

Jason D. Fridley

Resource availability dominates and alters the relationship between species diversity and ecosystem productivity in experimental plant communities

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Abstract Experimental evidence that plant species diversity has positive effects on biomass production appears to conflict with correlations of species diversity and standing biomass in natural communities. This may be due to the confounding effects of a third variable, resource availability, which has strong control over both diversity and productivity in natural systems and may conceal any positive effects of diversity on productivity. To test this hypothesis, I independently manipulated resource availability (soil fertility) and sown species diversity in a field experiment and measured their individual and interactive effects on productivity. Although fertility was a far stronger predictor of productivity than diversity, the effect of diversity on productivity significantly increased with fertility. Relative yield analyses indicated that plant mixtures of high fertility treatments significantly “overyielded,” or were more productive than expected based on monoculture yields of component species. In contrast, plant mixtures of low fertility treatments had significantly lower-than-expected yields. The effect of diversity on productivity was also driven by sampling effects, where more species-rich mixtures were more likely to include particularly productive species. Unexpectedly, the strength of sampling effects was largely insensitive to fertility, although the particular species most responsible for sampling effects did change with fertility. These results suggest that positive effects of species diversity on ecosystem productivity in natural systems are likely to be masked by variation in environmental factors among habitats.

Keywords Overyielding · Relative yield total · Sampling effect · Soil fertility · Species pool

Introduction

Plant species diversity has been shown to enhance ecosystem productivity (Naeem et al. 1994; Tilman et al. 1996, 1997a, 2001; Hector et al. 1999; Tilman 1999; Loreau 2000), but the reasons for this remain controversial (Huston 1997; Wardle 1999; Huston et al. 2000; Wardle et al. 2000). One common criticism of experiments that have investigated this relationship is that, in natural systems, plant diversity and productivity (measured as standing plant biomass) are either negatively correlated or show a unimodal pattern in diversity along a productivity gradient (Grime 1973; Huston 1979; Tilman 1982; Grace 1999; Waide et al. 1999). Most experiments in which production has been increased by enhancement of soil resource availability have shown a corresponding decline in species diversity (Kirchner 1977; Goldberg and Miller 1990; Gough et al. 2000). If increased production reduces diversity, can diversity nonetheless increase production? One possibility is that diversity does enhance production, but because factors such as resource availability control both diversity and production in natural systems, the positive effect of diversity on productivity is hidden when compared among ecosystems (Loreau 1998a, 2000; Tilman 1999). Studies that manipulate species diversity and resource availability independently could test for this possibility.

There is also disagreement concerning whether mechanisms by which diversity might promote productivity are likely to be similar in experimental and natural systems (Huston 1997; Wardle 1999; Huston et al. 2000; Wardle et al. 2000; Fridley 2001). In experiments where species assemblages are randomly constructed from a fixed species pool, species-rich plots have a higher probability of including those species that have the greatest individual effects on production, a phenomenon called the “sampling effect” (Aarssen 1997; Huston 1997; Tilman et al. 1997a). Determining whether sampling effects might apply in natural ecosystems has been difficult because no experiments have examined the sensitivity of sampling effects to environmental context. For ex-

J.D. Fridley (✉)
CB 3280, Coker Hall, University of North Carolina, Chapel Hill,
NC 27599–3280, USA
e-mail: fridley@unc.edu
Tel.: +1-919-9626934, Fax: +1-919-9626930

ample, sampling effects may be particularly important in environments that promote species dominance, where one or a few species have strong individual control over productivity (Fridley 2001). Resource availability often promotes species dominance in plant communities (Al-Mufti et al. 1977), suggesting that sampling effects should be greater in more fertile habitats. Higher production than expected from the sampling effect (“overyielding” *sensu* de Wit 1960; Trenbath 1974; Joliffe 1998) may be caused by complementary resource use or facilitative interactions among species (Vandermeer 1989; Tilman et al. 1997a, 2001; Hooper 1998; Hector et al. 1999). However, as for the sampling effect, the overyielding phenomenon is not well understood (Austin et al. 1988; Vandermeer 1989; Garnier et al. 1997; Fridley 2001).

To assess the relative degrees to which resource availability and species diversity influence productivity, whether these two factors interact, and whether resource availability alters the mechanisms by which diversity influences productivity, I performed a field experiment in which species diversity and resource availability were independently manipulated. I used a soil fertility gradient to manipulate resource availability and constructed plant communities of different levels of sown species richness and composition within these soil treatments. Specifically, my goals were to (1) test whether diversity directly enhances productivity by experimentally controlling resource availability; (2) determine the relative contribution of the sampling effect in enhancing production and the extent to which its role is affected by fertility, and (3) determine whether fertility influences the degree to which plant mixtures overyield.

Materials and methods

I constructed 360 raised-bed plots (50×50 cm, 15 cm deep) in an old field at Mason Farm Biological Reserve, North Carolina Botanical Garden, Chapel Hill, N.C., USA. Plots were arranged in three replicate blocks. Within size and climate restrictions, I chose a taxonomically diverse group of species with well-known growth characteristics (Table 1). These 10 species were grown in 10 compositions at each of three diversity levels (the 10 possible monocultures, 10 selected two-species “bicultures”, and the 10 possible nine-species “polycultures”). All 30 species compositions were grown at three fertility levels in each block, with all treatments ar-

ranged randomly within blocks. To examine the effect of monoculture density on overyielding analyses, each monoculture was also grown at half density at each fertility level in each of the replicate blocks. The 10 biculture species combinations were not chosen randomly; instead, combinations were chosen to provide a range of differences in species sizes (based on anticipated mature height), with the constraint that each species be represented in two compositions (Table 1). This deterministic construction of bicultures ensured that they would represent a full range of symmetric to asymmetric competitive interactions. Relatively large size disparities were represented by combinations of *Linum usitatissimum* + *Festuca ovina*, *Amaranthus hypochondriacus* + *F. ovina*, and *Fagopyrum esculentum* + *Satureja hortensis*; medium size disparities by *F. esculentum* + *Calendula officinalis*, *Borago officinalis* + *Hypericum perforatum*, *A. hypochondriacus* + *Avena sativa*, and *L. usitatissimum* + *A. sativa*; and small size disparities by *Achillea millefolium* + *H. perforatum*, *A. millefolium* + *S. hortensis*, and *B. officinalis* + *C. officinalis*.

Each plot was filled with a 1:1 mixture of sand and topsoil on top of porous black plastic, and plots of intermediate soil fertility were not further manipulated. Soil of high fertility plots was enriched with 125 g “Osmocote” slow-release fertilizer (6-month NPK; The Scotts Co., Marysville, Ohio, USA), equivalent to 90 g N, 30 g P, and 60 g K/m². I supplemented plots of low soil fertility with a 1:1 mixture of hardwood sawdust and table sugar, equivalent to 1.5 kg C/m². Soil additions for high and low fertility plots were performed on 31 May. In addition to reducing nutrient availability to plants, carbon supplementation may alter plant–microbe interactions and other soil processes (Schlesinger 1997); in this study, carbon addition strongly reduced biomass production but soil processes were not investigated.

I established experimental plant communities of different composition and diversity by sowing seed at two different times during the growing season. Total live seed mass rather than seed number was held constant at 4 g (2 g per seed addition) among plots to account for the differences in recruitment success among species of various seed sizes. Live seed mass was calculated by dividing desired live mass by the germination rate of the species (for monocultures), or by dividing the total live mass by 2 (for bicultures) or 9 (for polycultures) and then dividing this value by each species’ germination rate. Initial planting dates among eight of the ten species were spread over several weeks so that species would germinate at approximately the same time (Table 1). On 8 July, *A. hypochondriacus* and *A. sativa* were added to their respective plots to replace two species that failed germination and the second seed addition for the remaining eight species was performed. Seed of each species (except *A. hypochondriacus* and *A. sativa*) was added in two cohorts to generate more realistic communities of neighbors of different growth stages.

Plots were weeded weekly and watered daily with an automatic sprinkler irrigation system. *B. officinalis*, having gone to seed and senesced, was harvested from all plots on 2 August. *F. ovina* performed poorly and could not be accurately harvested. All remaining species were harvested on 17–19 August after all except

Table 1 Species of the experimental species pool. *Festuca ovina* (FEOV) was not harvested (see Materials and methods) and is not listed. Biculture pairings are the two species that co-inhabited bi-

cultures with the listed species. Biculture compositions were chosen to provide a range of differences in species sizes. Species nomenclature follows Kartesz (1994)

Species	Abbr.	Family	Life-history	Biculture pairings	First sowing
<i>Achillea millefolium</i>	ACMI	Asteraceae	Perennial herb	HYPE, SAHO	2 June
<i>Amaranthus hypochondriacus</i>	AMHY	Amaranthaceae	Annual herb	AVSA, FEOV	8 July
<i>Avena sativa</i>	AVSA	Poaceae	Annual grass	AMHY, LIUS	8 July
<i>Borago officinalis</i>	BOOF	Boraginaceae	Annual herb	CAOF, HYPE	1 June
<i>Calendula officinalis</i>	CAOF	Asteraceae	Annual herb	BOOF, FAES	1 June
<i>Fagopyrum esculentum</i>	FAES	Polygonaceae	Annual herb	CAOF, SAHO	21 June
<i>Hypericum perforatum</i>	HYPE	Hypericaceae	Perennial herb	ACMI, BOOF	9 June
<i>Linum usitatissimum</i>	LIUS	Linaceae	Annual herb	AVSA, FEOV	1 June
<i>Satureja hortensis</i>	SAHO	Labiatae	Annual herb	ACMI, FAES	9 June

Table 2 Summary tables for two type I SS ANOVA models describing treatment effects on total aboveground biomass. Model A includes the effects of fertility, seeded diversity, and the diversity–fertility interaction without considering other aspects of species composition. Model B describes the residual effects of diversity after accounting for the effects of particular species. Species terms are dummy variables that indicate source variation from the presence or absence of that species; only species that were significant predictors of productivity when listed in an ANOVA model by themselves are included. Note: Data were square-root transformed

Source of variation	df	SS	MS	F
Model A:				
Block	2	341.9	171.0	9.2**
Seeded diversity	2	941.6	470.8	25.4***
Fertility	2	2,765.9	1383.0	74.5***
Diversity × fertility	4	231.9	58.0	3.1*
Error	325	6,034.6	18.6	
Model B:				
Block	2	341.9	171.0	11.1***
Fertility	2	2,805.8	1,402.9	90.8***
<i>L. usitatissimum</i>	1	1,492.1	1,492.1	96.5***
<i>B. officinalis</i>	1	391.3	391.3	25.3***
<i>C. officinalis</i>	1	51.3	51.3	3.3
<i>F. esculentum</i>	1	0.1	0.1	0.0
<i>S. hortensis</i>	1	110.4	110.4	7.1**
<i>A. hypochondriacus</i>	1	79.3	79.3	5.1*
Seeded diversity	2	50.4	25.2	1.6
Error	323	4,993.2	15.5	

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

H. perforatum and *S. hortensis* had gone to seed. All aboveground biomass was dried to constant mass and each harvested individual plant was weighed to the nearest tenth gram.

I used type I SS fixed-effect ANOVA models to test square-root transformed total aboveground biomass against the main effects of fertility and diversity, their interaction, and the presence or absence of particular species. Several biomass values were excluded from these analyses, including all *F. ovina* monoculture values (not harvested) and six bare plots, leaving a total dataset of 336 plots. Monoculture density had no effect on monoculture production (Wilcoxon test, $P > 0.15$, $n_1 = 78$, $n_2 = 81$), probably because the half-density treatment was sufficient to maximize yield, so I pooled values from monoculture density treatments. Because diversity and species composition are highly correlated in this experimental design (i.e., the diversity of a given plot is perfectly described by the presence or absence of all species), a comparison of “diversity” effects versus “composition” effects had to be performed using separate models. A first model included only the effects of block, fertility, diversity, and the diversity–fertility interaction (Table 2 A). A second model included block, fertility, dummy variables describing the presence or absence of the six species that significantly influenced productivity when included alone in separate ANOVAs, and a diversity term listed last to assess whether seeded diversity could explain any residual variation (Table 2 B). Finally, I listed each composition-related variable first in a type I SS ANOVA to obtain the most liberal estimates for each factor’s magnitude of effect, or total sum of squares of the biomass response variable attributed to each factor (Welden and Slauson 1986). These factors are listed in Fig. 1.

I used two different metrics to estimateoveryielding. Relative yields were defined as a species’ biomass in mixed culture (biculture or polyculture) divided by its monoculture biomass for the same block and fertility level (de Wit 1960; Hector 1998). Relative yield totals (RYT) were the summed relative yields for all species in a particular mixture. D_{\max} was defined as: (total biomass of mixed culture – monoculture biomass of its component species with the largest monoculture value) / monoculture biomass of

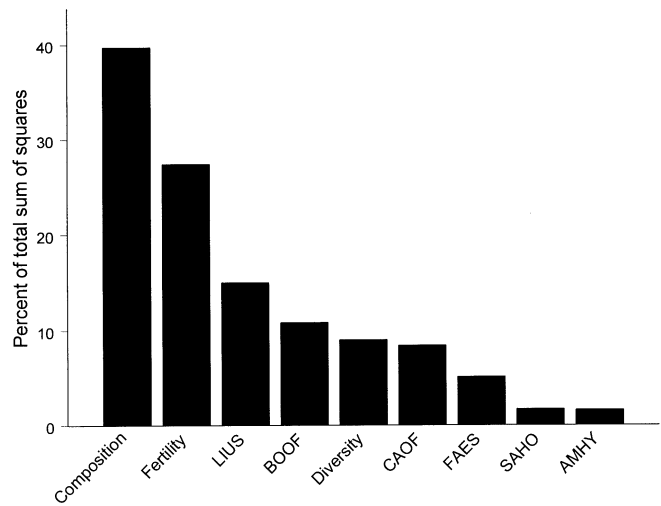


Fig. 1 Magnitudes of effect for significant factors predicting total aboveground biomass. Species diversity was a significant but weak predictor of productivity compared to fertility, total species composition, and the presence or absence of particular species (species codes listed in Table 1). Bars indicate the associated sum of squares for each factor predicting (square-root transformed) total aboveground biomass when listed individually in a type I SS ANOVA model

component species with largest monoculture value (Loreau 1998b; Hector et al. 1999). D_{\max} is a more stringent test than RYT for the detection ofoveryielding, but RYT is a better descriptor of the mechanisms underlyingoveryielding, and caution must be used in the interpretation of both metrics (Garnier et al. 1997; Loreau 1998b; Fridley 2001). I square-root transformed RYT and D_{\max} values for fixed-effect ANOVAs to achieve normal residual distributions, and zero values (due to bare plots) and several spuriously high values (>5) were excluded.

I also measured the role of sampling effects among fertility levels in two ways. To compare total sampling effects among fertility levels, I used the “selection effect” metric of the “additive partition of biodiversity effects” technique of Loreau and Hector (2001). This estimates a sampling effect for each plant mixture by calculating the covariance between species’ monoculture yields and their deviance from expected relative yields in mixture (based on their planted proportions), multiplied by the total number of species in mixture. If species of higher-than-average monoculture values dominate a mixture, the associated selection effect is positive; dominance by smaller, less productive species leads to negative selection effect values. Selection effects were square-root transformed within fertility levels to achieve normality (following Loreau and Hector 2001). To determine which species were most responsible for sampling effects at each level of fertility, I calculated the magnitude of effect for each species as dummy variables in separate ANOVAs for each fertility level (Hector et al. 1999).

Results

Soil fertility, sown species diversity, and species composition were all significant predictors of total aboveground biomass (Table 2). When listed alone in separate ANOVA models, total species composition had the strongest effect on production, explaining 40% of the variation in biomass among plots, followed by soil fertility (27%), the presence of *L. usitatissimum* (15%), *B. officinalis* (11%), diversity, and the presence of four other

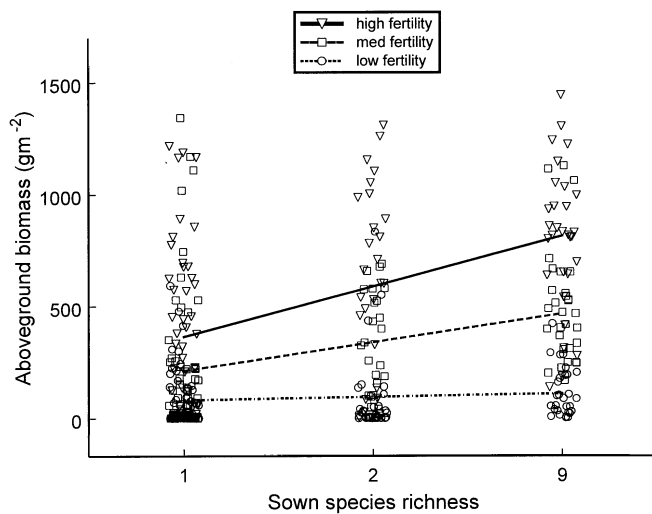


Fig. 2 The interaction between sown species diversity and soil fertility in the control of total aboveground biomass. The effect of diversity increased with fertility. Linear regression lines are for fertility treatment subsets of plot biomass data. Data values are jittered along the x -axis for clarity

species (Fig. 1). Diversity only accounted for 9% of the total sum of squares for plot biomass, even when other aspects of species composition were not considered, and was not a significant predictor of production after accounting for the effects of composition (Table 2). In addition, there was a significant interaction between fertility and diversity in the control of production ($P < 0.05$): the diversity effect was marginal in plots of low fertility but increased with nutrient availability, as shown by differences in slopes of separate regression lines for each fertility level (Fig. 2). Production was also significantly influenced by blocking treatment, likely due to slightly different flow rates in the irrigation system, the sprinklers of which were grouped by block.

The effect of the presence or absence of particular species on production, a measure of the sampling effect, was large (Fig. 1), and positive “selection” effects were observed at each level of fertility (Fig. 3). Although calculated selection effects were significantly higher in plots of intermediate fertility than in those of low fertility (Wilcoxon test, $P < 0.001$, $n_1 = 46$, $n_2 = 50$), there was no clear evidence that fertility promoted sampling effects across the whole fertility gradient due to the wide variation of the selection effect metric at the highest fertility level (Fig. 3). Moreover, the two species that had the greatest individual effects on production, *L. usitatissimum* and *B. officinalis*, had their peak effects on opposite sides of the fertility gradient (Fig. 4). Thus, although there was no overall trend of sampling effect magnitude along the fertility gradient, the particular species responsible for positive sampling effects did change with fertility.

As measured by the RYT, overyielding in plant mixtures was significantly affected by fertility ($P < 0.01$, $n = 133$) but not by whether the mixture included two or

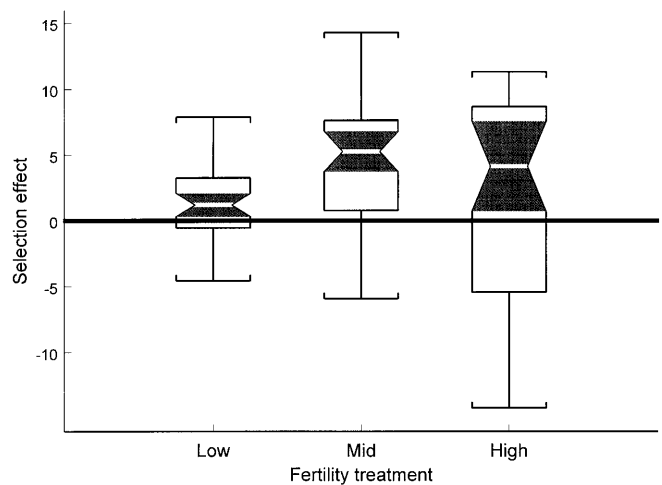


Fig. 3 Sampling effects in plant mixtures among fertility levels, as calculated by the “selection effect” technique of Loreau and Hector (2001). Positive sampling effects occurred at each fertility level. Box plots indicate the range of the data between brackets, the middle two quartiles within the *box*, the median value as the *white midline*, 95% confidence intervals as *shaded and notched areas*, and extreme outliers as *dots*. Selection effect values were square-root transformed

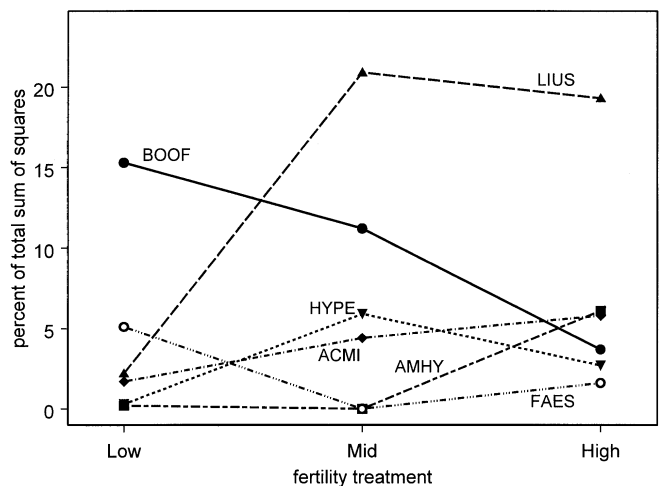


Fig. 4 Magnitudes of effect for the presence or absence of certain species separated into three fertility treatments. *Borago officinalis* (BOOF) and *Linum usitatissimum* (LIUS) traded-off in importance along the fertility gradient. Percentage of total sum of squares values were derived from ANOVAs of treatment and species effects on biomass performed separately for each fertility level. See Table 1 for species codes

nine species ($P > 0.5$). Bicultures and polycultures exhibited significant overyielding at high fertility (Wilcoxon, $\mu > 1$, $P < 0.05$, $n = 43$) and significant underyielding at low fertility ($\mu < 1$, $P < 0.05$, $n = 43$). At intermediate fertility RYT values were not significantly different from unity ($P > 0.5$, $n = 47$) (Fig. 5). However, a more conservative overyielding estimate, by the calculation of D_{\max} values, did not indicate overyielding, whether analyzing plant mixtures as a group or within fertility levels (Wilcoxon, $\mu = 0$, $P < 0.001$, $n = 163$), although low fertility D_{\max} values

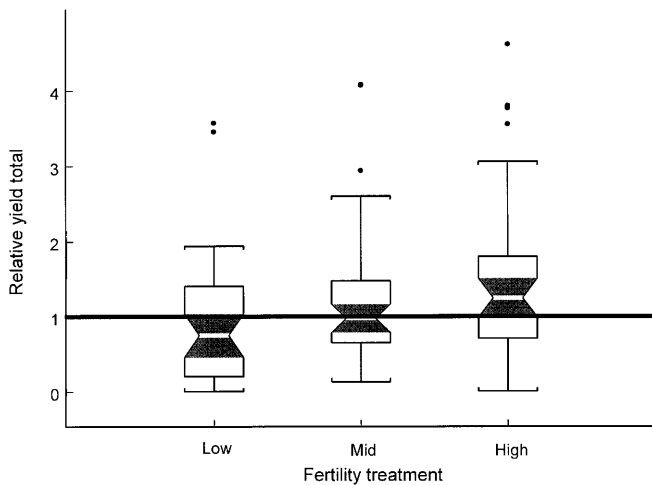


Fig. 5 Overyielding in plant mixtures among fertility levels, as calculated by the relative yield total (RYT). Mixtures of high fertility overyielded; those of low fertility underyielded. Box plot specifications are the same as those listed in Fig. 3. Overyielding is indicated by RYT values above unity; values below unity constitute underyielding

were significantly lower than those of medium fertility (Wilcoxon, $P < 0.05$).

Discussion

When manipulated independently in a field experiment using artificial plant communities, soil fertility, sown species diversity, and species composition all significantly influenced productivity. Composition and fertility had much larger effects on production than diversity (Fig. 1), which indicates that, although the richness of the potential colonizing species pool can play a role in ecosystem function, its effects are likely to be overwhelmed by site differences and species identity (Loreau 1998a, 2000; Wardle et al. 2000). The relative importance of these factors could be influenced by experimental design, including the range of the fertility gradient, the traits of the species chosen, and the selected biculture compositions. However, it is likely that the relatively large effects of species identity and environmental factors, compared to the much smaller effects of species diversity, can be generalized. Of the two large-scale diversity–productivity experiments conducted to date, the results of Hector et al. (1999) suggest that the effects of environmental factors on productivity are, at a minimum, nearly twice as large as those of species diversity; Tilman et al. (2001) did not separate magnitude of effect estimates for species diversity from those of composition.

On average, sown species diversity had little effect on production in plots of low fertility, but species-rich plots were twice as productive as monoculture plots at high fertility (Fig. 2). Part of this interaction can be explained by the effects of fertility on overyielding, as measured by relative yields (Fig. 5). Why did plant mixtures in high-fertility plots overyield? There are two possibilities. The

first is that soil fertility promoted complementary resource use among species, allowing the capture of more total resources in mixtures compared to monocultures (Austin et al. 1988; Vandermeer 1989; Hooper 1998). The species used, however, were of similar growth types and life-histories and the plots were small and probably contained little heterogeneity other than a vertical light gradient. Complementary use of any resource other than light was therefore unlikely; light partitioning has been suggested as a mechanism of diversity effects (Naeem et al. 1994) but it is unclear whether this would be promoted by soil fertility.

The other possible explanation is that fertility promoted facilitative interactions among species, such that “nurse plant”-type interactions (Turner et al. 1966) occurred in the most fertile plots. Plot substrates were 50% sand; although watered daily, plants may have been susceptible to water stress, particularly at midday. Seeds were added in two cohorts, such that seedlings of species that could not establish due to water stress in the first cohort may have been protected by canopy shade if a suitable canopy was established prior to second sowing. Plots of high fertility had such a canopy by the time of second cohort addition, while those of low fertility generally had small plants with no canopy. Indeed, plot biomass, a reasonable estimator of canopy extent, was a strong predictor of relative yield total ($R^2 = 0.72$, unpublished analysis). However, greater canopy extent with added soil nutrients might also lead to greater water stress for understory seedlings due to a higher total rate of plot water consumption, especially in sandy soil (Ewers et al. 2000; Phillips et al. 2001). A more physiological approach is required to fully determine mechanisms responsible for this fertility–overyielding interaction.

A much larger effect of diversity on production occurred by means of sampling effects for particularly influential species, consistent with other similar studies of experimental plant communities (Tilman et al. 1996; Huston 1997; Tilman 1997; Hector et al. 1999; Huston et al. 2000; Leps et al. 2001; but see Tilman et al. 2001). However, despite the expectation that sampling effects promoting ecosystem productivity should increase with soil fertility, there was little evidence that this occurred as estimated by the selection effect metric over all three fertility levels (Fig. 3). The explanation of this relative insensitivity of sampling effects to fertility may be that fertility does promote a sampling effect for fast-growing, competitive species, but a different sampling effect for species tolerant of stressful conditions operated in plots of low fertility, exhibited by the reversal of the importance of *B. officinalis* and *L. usitatissimum* along the fertility gradient (Fig. 4). Thus, in addition to the increasing probability of selecting more competitive species in species-rich assemblages, sampling effects should also include the greater likelihood of selecting species better adapted to particular habitats, such as those of high nutrient stress. These two separate phenomena have been termed the “performance” and “habitat” sampling effects, respectively (Fridley 2001).

Because this experiment included variation of seeded species diversity rather than a manipulation of standing plot diversity, it may offer grounds for reconciling the apparent conflict between the often negative effects of increased production on diversity and the positive average effects of diversity on productivity in randomly assembled diversity experiments. This paradox may be resolved by recognizing that diversity is being considered at different scales. High local production may reduce local diversity due to competitive dominance, especially for light (Grime 1979; Huston 1979; Tilman 1982; Grace 1999). However, a larger pool of potential colonizing species represents a larger range of species traits from which local environmental conditions “sample,” thereby increasing the probability of establishment of species with large individual effects on local production (Tilman 1999; Fridley 2001). In the first instance local, realized diversity is the result of a competitive filtering of the species pool available to colonize a particular ecosystem (Pärtel et al. 1996); in the latter, the diversity of the species pool itself directly affects local production. In this experiment, diversity treatments modeled variation in species pool diversity, not local diversity (although these measures of diversity were correlated, as they often are in natural systems; Cornell 1999). Seeded diversity promoted production largely by means of sampling effects for both highly productive species and stress-tolerant species. At the same time, the considerably greater effect of fertility on production in this experiment suggests that local environmental conditions should have much stronger effects on local ecosystem function than the diversity of the species pool.

Although the design of this study was similar to other plant diversity–productivity experiments (e.g., Naeem et al. 1996; Tilman et al. 1996; Symstad et al. 1998; Hector et al. 1999; Naeem et al. 1999), two caveats in extrapolating these results must be emphasized. First, seven of the ten species of the species pool were annuals; although taxonomically diverse, these ruderals (*sensu* Grime 1973) would not be expected to exhibit the same range of morphological and physiological diversity of a more natural, perennial community. In particular, studies using species of greater functional diversity, conducted within larger plots, and of longer duration would be more likely to generate complementary species relationships, especially those based on phenology (Tilman et al. 1997b; Hooper 1998). Indeed, a consortium of researchers using similar experimental communities, but over 2 years and with ambient species pools, concluded that sown species diversity had similar effects on production across a wide range of environmental conditions (Hector et al. 1999; but see Huston et al. 2000). (Interestingly, their data also indicate that diversity had no effect on production at their least productive site, consistent with the present study.) Second, if sampling effects for especially productive or stress-adapted species are a primary means by which diversity enhances productivity, species identity and environmental context will play a large role in generating diversity–productivity relationships. It is

therefore particularly important that interactions between local and regional processes in the control of ecosystem function be investigated using a wide range of species pools and environmental gradients.

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