

SCALE-DEPENDENT RESPONSES OF PLANT BIODIVERSITY TO NITROGEN ENRICHMENT

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Abstract. Experimental studies demonstrating that nitrogen (N) enrichment reduces plant diversity within individual plots have led to the conclusion that anthropogenic N enrichment is a threat to global biodiversity. These conclusions overlook the influence of spatial scale, however, as N enrichment may alter β diversity (i.e., how similar plots are in their species composition), which would likely alter the degree to which N-induced changes in diversity within localities translate to changes in diversity at larger scales that are relevant to policy and management. Currently, it is unclear how N enrichment affects biodiversity at scales larger than a small plot. We synthesized data from 18 N-enrichment experiments across North America to examine the effects of N enrichment on plant species diversity at three spatial scales: small (within plots), intermediate (among plots), and large (within and among plots). We found that N enrichment reduced plant diversity within plots by an average of 25% (ranging from a reduction of 61% to an increase of 5%) and frequently enhanced β diversity. The extent to which N enrichment altered β diversity, however, varied substantially among sites (from a 22% increase to an 18% reduction) and was contingent on site productivity. Specifically, N enrichment enhanced β diversity at low-productivity sites but reduced β diversity at high-productivity sites. N-induced changes in β diversity generally reduced the extent of species loss at larger scales to an average of 22% (ranging from a reduction of 54% to an increase of 18%). Our results demonstrate that N enrichment often reduces biodiversity at both local and regional scales, but that a focus on the effects of N enrichment on biodiversity at small spatial scales may often overestimate (and sometimes underestimate) declines in regional biodiversity by failing to recognize the effects of N on β diversity.

Key words: *alpha diversity; beta diversity; gamma diversity; herbaceous plant communities; nitrogen enrichment; productivity; species composition; species diversity.*

INTRODUCTION

Human activities have doubled the global availability of N (Vitousek et al. 2002, Galloway et al. 2004). Primary production is often limited by the availability of reactive N in terrestrial ecosystems (Vitousek and Howarth 1991), and experimental evidence suggests that N enrichment often leads to increased primary production and reduced biodiversity of plants (Silvertown 1980, Wedin and Tilman 1996, Gough et al. 2000, Suding et al. 2005). Consequently, increased N availability is recognized as one of the major causes of biodiversity decline in terrestrial ecosystems (Sala et al. 2000, Stevens et al. 2004, Phoenix et al. 2006).

Studies of N-mediated losses in plant biodiversity, however, have usually focused on α diversity (the number of species coexisting within a relatively small local community or patch; Whittaker 1972). Relatively little is known about the effects of N enrichment on biodiversity at large spatial scales (i.e., the number of species present in a region; γ diversity) relevant to management and policy concerns. A change in γ diversity can occur if (1) there is a change in the average α diversity in the patches comprising the region and/or (2) there is a change in the amount of β diversity (the degree to which different patches are similar in their species composition) among patches within the region (Whittaker 1972, Lande 1996). Consequently, to understand how N enrichment affects biodiversity at large spatial scales requires study of how both α and β diversity respond to N enrichment.

Three sets of models make different predictions about the effects of nutrient enrichment on β diversity. First, N enrichment may reduce β diversity by reducing micro-

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TABLE 1. List of the seven field stations (in six U.S. States) from which we obtained data from nitrogen-manipulation experiments conducted in herbaceous plant communities.

Field station	Location†	No. experiments	Code‡
Arctic LTER	AK	5	ARC1–ARC5
Cedar Creek LTER	MN	2	CDR1, CDR2
Jasper Ridge Biological Station	CA	2	JRG1, JRG2
Kellog Biological Station	MI	2	KBS1, KBS2
Konza LTER	KS	4	KNZ1–KNZ4
Niwot Ridge LTER	CO	1	NWT1
Shortgrass Steppe LTER	CO	2	SGS1, SGS2

Note: LTER indicates a Long-term Ecological Research site.

† Key to abbreviations: AK, Arkansas; CA, California; CO, Colorado; KS, Kansas; MI, Michigan; MN, Minnesota.

‡ Code represents the abbreviation for a particular field station and experiment. The first three letters of the code correspond to one of the seven field stations where the experiments were conducted, and the number corresponds to one of the experiments conducted at a particular field station; stations are distinguished by different symbols in the figures.

environmental heterogeneity in N availability and allowing a few species that are adapted for higher N levels to spread and dominate local communities (i.e., the *biotic-homogenization hypothesis*; Huston 1979, Tilman 1988, Wisheu and Keddy 1992). Second, the increase in productivity following nutrient enrichment may cause β diversity to increase because (1) the number of alternate community states is higher in more productive areas or (2) temporal stochasticity plays a more important role in regulating species composition in more productive areas (i.e., the *biotic-divergence hypothesis*; Chase and Leibold 2002, 2003, Chase 2003). Third, the effect of nutrient enrichment on β diversity may depend on the natural productivity of a site if the association between β diversity and productivity is unimodal. In this case, nutrient enrichment enhances β diversity in less productive sites and reduces β diversity in more productive sites (i.e., the *productivity-dependent biotic-homogenization hypothesis*; Holt et al. 1994, Van der Koppel et al. 1996, Chase 1999, Chase et al. 2000, Diehl and Feiel 2000). Such unimodal associations can be produced by a variety of mechanisms (e.g., changes in consumer efficiency or change in prey tolerance to consumption) that may vary in importance along a productivity gradient (Scheiner and Willig 2005).

Empirical work assessing the association between β diversity and productivity has provided support for the biotic-homogeneity hypothesis (Pastor et al. 1996), the biotic-heterogeneity hypothesis (Chase and Leibold 2002, Harrison et al. 2006), and the productivity-dependent biotic-homogenization hypothesis (Chalcraft et al. 2004). Experimental work at one site (Inouye and Tilman 1995) demonstrated that N enrichment reduces β diversity. These different predictions and results make it difficult to generalize how N enrichment will influence diversity at scales larger than a small plot. Although results from a single N-enrichment experiment could be used to evaluate whether N enrichment alters β diversity in one location, an analysis of data from multiple N-enrichment experiments conducted over a broad range of productivity is necessary to (1) test for the generality

of responses and (2) evaluate which set of models better predicts how N enrichment will affect β diversity across a natural productivity gradient.

METHODS

To gain a more general understanding of how N enrichment affects biodiversity at multiple spatial scales, we synthesized data from 18 N-fertilization experiments in herbaceous plant communities that encompass a wide range of natural productivity (100–724 g of aboveground biomass per square meter per year) to address how N enrichment affects α , β , and γ diversity. Our experiments represent all of the N-enrichment experiments conducted on terrestrial herbaceous plant communities considered by Suding et al. (2005) in their meta-analysis of the effects of N enrichment on α diversity. Data from these experiments are provided in Cleland et al. (2008). The experiments included in our study were conducted at seven field stations in North America (Table 1). Although the experiments differed in their specific designs (Appendix), all experiments had (1) replicate plots that received no supplemental N (i.e., unfertilized plots) and replicate plots that received supplemental N (i.e., fertilized plots) and (2) measurements on the relative abundances of individual species and annual aboveground net primary productivity (ANPP) in each replicate plot.

Species composition for a replicate plot was estimated in one of two ways; biomass harvests (Cedar Creek LTER [CDR] and Konza Biological Station [KBS]) or nondestructive cover estimates (all other sites) of sample plots located within the replicate plot. For biomass harvests, we averaged the last three years of sample plot data because researchers at sites employing this technique believed that this estimate provided a better estimate of species composition of the replicate plot (i.e., the unit to which N was applied). For cover estimates, we used the most recent year of species composition data available.

We measured α , β , and γ diversity for each treatment (i.e., fertilized vs. unfertilized) in each of the 18 experiments. For each treatment α diversity was measured as the mean number of plant species located within each replicate plot within the treatment. We measured β diversity for each treatment as the average pairwise Jaccard distance in plant species composition among all replicate plots within the treatment (i.e., β_{jacc}). β_{jacc} for a given pair of plots is estimated as

$$\beta_{\text{jacc}} = 1 - \frac{a}{a + b + c}$$

where a represents the number of species that both plots have in common, b is the number of species that are unique to one plot, and c is the number of species that are unique to the second plot. β_{jacc} approximates β diversity as conceptualized by Whittaker (1972) and Lande (1996) as both incorporate spatial variation in species composition among localities that is due to (1) some localities containing more species than other localities and/or (2) some species that are present in one locality being replaced by other species in a different locality, independent of differences in the number of species present in each locality (Koleff et al. 2003). As such, β diversity can be broken into two subcomponents: one that measures spatial variation in species composition attributable to spatial variation in α diversity (i.e., β_{gl}) and another that measures spatial variation in species composition not attributable to spatial variation in α diversity (i.e., β_{sim}) (Lennon et al. 2001, Koleff et al. 2003). For a given pair of plots, β_{gl} is estimated as

$$\beta_{\text{gl}} = \frac{2|b - c|}{2a + b + c}$$

and β_{sim} is estimated as

$$\beta_{\text{sim}} = \frac{\min(b, c)}{\min(b, c) + a}$$

β_{sim} provides an estimate for spatial variation in species composition between two localities after adjusting for differences in their α diversity (Lennon et al. 2001, Koleff et al. 2003). We measured both of these subcomponents of β diversity to determine whether N enrichment alters β diversity by changing one or both of these potential sources of variation in species composition. We report β_{sim} and β_{gl} for a given experiment as the average pairwise β_{sim} and β_{gl} values among all replicate plots within the treatment. We estimated γ diversity for each treatment as the total number of unique plant species found on all replicate plots within the treatment.

We measured the effect of N enrichment in each experiment on each of our biodiversity measures as

$$\ln\left(\frac{D_{\text{fert}}}{D_{\text{cont}}}\right)$$

where D is the value of a particular measure of diversity

in fertilized (fert) and control (cont) plots. Negative log ratios indicate that fertilized plots have lower values of a biodiversity measure (e.g., lower β diversity) while positive log ratios indicate that fertilized plots have higher values of a biodiversity measure. We determined that N addition caused a significant change in a measure of biodiversity if the observed log ratio exceeded 95% of the log ratios produced by 10 000 iterations of a null model that randomly assigned treatment identities to individual plots. Because our null model randomly assigned treatment identities to individual plots, it assumed that there is actually no difference in a particular diversity measure between control and treatment plots during any given iteration [i.e., $H_0: \ln(D_{\text{fert}}/D_{\text{cont}}) = 0$]. We used the programming language R (R Development Core Team 2007) for performing our null-model iterations.

We used regression analysis to determine if the effect of N enrichment on a particular measure of biodiversity in each experiment was dependent on the natural aboveground net primary production (ANPP) of the site in which the experiment was conducted (as measured on control plots). Different experiments conducted at the same field station have the potential to be considered interdependent in regression analysis. As a result, we also calculated the mean log response ratio and the mean ANPP of all unfertilized plots for all experiments conducted at each field station and performed a regression analysis on this reduced data set (with each data point representing one field station). For all regression analyses the procedure PROC GLM in SAS for Windows (SAS Institute 2002) was used.

RESULTS

N fertilization was associated with a reduction in α diversity in 17 of 18 experiments but the effects were only significant in 11 experiments (solid symbols in Fig. 1). The degree to which N enrichment reduced α diversity was not dependent on site productivity (Fig. 1).

β_{jacc} diversity was significantly altered by N enrichment in 11 of 18 experiments (solid symbols in Fig. 2A), increasing in 8 and decreasing in 3 experiments. The response of β_{jacc} diversity to N enrichment was related to site productivity (Fig. 2A). Specifically, N enrichment enhanced β_{jacc} diversity in less productive sites and reduced β_{jacc} diversity in more productive sites. N enrichment altered the component of β diversity that is independent of spatial variation in α diversity (i.e., β_{sim} diversity) in 13 of 18 experiments (solid symbols in Fig. 2B), increasing in 6 and decreasing in 7 experiments. Variation in the response of β_{sim} diversity to N enrichment was not related to site productivity (Fig. 2B). N enrichment also affected β diversity by altering the extent of spatial variation in α diversity (i.e., β_{gl}) in 12 of 18 experiments (solid symbols in Fig. 2C), increasing in 10 and decreasing in 2 experiments. The magnitude of the effect varied with productivity (Fig. 2C); specifically, N enrichment increased β_{gl} in

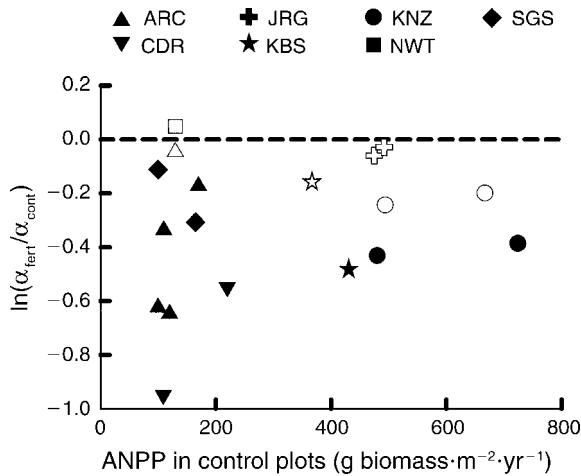


FIG. 1. The effect of N enrichment (fert = fertilized; cont = control) on α diversity in locations differing in their annual aboveground net primary productivity (ANPP). Positive log ratios indicate that diversity is enhanced by N enrichment while negative log ratios indicate that diversity is reduced by N enrichment. Solid symbols indicate that the effect of N enrichment on diversity is significantly different than 0 ($P < 0.05$) while open symbols indicate that the observed effect is not different than 0. The natural productivity of a site where an experiment was conducted did not alter the effect of N enrichment on α diversity ($n = 18$ experiments, $P = 0.42$, $R^2 = 0.04$). See Table 1 for full names of stations.

unproductive regions and reduced β_{gl} in productive regions. Although the effect of N on β_{jacc} was positively correlated with the effect of N on β_{sim} ($n = 18$ experiments, $r = 0.53$, $P = 0.024$) and on β_{gl} ($n = 18$, $r = 0.49$, $P = 0.038$), there was a trend for the effect of N on β_{gl} to be negatively correlated with the effect of N on β_{sim} ($n = 18$ experiments, $r = -0.42$, $P = 0.087$).

N enrichment was associated with a reduction in γ diversity in 16 of 18 experiments but the effects were only significant in 8 experiments (solid symbols in Fig. 3). The effects of N enrichment on γ diversity did not depend on site productivity (Fig. 3). A regression of the response of γ diversity to N enrichment on the response of α diversity to N enrichment (with the y intercept fixed to 0) estimated a slope of 0.863 ± 0.068 (mean \pm SE). A hypothesis test on this slope estimate indicates that there is a low probability that the slope is equal to 1 ($F_{1,17} = 4.085$, $P = 0.059$), which indicates that the response of α diversity to N enrichment generally overestimates the response of γ diversity to N enrichment.

Regressions that focused on the mean log responses of biodiversity measures and mean ANPP (aboveground net primary production) for all experiments conducted at each field station (i.e., each data point in the regression was represented by one field station rather than each experiment) were consistent with the regression results reported above, except for the response of β_{gl} , for which ANPP did not explain a significant amount of variation ($n = 7$, $P = 0.27$, $R^2 = 0.23$).

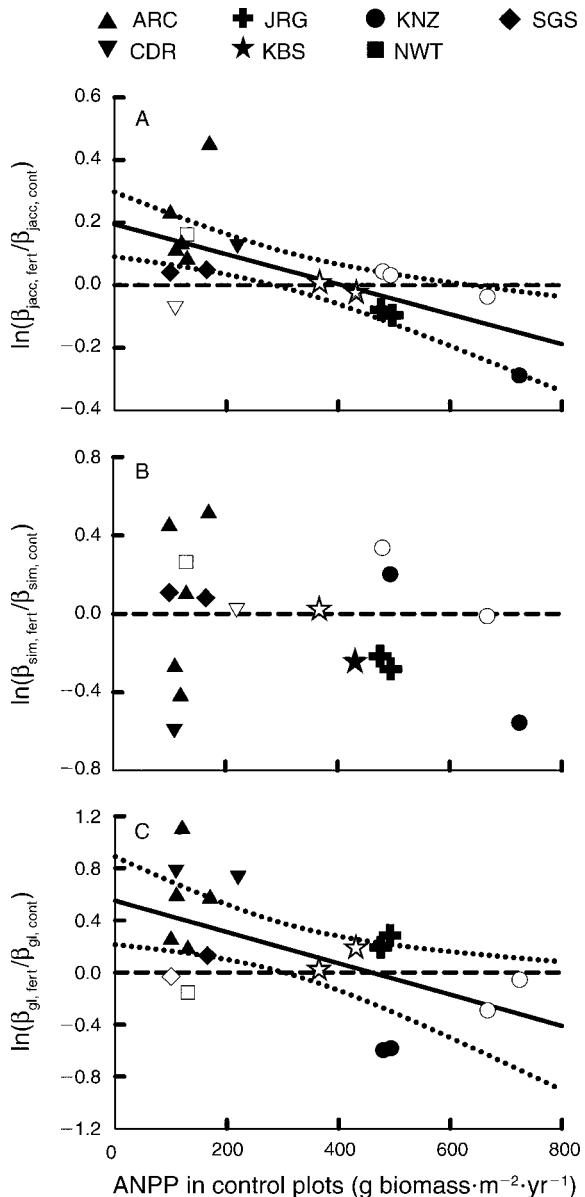


FIG. 2. The effect of N enrichment on β diversity in locations differing in their annual aboveground net primary productivity (ANPP). Positive log ratios indicate that diversity is enhanced by N enrichment while negative log ratios indicate that diversity is reduced by N enrichment. Solid symbols indicate that the effect of N enrichment on diversity is significantly different than 0 ($P < 0.05$) while open symbols indicate that the observed effect is not different than 0. The natural productivity of a site where an experiment was conducted altered the effect of N enrichment on (A) β_{jacc} ($n = 18$ experiments, $P = 0.003$, $R^2 = 0.53$) and (B) β_{gl} ($n = 18$, $P = 0.02$, $R^2 = 0.31$) but not on (C) β_{sim} ($n = 18$, $P = 0.35$, $R^2 = 0.05$). The solid line in (A) and (C) represents the estimated linear function, and the dotted line in (A) and (C) represents the 95% confidence interval associated with the estimated linear function. See Table 1 for full names of stations.

DISCUSSION

Although the fact that N enrichment reduces biodiversity at the local scale is well established (e.g., Silvertown 1980, Wedin and Tilman 1996, Gough et al. 2000, Stevens et al. 2004, Suding et al. 2005), it is less clear how N enrichment affects biodiversity at larger spatial scales. We found that N enrichment often alters biodiversity at local (within a plot), intermediate (among plots), and regional (within and among plots) spatial scales. N enrichment generally reduced biodiversity at local (by 25%) and regional (by 22%) scales but the actual response varied substantially (ranging from a 61% reduction to a 5% increase in α diversity and from a 54% reduction to an 18% increase in γ diversity) among experiments. We also observed N induced changes in biodiversity at intermediate scales (i.e., β diversity) but the direction and magnitude of the effect depended on site productivity. These results caution against the assumption that effects at small spatial scales translate neatly to large spatial scales, and highlight the need for explicit incorporation of multiple spatial scales to accurately assess the threat of anthropogenic N deposition on herbaceous plant biodiversity.

N-induced changes in β diversity (i.e., β_{jacc} , the average pairwise Jaccard distance in plant species composition among all plots within the treatment) were the result of N enrichment altering (1) spatial variation in α diversity and (2) the extent to which species replace each other independently of variation in α diversity. Evidence for this conclusion was based on the result that N-induced changes in β diversity were positively associated with both β_{gl} (spatial variation in species composition attributable to spatial variation in α diversity) and β_{sim} (spatial variation in species composition *not* attributable to spatial variation in α diversity) and by the observation that the number of experiments in which N altered β_{gl} and β_{sim} were the same (13 experiments). The direction of the effect of N on β_{sim} , however, was often in the opposite direction of the effect of N on β_{gl} (Table 2) and there was a trend for these two effects to be negatively correlated. Two important conclusions can be made from these results. First, the opposing responses of each subcomponent of β -diversity to N enrichment appears to constrain the extent to which β diversity can respond to N enrichment. Second, although β_{gl} and β_{sim} represent mathematically independent components of β diversity (Lennon et al. 2001, Koleff et al. 2003), the correlation between the responses of each subcomponent of β diversity to N enrichment suggests that the mechanisms affecting each subcomponent are not entirely independent. The fact that the effect of N on β_{gl} varied across a productivity gradient while the effect of N on β_{sim} did not, however, suggests that N enrichment may also affect β_{gl} through some additional mechanisms that do not affect β_{sim} . We believe that future efforts directed toward exploring mechanisms that affect β_{gl} and β_{sim} would greatly improve our understanding of scale-dependent changes

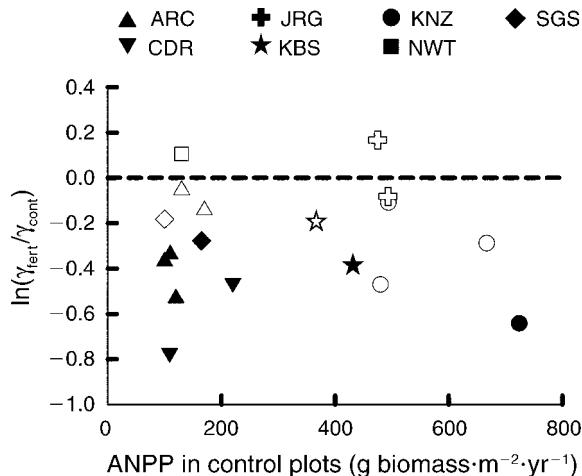


FIG. 3. The effect of N enrichment on γ diversity in locations differing in their annual aboveground net primary productivity (ANPP). Positive log ratios indicate that diversity is enhanced by N enrichment while negative log ratios indicate that diversity is reduced by N enrichment. Solid symbols indicate that the effect of N enrichment on diversity is significantly different than 0 ($P < 0.05$) while open symbols indicate that the observed effect is not different than 0. The natural productivity of a site where an experiment was conducted did not alter the effect of N enrichment on γ diversity ($n = 18$ experiments, $P = 0.30$, $R^2 = 0.03$). See Table 1 for full names of stations.

in biodiversity. For example, among-patch variation in colonization history may cause α diversity to be reduced to different extents (i.e., enhance β_{gl}) following N enrichment because variation in colonization history alters how changes in productivity affect biodiversity (Fukami and Morin 2003).

N-induced changes in β diversity (i.e., β_{jacc}) were most consistent with the productivity-dependent biotic-homogenization hypothesis; β diversity was enhanced in less productive sites and reduced in more productive sites. This pattern was found regardless of whether the unit of analysis was an individual experiment or an average response at an individual field station. Although our results are consistent with model-based predictions of productivity-dependent biotic homogenization (e.g., Holt et al. 1994, Van der Koppel et al. 1996, Chase 1999, Chase et al. 2000, Diehl and Feiße 2000), we do not have sufficient information to evaluate any of the associated mechanisms that are proposed by these models. Nonetheless, our analysis of 18 experiments conducted in various locations across North America suggest that models predicting productivity-dependent biotic homogenization have applications for a diverse array of terrestrial herbaceous plant communities (e.g., old fields, tundra, annual grasslands, tallgrass prairie) across broad geographic scales. Consequently, future efforts designed to test mechanisms through which N enrichment affects β diversity in herbaceous plant communities should focus on hypothesized mechanisms that predict productivity-dependent biotic homogenization.

TABLE 2. Summary of responses by α , β_{jacc} , β_{sim} , β_{gl} , and γ diversity to N enrichment for 18 experiments, by category (1–5).

Category	Experiment	Response of diversity measures to N enrichment †				
		α	β			γ
			jacc	sim	gl	
1	KBS2	0	0	0	0	0
1	NWT1	0	0	0	0	0
1	KNZ4	0	0	0	0	0
1	KNZ3	0	0	↑	↓	0
1	JRG1	0	↓	↓	↑	0
1	JRG2	0	↓	↓	↑	0
1	ARC3	0	↑	↑	↑	0
1	KNZ1	↓	0	0	↓	0
2	ARC2	↓	↑	↑	↑	0
2	SGS1	↓	↑	↑	0	0
3	CDR1	↓	0	↓	↑	↓
3	KBS1	↓	0	↓	↑	↓
4	CDR2	↓	↑	0	↑	↓
4	ARC1	↓	↑	↑	↑	↓
4	SGS2	↓	↑	↑	↑	↓
4	ARC4	↓	↑	↓	↑	↓
4	ARC5	↓	↑	↓	↑	↓
5	KNZ2	↓	↓	↓	0	↓
Total declines		11	3	7	2	8
Total increases		0	8	6	11	0

Notes: Responses are divided into five categories according to their nature of response as follows: (1) no change in γ diversity as a result of weak changes in either α or β_{jacc} diversity, (2) no change in γ diversity as a result of an increase in β_{jacc} diversity compensating for reductions in α diversity, (3) reductions in γ diversity as the result of reductions in α diversity but no change in β_{jacc} diversity, (4) reductions in γ diversity but increases in β_{jacc} diversity minimize the effect of reductions in α diversity, and (5) reductions in γ diversity as a result of reductions in both α and β_{jacc} diversity. Experiments are abbreviated as in Table 1.

† β_{jacc} measures spatial diversity in species composition that is attributable to (a) among-locality variation in α diversity (i.e., β_{gl}) and (b) among-locality substitution of species that is independent of among-locality variation in α diversity (i.e., β_{sim}) (Lennon et al. 2001, Koleff et al. 2003). Key: ↑, significant increase; ↓, significant decrease; 0, no significant change ($P < 0.05$).

Was the increase in β diversity that was commonly observed sufficient to maintain γ diversity despite reductions in α diversity? The increase in β diversity following N enrichment was only sufficient to maintain γ diversity despite reductions in α diversity in two experiments (Table 2: Category 2) but reduced the extent to which γ diversity declined in five experiments (Table 2: Category 4). An increase in β diversity was never sufficient to increase γ diversity even when α diversity was not affected by N enrichment. In one highly productive site, a reduction in γ diversity was associated with a reduction in both α and β diversity, suggesting that the extent of reduction in γ diversity was even greater than expected on the basis of responses by α diversity alone (Table 2: Category 5). This suggests that highly productive herbaceous communities may be especially sensitive to species loss through concomitant reductions in both α and β diversity following N enrichment.

In summary, experiments that only focus on α diversity may frequently overestimate (8 of 11 experiments where α diversity changed) or sometimes underestimate (1 of 11 experiments where α diversity changed) effects of N enrichment at larger spatial scales because N enrichment alters β diversity. Our analyses also show

that the effect of N enrichment on β diversity was consistent with the productivity-dependent biotic-homogenization hypothesis. N enrichment created spatial variation in the species composition of unproductive sites but reduced spatial variation in the species composition of productive sites. Consequently, at highly productive sites, there is a potential for biodiversity loss at large spatial scales to be even greater than expected on the basis of studies focusing on α diversity alone. Extrapolating results of experiments across spatial scales has proven to be a great challenge in ecology. Our results indicate that incorporating processes that affect both α and β diversity will greatly enhance our understanding of how N enrichment affects biodiversity at spatial scales that are of particular concern for conservation biology.

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APPENDIX

A table summarizing each of the experiments included in this study (*Ecological Archives* E089-123-A1).