, soil cation exchange capacity, which measures the soil’s buffering capacity to acidification, is a major predictor of species loss following N addition in various systems (3, 6).

Another potential mechanism of species loss following N addition involves excessive N uptake. Extreme levels of N availability could increase N uptake and may result in toxic levels of N in plant tissue. Such levels of N can cause elongation of the vegetative phase in plants, delaying or preventing maturation, as well as increased susceptibility to temperature-related stress or drought (13, 33, 48).

N addition may also change the composition, diversity, and abundance of the microbial community (47, 49, 50). Such changes can alter various processes of plant–soil feedbacks,

thereby favoring certain species over others and ultimately leading to competitive exclusions (35, 49).

While our results support the conclusion that N is the main driver of species loss in resource addition experiments, further experiments are necessary to better understand the mechanisms underlying this effect.

Methodological Issues. An inherent limitation of meta-analyses focusing on experimental studies is among-studies variability in the experimental design. In our meta-analysis, this variability is expressed by differences in the kinds of resources added, their absolute and relative amounts, the size of the experimental plots, the number of replicates, the duration of the experiment, etc. Additionally, our data are strongly unbalanced in the representation of the various experimental treatments, with some treatments, particularly N addition, having a much larger sample size than other treatments (Fig. 1B). These sources of variance, together with potential publication bias, could have affected our results and conclusions.

To evaluate the sensitivity of our results to these issues, we repeated all our analyses using two independent subsets of the data: the 45 sites of the standardized “NutNet” experimental network (8) and all other sites for which we had data (a total of 54 sites). Since data obtained from the “NutNet” network do not suffer from any of the above issues, a comparison of the results obtained from the two subsets of data allowed us to assess the sensitivity of our results to noise caused by inconsistency in the experimental design and publication bias. Furthermore, a strong consistency in the results obtained from the two datasets can be interpreted as significant support for our conclusions.

Comparing the patterns obtained for the two independent datasets revealed a high degree of similarity in both the general patterns (*SI Appendix*, Figs. S5–S9) and the statistical models (*SI Appendix*, Tables S8–S10). This strong consistency indicates that our findings are not mere artifacts of noise or biases in the data and further supports our conclusions.

Still, it should be emphasized that our study does not cover all previously proposed explanations for the negative effect of nutrient enrichment on species richness. For example, one particular hypothesis that could not be tested with our data is that the decline of richness under high levels of resources reflects a pure sampling effect of a decrease in the number of individuals (51). According to this hypothesis, increasing soil resources leads to an increase in average plant size, and this increase leads to a corresponding increase in the skewness of the plant size distribution (i.e., an increase in the relative frequency of relatively small plants). Since smaller plants are more likely to die than larger plants, this process reduces the number of individuals and decreases the number of species by a pure sampling effect (51, 52).

Finally, it should also be pointed out that we do not claim that competition is not important as a driver of species loss under high levels of soil resources. On the contrary, there are strong experimental indications that high levels of soil resources may reduce richness by increasing competition for light (26, 27). Nevertheless, what can be learned from our analysis is that the overall contribution of this mechanism to species loss in resource addition experiments is lower than that of N-specific effects.

Conclusion and Implications. This global-scale analysis provides strong support for the nitrogen detriment hypothesis, modest support for the biomass-driven competition hypothesis, and insufficient support for the niche dimension hypothesis.

The finding that N enrichment leads to the most detrimental effect on species richness has major implications for nature conservation (9, 13, 53), since N eutrophication is one of the main threats to biodiversity in this century (11). The fact that a low-diversity state could persist even decades after the reduction of N inputs makes this problem even more acute (54). Our results support previous suggestions concerning the need to reduce anthropogenic N emissions. Such efforts have been successful in some countries, but, in most parts of the world, the N deposition rate is still increasing (55). They also imply that future research should devote more efforts to identifying the specific mechanisms underlying the negative effect of N on species richness.

Methods

Literature Search. The basic criterion for inclusion of a study in the dataset was reporting results of species richness of herbaceous plants in experiments that include manipulation of at least one of the following soil resources: N, P, K, and water. We focused on these resources because other resource manipulations were too rare for statistical analyses.

We conducted our initial search in the Web of Science search engine, using the following phrase: “(richness OR *diversity OR “species loss” OR composition OR “community”) AND (“resource addition” OR “resource availability” OR “nutrient addition” OR “nutrient enrichment” OR “nutrient availability” OR (nitrogen AND addition*) OR (nitrogen AND enrichment*) OR “nitrogen availability” OR (phosphorus AND addition*) OR (phosphorus AND enrichment*) OR “phosphorus availability” OR (potassium AND addition*) OR (potassium AND enrichment*) OR “potassium availability” OR (water AND addition*) OR “water availability” OR irrigation) AND experiment* AND (grassland* OR herbaceous OR annual*)”. This search yielded 2,213 results (1 April 2021). After screening manually through the titles and abstracts, 319 papers were found to be potentially relevant. An additional 107 studies were collected from references within these papers. A deeper scanning of the main text of these papers produced a final directory of 164 papers that reported richness responses to resource manipulations (*SI Appendix*, Appendix 1).

Dataset Construction. Based on the data obtained from the 164 papers, we constructed a unified database where each record (row) represents the application of a single experimental treatment in a specific site and at a specific time. An experimental treatment was defined as the addition of a certain amount of a given resource to a set of replicated plots or, in cases of multiple resources, the application of a particular combination of resources to a set of replicated plots. Sets of control plots were also regarded as treatments with respect to their representation in the database. If a study reported data for multiple years, we recorded only the last year of observation. In cases where the same plot was sampled several times during the same year, a single time (the one with the highest mean richness in control plots) was selected for the analysis. When data were only reported in figures, we used the digitizing program GetData (56) to extract the relevant numerical data. This procedure resulted in 1,737 records, where each record represents the application of a single resource (e.g., P), a combination of resources (e.g., N and water), or a control group, and the corresponding species richness and biomass data (if available). Only treatments for which there was an appropriate control group were included in this dataset, and a given control group could be used as a reference to one or more resource addition treatments in the same site. We, therefore, coded the treatments in a manner that allowed us to relate each treatment to its relevant control. We termed this code “Cluster ID” and used it as a random variable in all analyses.

The above dataset was further refined to exclude several undesirable characteristics. Some studies were removed due to the use of unconventional measures that proved troublesome compared to the majority of the papers (e.g., reporting average species richness of specific functional groups rather than the entire community). When the same resource was added using different fertilizers, one type was chosen at random to prevent the disproportional weight of such studies in the analysis. In cases of studies reporting richness at multiple scales within the same plot (e.g., 1 m² and 10 m²), a single spatial scale was chosen based on the most common sampling unit size in the dataset (1 m²)

prevent pseudoreplication. Two studies showing extreme values of biomass or richness (at least 5 times greater than any other paper) were also removed from the dataset, as they were considered outliers.

Our statistical analyses (see below) were designed to distinguish between two types of predictors representing resource addition: quantitative data (the amount of each resource in the relevant treatment) and binary data (the presence or absence of each resource in a given treatment). We, therefore, created two subsets of data: 1) a quantitative dataset including all treatments where each treatment was characterized by the amount of each resource added; and 2) a binary dataset, where treatments were characterized by the presence or absence of each resource. The latter dataset was further reduced to equalize the weight of experiments applying single versus multiple amounts of resources when using the binary dataset. Specifically, if different amounts of the same (single) resource were applied in the same experiment, only a single amount was selected for the binary dataset—the one that was most common in the rest of the experiments (10 g·m⁻²·y⁻¹ for nutrients and 180 mm for water). The final binary dataset included 1,004 records distributed over 150 different locations (Fig. 1 and *SI Appendix, Appendix 1 and Table S1*). Biomass data were available for 630 of these records, distributed over 99 locations.

Most of our analyses used the binary dataset, except for testing the effects of all combinations of resources on species richness, which was applied on both datasets to test robustness.

Data Analysis. All our analyses are based on mixed-effects models with cluster IDs treated as a random effect to account for differences between sites. To meet the assumption of the model, we have log₁₀-transformed biomass and species richness which improved the normality and minimized heteroscedasticity of the data. All statistical analyses were performed in R version 4.1.1 using the packages MuMIn, lme4, lmerTest, and piecewiseSEM (57–60).

We started by testing each hypothesis separately. First, the prediction that increasing biomass reduces richness was tested using both linear and quadratic models. Next, we tested the effect of the number of added resources on species richness. The number of added resources was treated as a continuous variable or a set of dummy variables for each resource level. In the dummy variable model, each treatment was assigned to one of five categories based on the number of resources added in that treatment (zero, one, two, three, or four resources). However, the last category was omitted due to the small sample size ($n = 3$). Lastly, we tested the prediction that the presence of N reduces species richness while other resources do not. In this model, all combinations of experimental treatments were classified into three groups: control treatments (no addition), resource addition treatments without N, and resource addition treatments with N. According to the nitrogen detriment hypothesis, resource addition treatments without N should not differ in richness from the control treatments, and both treatments should show higher richness than resource addition treatments with N.

In the second step, we incorporated the effects of biomass (including its linear and quadratic terms), the number of added resources, and N in a single integrated model. Two types of models were used for this purpose: a multiple regression model and a SEM. To better interpret the regression model results,

we also compared the predictive power of regression models incorporating all possible combinations of biomass, the number of added resources, and N, based on their AICc (61). Differences in AICc values obtained for selected pairs of models were also expressed as evidence ratio [the ratio between their Akaike weights (62)] to interpret the magnitude of the observed differences more intuitively.

The second type of model (SEM) was designed for separating the direct and biomass-mediated effects of N and the number of added resources on species richness. The first equation of the SEM included the number of added resources and N as predictors of a composite variable representing the predicted species richness by the linear and quadratic terms of biomass. The second equation included the composite variable, the number of added resources, and N as predictors of species richness. Biomass was incorporated as a composite variable to account for its unimodal effect on species richness (see ref. 39 for details on incorporating quadratic relationships in SEM using composite variables). This approach enables calculating indirect effects through biomass by multiplying the relevant coefficients (arrows in Fig. 3). However, caution is needed in interpreting the signs of the arrows; for example, a negative effect of nitrogen on the composite variable does not represent a negative effect on biomass but a negative effect on species richness as predicted by biomass. In other words, the coefficients related to the composite variable should not be interpreted as effects of, or on, biomass.

The analysis of the SEM started with a saturated model that included all the potential paths, which we later compared to simpler models by removing paths (19). We compared the AICc scores of all potential submodels and ultimately chose the saturated model because it best fitted the data (i.e., had the lowest AICc score). We have also built an alternative SEM in which biomass and richness were incorporated in terms of their effect size instead of their actual values (everything else was the same). The effect size was calculated as the log₁₀-transformed ratio between treatment and control values (63).

The third phase of the analysis aimed to compare the effects of the four types of resources (N, P, K, and water) on biomass and species richness using multiple regressions. Specifically, we tested whether each combination of the four resources affects biomass, and whether the effects of the resources on species richness are mediated by biomass. For the second aim, we compared the effects of each resource on species richness in a model that included only the resources and a model that also included biomass. The model without biomass estimates the combined effects of the direct and biomass-mediated effects, while the model that includes biomass estimates the direct effect of each resource combination.

Data Availability. The csv files and R file have been deposited in Figshare, <https://figshare.com/s/d2933788bc55814b47f3> (64). Previously published data were used for this work (8, 27, 34, 43, 44, 53, 65–196).

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