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Realistically Low Species Evenness Does Not Alter Grassland Species-Richness-Productivity Relationships

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Keywords

grasslands, prairies, primary productivity, rank–abundance relationships, species diversity, species evenness, species richness

Disciplines

Biodiversity | Ecology and Evolutionary Biology

Comments

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REALISTICALLY LOW SPECIES EVENNESS DOES NOT ALTER GRASSLAND SPECIES-RICHNESS–PRODUCTIVITY RELATIONSHIPS

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Abstract. Biodiversity is declining worldwide from reductions in both species richness and evenness. Field experiments have shown that primary productivity is often reduced when richness of plant species is lowered. However, experiments testing richness effects have used evenness levels that are much higher than normally encountered in plant communities and have been based on the assumption that species extinctions are random. We experimentally varied, for the first time, both species richness (1–8 perennial species/m²) and species evenness (near maximal vs. realistically low) in grassland plots. Net primary productivity (NPP) and ecosystem CO₂ uptake declined when richness was reduced, and reductions were similar between evenness treatments. Richness effects were associated more with a selection effect than with complementarity (found only with high evenness). Importantly, extinctions in plots during the second year were not random, but were greater at low than at high evenness (i.e., with increased rarity) and in species with low aboveground growth rates. Thus, species evenness can affect grassland ecosystem processes indirectly by affecting species richness, and it will be imperative to understand how nonrandom extinctions affect NPP in future studies. Our results indicate that richness studies may not be biased by using mixtures with artificially high evenness levels, but the results also demonstrate that results from these studies are directly applicable only to communities in which plant extinctions are random.

Key words: grasslands; prairies; primary productivity; rank–abundance relationships; species diversity; species evenness; species richness.

INTRODUCTION

Biodiversity is declining worldwide from reductions in both species richness and evenness (Pimm et al. 1995, Chapin et al. 2000, Sala et al. 2000). Species richness is the number of species, and evenness is the equitability of relative abundance or biomass among species. Several studies have found log-linear reductions in plant productivity when species richness was experimentally lowered at the plant neighborhood scale (i.e., small plots; Schapfer and Schmid 1999, Loreau et al. 2001). These results, which were well replicated both within (Tilman et al. 1996, 2001) and among sites (Hector et al. 1999), suggest that ecosystem services may be impaired by a reduction in small-scale species richness. However, two important complications in these experiments have prevented many scientists from accepting their relevance to real communities.

First, experimental plots usually are created with seed mixes that maximized species evenness. Species evenness is usually much lower than maximum in real communities (Huston 1997, Grime 1998), with a few dominant species being relatively abundant and many

species being rare. Species evenness has been shown to be an equally or more important component of small-scale plant diversity than species richness. Evenness alone accounted for 53% of the variation in species diversity (Shannon's H'), whereas species richness accounted for only 6% of the variation across community types in a recent literature review (Stirling and Wilsey 2001). Furthermore, experiments have shown that evenness can be important to grassland primary productivity and invasion resistance (Wilsey and Potvin 2000, Wilsey and Polley 2002). Schwartz et al. (2000) argued that primary productivity would have saturated at a much lower species richness level in productivity–richness studies if a realistically low species evenness was used. In communities with very low species evenness (i.e., having one or a few species having very high relative abundance), the community may behave much more like the dominant species would in monoculture (Mulder et al. 2001).

Second, the mechanism responsible for the decrease in net primary productivity (NPP) with lowered species richness is still largely in doubt because experimental mixtures were assembled from random draws from a species pool (Aarssen 1997, Huston 1997, Smith and Knapp 2003). As a result, local extinction of species is simulated as a random process, contrary to the pattern of greater regional extinction rates in rare species

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PLATE 1. The experimental field plots (foreground) on 7 July 2002. Photo credit: Katherine Jones.

(Fischer and Stocklin 1997, Duncan and Young 2000). Positive richness–productivity relationships may arise due to the greater probability of including a species with more extreme traits as the number of species increases (Aarssen 1997, Huston 1997, Tilman et al. 1997), rather than by complementary resource use or facilitation among species (Tilman et al. 1997, 2001, Loreau and Hector 2001, Mulder et al. 2001). A prediction arising from the selection effect hypothesis is that the most productive species in monoculture will dominate mixtures and cause their productivities to be higher than in plots without these species (Loreau and Hector 2001). Alternatively, the complementarity hypothesis predicts that functional differences among species enable greater resource uptake by the community as a whole, and that the species that do better in mixture are not necessarily the ones that grow best in monoculture (Loreau and Hector 2001, Tilman et al. 2001). By using a maximally even species distribution, previous richness experiments may have overestimated the complementarity effect. This would make results difficult to apply to real communities, where evenness is lower than maximum (May 1981, Tokeshi 1993, Huston 1997, Grime 1998, Smith and Knapp 2003). Virtually nothing is known about whether evenness affects the species interactions underlying the complementarity effect. At lower than maximal evenness, the idiosyncratic effects of dominant species may dampen or eliminate complementarity effects if evenness affects the outcome of species interactions.

We varied, for the first time, both species richness and evenness in the same experiment to test the hypothesis that realistically low levels of species evenness constrain productivity responses to species richness. By planting plots with both high and low evenness, and by monitoring plots over time, we also were able to test the hypothesis that extinction rates are higher with low evenness at the plant neighborhood scale.

Varying species evenness provides a way of testing for diversity effects without having the sampling effect (Wilsey and Potvin 2000, Loreau et al. 2001, Wilsey and Polley 2002, Polley et al. 2003), because species diversity can be varied without changing the identity of species within plots. Furthermore, by planting equal-sized transplants into field plots, rather than seeding plots as in earlier studies, we were able to control initial plant density and minimize differential establishment across species. We tested the hypothesis that having realistically low species evenness will constrain plant productivity responses to species richness. If relationships turn out to be similar between evenness treatments, then it would suggest that species evenness and richness have additive effects, and that previous studies of species richness with maximal evenness may be applicable to real grassland communities.

METHODS

Experimental design

Evenness can be varied either by increasing the abundance of one species (Nijs and Roy 2000, Wilsey and Potvin 2000, Wilsey and Polley 2002) or by varying rank–abundance relationships among all species. Natural and semi-natural communities have rank–abundance slopes that are much lower than zero, and it has been shown that slopes become steeper with excessive stress or disturbance (Bazzaz 1975, May 1981, Lugo 1991, Tokeshi 1993). We varied species evenness in experimental plots by varying the slope of rank–abundance relationships in communities with the same species richness and plant densities. Thus, we compared communities with realistically steep rank–abundance slopes with communities that have unrealistically shallow slopes.

We compared planted experimental communities with maximal evenness to communities with a geometric distribution of abundances among species found

in the Blackland Prairie Region of Central Texas, USA (see Plate 1). The soil at the site is a vertisol, and the climate is subhumid with an average of 864 mm of rainfall per year. We varied both richness and evenness in a factorial design in $75 \times 1 \times 1$ m plots, each planted with 96 equal-sized transplants. Species richnesses of 2, 4, and 8 were established by randomly drawing species from a larger pool of 13 frequent Texas Blackland perennial prairie species. Legumes were not included because they normally compose only $\sim 1\%$ of the productivity of Blackland prairie communities (Wilsey and Polley 2003). Species used were *Schizachyrium scoparium*, *Sporobolus asper*, *Bothriochloa saccharoides*, *Bouteloua curtipendula*, *Sorghastrum nutans*, *Bothriochloa ischaemum*, *Paspalum dilatatum*, and *Panicum coloratum* (C_4 grasses), *Nassella leucotricha* (C_3 grass), and *Ratibida columnifera*, *Oenothera speciosa*, *Salvia azurea*, and *Echinacea purpurea* (C_3 forbs). Random draws (six for each of the 2-, 4-, and 8-species treatments) were made from these 13 species. After draws were made, we randomly assigned relative abundance positions for communities to have either maximal evenness (or equal distribution of abundance and initial biomass among species, 48 individuals each in 2-species mixes, 24 each in 4-species mixtures, and 12 individuals each in 8-species mixtures) or a more realistically low evenness based on a geometric distribution among species which produced rank-abundance slopes of approximately -0.30 (64:32 in 2-species, 51:26:13:6 for 4-species, and 47:24:12:6:3:2:1:1 in 8-species mixtures). Thus, for each random draw, the high and low evenness treatments had the same species. The evenness treatments had slopes that are at the extremes of the normal range of Blackland prairie communities (H. W. Polley, J. D. Derner, and B. J. Wilsey, unpublished data). Three replicate monocultures were also planted for each of the 13 species. Thus, there were 3 richness levels \times 2 evenness levels \times 6 replicates (random draws) = 36 + 39 monocultures = 75 plots (and $75 \times 96 = 7200$ plants). Treatments were randomly assigned within 3 blocks, each with 25 plots.

We planted each plot during 19–25 April 2001. Plants were grown in greenhouses in Blackland soil taken from the field, trimmed to equal size, and then transplanted from square 10-cm pots back into the same field on lands of the Grassland, Soil, and Water Research Lab, Temple, Texas. There was $>95\%$ survival among transplants during the initial planting; plants that did not survive the original planting were replaced ~ 2 wk later. Plants achieved complete canopy closure during the first growing season. Plots were hand weeded when necessary.

Net primary productivity

Aboveground plant productivity was estimated by measuring peak biomass during October of each year by clipping all plants to 2 cm height. Peak biomass is a reasonably good estimator of net aboveground pri-

mary productivity in this system because frost kills aboveground biomass during the winter and there is no carryover from year to year. A 45 cm deep soil core (4.2 cm diameter) was removed from each plot during fall 2001. During 2002, this sampling regime was increased to two cores per plot. Each core was sectioned into an upper “shallow” (<20 cm) and lower “deep” (20–45 cm) layer to examine differences in rooting depth. Root productivity cannot be directly estimated with peak root biomass, because some root biomass carries over from year to year. Nevertheless, biomass provides a relative measure of root accumulation that was comparable between treatments.

We tested for main effects of richness, evenness, and their interaction with a randomized-block split-plot repeated-measures ANOVA, with richness effects in the main plot (using $\text{rep}[\text{block} \times \text{richness}]$ as the error term), and evenness effects and interactions in the subplot. Thus, with this design, evenness and richness \times evenness interactions were tested after we accounted for differences in species composition ($\text{rep}[\text{block} \times \text{richness}]$). A priori linear and log-linear contrasts were used to test for richness effects. Means from each treatment were compared to the average value of all monocultures (Loreau and Hector 2001) to determine if overyielding occurred in plots, and if overyielding responses among richness groups were affected by species evenness. The additive partitioning method outlined by Loreau and Hector (2001) was employed to partition these net effects into selection and complementarity effects.

Ecosystem CO_2 exchange

Net ecosystem CO_2 exchange (NEE) was measured on replicates 1, 3, and 5 of treatments during June 2001, and on replicates 2, 4, and 6 during October 2001, and on all plots during June 2002, with a temperature and humidity-controlled clear polycarbonate chamber placed over 50×50 cm angle iron collars placed to 5 cm below the soil surface (Angell and Svejcar 1999, Stocker et al. 1999, LeCain et al. 2000). Thus, ANOVAs were similar to productivity models, except that time was not treated as a repeated-measures term (years were analyzed separately). The chamber was connected to a LI-COR 6262 infrared gas analyzer (LI-COR, Lincoln, Nebraska, USA) and was operated in a closed configuration. Temperature and relative humidity within the chamber were controlled by pumping ice water through a small car radiator attached to the inside of the chamber (Waddington and Roulet 1996, Wilsey et al. 2002). A fan blew air over the radiator, mixing air and distributing cool air within the chamber. Temperature was maintained within $2^\circ C$ of ambient temperatures during measurements. A LI-COR PAR sensor was placed inside the top of the chamber (Wilsey et al. 2002). Measurements of CO_2 within the chamber were made every 5 s for 90 s, and remained linear during the duration of the sampling period. A slope of the CO_2

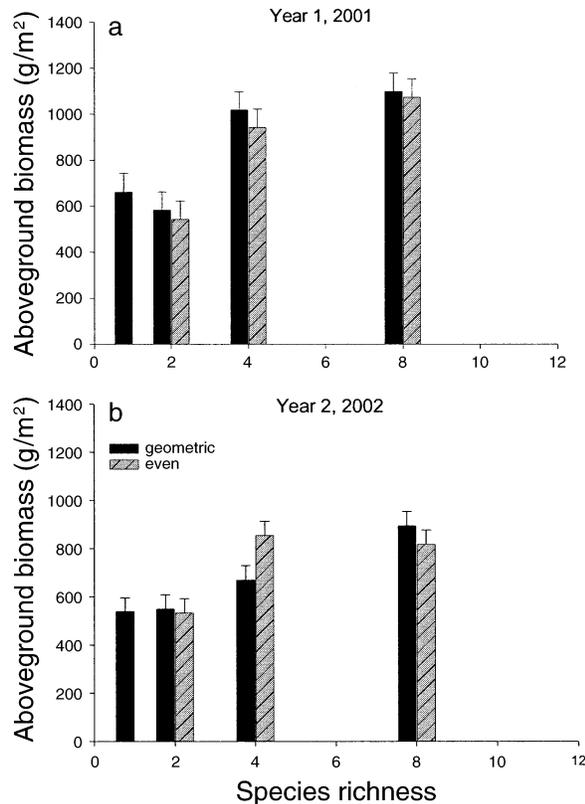


FIG. 1. Peak aboveground biomass (least-square means + 1 SE) in experimental plots planted with 1, 2, 4, or 8 species either with high or low (geometric) species evenness during (a) 2001 and (b) 2002 in the Blackland Prairie Region, Texas, USA.

concentration in the chamber over time was then calculated (micromoles per mole per second). The slope was multiplied by the effective volume of the chamber (44.6 mol/m^2), which results in a carbon flux in micromoles per square meter per second (Ruimy et al. 1995).

Measurements of NEE were made under three light conditions: ambient light, reduced light, by placing a shade screen over the chamber, and under darkness, by placing a black shade cloth over the chamber (Wilsey et al. 2002). The NEE and light measurements were used to develop regression relationships between PPFD (photosynthetic photon flux density) and NEE following Ruimy et al. (1995). We fit the following linear and hyperbolic equations:

$$\text{NEE} = \alpha \text{PPFD} - R \text{ (linear)}$$

$$\text{NEE} = \frac{\alpha \text{PPFD} \times \text{NEE}_{\max}}{\alpha \text{PPFD} + \text{NEE}_{\max}} - R \text{ (hyperbolic)}$$

where α is apparent quantum yield (initial slope in the hyperbolic equation), NEE_{\max} is NEE maximum, and R is dark respiration rate, or NEE at $\text{PPFD} = 0$. Net CO_2 uptake (NEE_{1800}) was then derived from the data as NEE with PPFD of $1800 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, or at optimum light. Gross productivity was derived as $R + \text{NEE}_{1800}$.

Local extinction rates

We tested whether local extinction rates varied among richness and evenness treatments by subtracting richness levels at the end of the second growing season from planted values, and then conducting an ANOVA as explained in the previous section. The local extinction rate for each species was calculated as the number of plots from which it went extinct divided by the number of plots in which it was planted. Because the identity of dominant and rare species within a given evenness treatment was determined randomly, mean relative abundances did not vary across species. Local extinction rates did not differ between grasses and forbs ($P > 0.10$).

RESULTS

During the two years of our experiment, aboveground peak biomass was log-linearly related to planted species richness (contrast $F_{1,13} = 9.9$, $P = 0.01$; Fig. 1). Significant effects of richness were found during both years (richness \times year interaction, $F_{2,13} = 1.2$, $P = 0.3$), and species richness accounted for 37% and 25% of the variation in biomass in 2001 and 2002, respectively. Peak biomass did not significantly differ between species evenness treatments ($F_{1,15} = 0.9$, $P = 0.3$), and the log-linear increase in peak biomass was similar between the high and low evenness distributions (interaction, $F_{2,15} = 1.8$, $P = 0.2$).

Biomass of shallow roots ($<20 \text{ cm}$) also increased log-linearly with species richness ($F_{1,13} = 5.3$, $P = 0.04$, r^2 values = 0.10, 0.29 for year 1 and 2, respectively), and this effect was found in both years (Table 1). Shallow-root biomass tended to be greater at high (136.5 g/m^2) than at low evenness (104.1 g/m^2) during year 1 ($F_{1,15} = 3.2$, $P = 0.09$), but evenness did not alter the richness effect (interaction, $P = 0.7$). Deep

TABLE 1. Shallow- and deep-root biomass (least-square means for mixtures and means for monocultures, with 1 SE in parentheses) in experimental plots planted with 1, 2, 4, or 8 species, either with high evenness (E) or low evenness (geometric, G).

Richness	Evenness	Shallow (<20 cm)	Deep (20–45 cm)
2001 (year 1)			
1		116.7 (12.3)	52.8 (7.3)
2	E	103.1 (30.1)	48.7 (11.3)
	G	79.5 (30.1)	55.3 (11.3)
4	E	171.4 (30.1)	37.4 (11.3)
	G	115.3 (30.1)	59.9 (11.3)
8	E	135.0 (30.1)	59.3 (11.3)
	G	117.5 (30.1)	42.2 (11.3)
2002 (year 2)			
1		169.2 (22.4)	40.0 (6.1)
2	E	79.7 (28.1)	22.1 (6.2)
	G	102.8 (28.1)	28.2 (6.2)
4	E	193.8 (28.1)	39.1 (6.2)
	G	238.1 (28.1)	40.8 (6.2)
8	E	213.1 (28.1)	53.5 (6.2)
	G	197.3 (28.1)	23.6 (6.2)

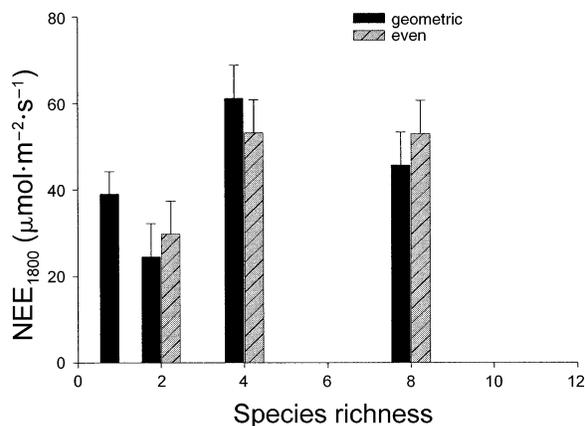


FIG. 2. Net ecosystem CO₂ exchange (NEE₁₈₀₀; least-square means + 1 SE) at full light in experimental Blackland Prairie plots planted with 1, 2, 4, or 8 species either with high or low (geometric) species evenness during June 2001.

roots (20–45 cm) increased with species richness only in high evenness plots ($F_{2,15} = 5.4$, $P = 0.02$), and this effect was linear in nature (linear contrast, $F_{1,13} = 5.7$, $P = 0.03$ in high evenness plots, $F_{1,13} = 2.7$, $P = 0.12$ in low evenness plots) (Table 1).

Ecosystem CO₂ uptake (NEE₁₈₀₀) increased significantly as species richness increased (Fig. 2), but only for the June dates (month × richness interaction for year 1, $F_{2,13} = 7.3$, $P < 0.01$; log-linear contrast for year 2, $F_{1,15} = 4.1$, $P = 0.06$). During June of 2001, NEE₁₈₀₀ increased log-linearly with richness (log-linear contrast for June, $F_{1,6} = 7.3$, $P = 0.03$). There was no significant difference among richness treatments in ecosystem respiration (all P values > 0.10). Respiration was higher during June (12.0 ± 0.9 μmol·mol⁻¹·s⁻¹ [mean ± 1 SE]) than during October of 2001 (4.8 ± 0.3 μmol·mol⁻¹·s⁻¹). Gross primary productivity generally followed the trends in NEE₁₈₀₀ (see Appendix): It increased with species richness during June of both years (month × richness interaction, $F_{2,13} = 7.1$, $P = 0.01$; log-linear contrast, $F_{1,6} = 8.0$, $P = 0.03$ during year 1, $F_{1,15} = 4.9$, $P = 0.04$ during year 2), and ranged from 45.6 μmol·mol⁻¹·s⁻¹ (2 species) to 62.0 (8 species) μmol·mol⁻¹·s⁻¹ in June 2001. All CO₂ exchange variables were similar between the two evenness treatments, and the relationships between CO₂ response variables and species richness were not significantly different between evenness treatments (all P values > 0.10).

Relative yield analyses indicated that diverse mixtures yielded more than expected from monocultures. The net biodiversity effect was significantly greater than 0 (t tests: year 1, $t = 3.1$, $P < 0.01$; year 2, $t = 4.7$, $P < 0.01$). It increased with increasing species richness ($F_{1,13} = 7.6$, $P = 0.02$), and this increase was similar between high and low evenness treatments ($F_{2,15} = 0.5$, $P = 0.6$) (see Appendix). The C₄ grass *Panicum coloratum* over-yielded by a very large margin during

both years ($t = 5.0$ and 7.6 , respectively, P values < 0.01), and *Bouteloua curtipendula*, *Paspalum dilatatum* (C₄ grasses; year 1, $t = 3.9$, $P = 0.02$; year 2, $t = 2.2$, $P < 0.04$), and *Ratibida columnifera* (C₃ forb; $t = 3.7$, $P < 0.01$) significantly over-yielded during the first and second years, respectively. The C₄ grasses *Sorghastrum nutans* ($t = -4.9$, -17.5 , for both years respectively), *Sporobolus asper* ($t = -7.5$, -3.1), *Bothriochloa saccharoides* ($t = -4.4$, -4.9), and the C₃ forb *Echinacea purpurea* under-yielded both years ($t = -13.4$, -44.2 ; all P values < 0.01 for all species for both years), and *Schizachyrium scoparium* ($t = -18.4$, $P < 0.01$) and *Bothriochloa ischaemum* ($t = -7.0$, $P < 0.01$), and the C₃ grass *Nassella leucotricha* ($t = -6.7$, $P < 0.01$) significantly under-yielded during year 2. Partitioning the net effect into selection and complementarity components suggested that the net effect was mostly a selection effect. Like the net effect, the selection effect was significantly greater than 0 (t tests: year 1, $t = 3.7$, $P < 0.01$; year 2, $t = 5.7$, $P < 0.01$). The selection effect increased with species richness ($F_{1,13} = 10.6$, $P < 0.01$), and the increase was similar between high and low evenness ($F_{2,15} = 0.3$, $P = 0.7$; Fig. 3). The complementarity effect was detectable only in high evenness communities during the first year (time × richness × evenness interaction, $F_{2,15} = 4.2$, $P = 0.04$; Fig. 3).

By the end of year 2, there was no longer a significant difference in actual evenness between the evenness treatments (slopes of species rank–abundance relationships = -0.27 in even plots and -0.35 in geometric plots). Because of the changes in richness and evenness, we reanalyzed data using the actual measures with regression models. The general trends were similar to those made with planted values. Peak biomass increased with actual species richness during both years of the study ($F_{1,2} = 32.8$, $P = 0.03$, $r^2 = 0.26$ main effect), there were no significant effects of evenness, and there were no interactions between richness and evenness. Root biomass increased with actual richness, but significantly so only during year 2 (shallow, $F_{1,5} = 12.5$, $P = 0.02$; deep, $F_{1,5} = 17.8$, $P < 0.01$).

Local extinctions, which began during the second growing season, were greatest in plots with the highest richness (8) and lowest evenness (evenness × richness interaction, $F_{2,15} = 4.1$, $P = 0.04$). Local extinctions were ~8% in 2- and 4-species mixtures. In 8-species mixtures, local extinction rates were 23% in high evenness plots and 46% in low evenness plots. Extinction rate also varied across species: it was highest in species with low aboveground productivity rates and it declined with increasing productivity according to the highly significant ($P < 0.01$, $r^2 = 0.83$) equation (Fig. 4):

$$\text{local extinction rate} = 0.93 \times e^{-4.2(\text{productivity in monoculture})}$$

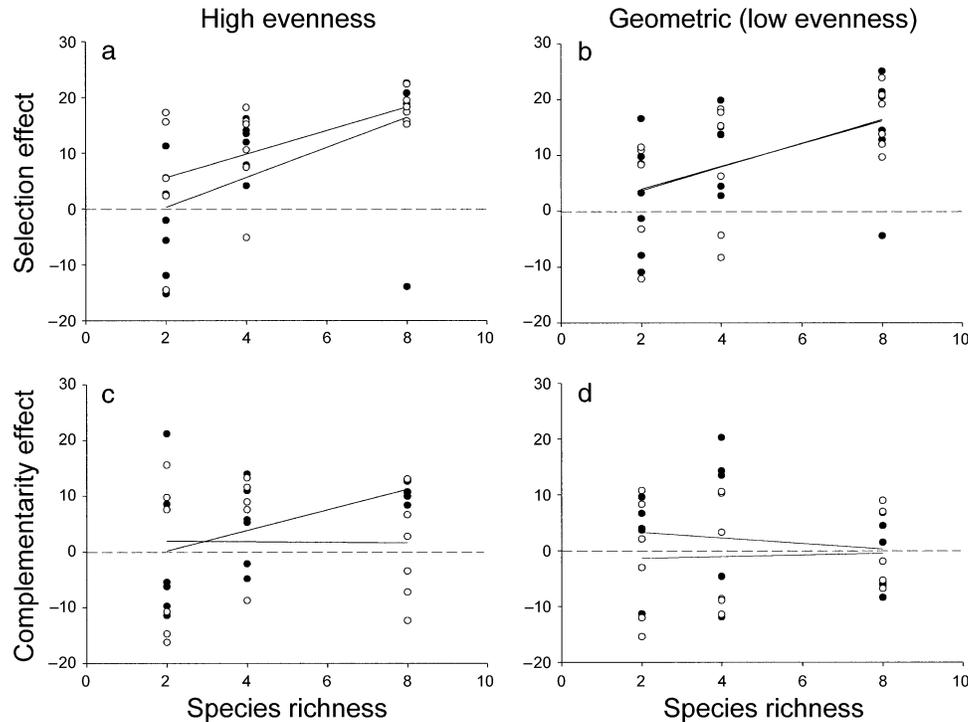


FIG. 3. (a, b) Net selection effect and (c, d) complementarity effect in experimental Blackland Prairie plots planted with 1, 2, 4, or 8 species either with (a, c) high or (b, d) low species evenness during 2001 (solid circles) and 2002 (open circles).

DISCUSSION

Several have argued that if studies of productivity–richness relationships were seeded with a more realistically low species evenness (Huston 1997, Grime 1998, Smith and Knapp 2003), they would have found little or no change in productivity. Differences in relative abundances among species did develop over time in earlier richness experiments, but evenness remained much higher than in natural communities. For example, after establishment occurred in the study by Tilman et

al. (1996, 2001), the relative abundance of the most abundant species was still only 14% in species-rich plots (Tilman et al. 2002). In the present experiment, we found that planting experimental plots with realistically low species evenness did not change the relationship between ecosystem response variables and species richness, but it did have significant indirect effects through changes in local extinction rates. Responses of peak biomass and net ecosystem CO₂ uptake to increased species richness were especially large in this periodically water-limited ecosystem, and were equally large at both evenness levels. Evenness had occasional and subtle effects on richness relationships, such as causing species complementarity to occur only in high evenness plots during the first year, and causing effects of richness on deep-root biomass to vary, but it did not change overall productivity–richness relationships.

Species evenness increased belowground and total productivity in a Québec old field largely independently of dominant species identity (Wilsey and Potvin 2000). Our first-year results were consistent with this study for root biomass only (which were only approaching significance), and there was no relationship with evenness in a second study with an annual community in central Texas (Polley et al. 2003). The fact that effects of species evenness on productivity are inconsistent suggests that reductions in this important component of species diversity may not always have

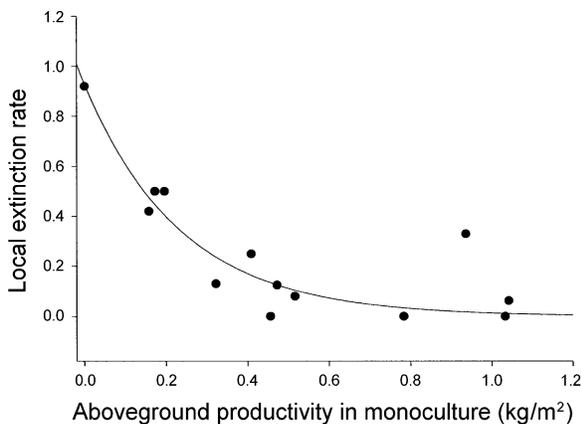


FIG. 4. Relationship between local extinction rate (no. of plots extinct/no. of plots planted) and relative growth rate of each species in monocultures.

large direct impacts on primary productivity and may depend on the composition and dissimilarity of species in the mixtures (Nijs and Roy 2000).

Our results also indicate that species richness effects were primarily a result of the selection effect. Plots with a greater number of species were more likely to contain *Panicum coloratum*, *Bouteloua curtipendula*, and *Ratibida columnifera*, which over-yielded in mixture. These species (especially *Panicum coloratum*) were also the species that did best in monoculture. These results contrast with the results of Tilman et al. (2001) and Loreau and Hector (2001), who both found that their results were mostly explained by the complementarity effects. In contrast to these other studies, we did not use legumes because they make up only ~1% of primary productivity in this system (Wilsey and Polley 2003). This suggests that the presence of legumes may be at least partly responsible for the reported complementarity effects in earlier studies (but not entirely, as complementarity effects were found without legumes by van Ruijven and Berendse 2003). Nevertheless, our results indicate that the complementarity effect may not be found in all grassland types, and further research is needed that directly (experimentally) varies the functional differences among species (Hooper and Vitousek 1997) to make further progress in this area.

Although varying species evenness did not change richness–productivity or richness–C exchange relationships, reduced evenness did contribute to an increase in local extinctions during the second year of the study. The maintenance of species richness also depends on species replenishment (i.e., immigration) from the meta-community, and this was not measured here. However, seedling recruitment rate was estimated to be close to zero in this system in an earlier seed addition experiment (Wilsey and Polley 2003). Plant extinctions at the regional level (Fischer and Stocklin 1997, Duncan and Young 2000) and invertebrate extinctions at the local level (Gonzalez and Chaneton 2002) have been reported to be higher among rare species. To our knowledge, this is the first documented case of increased local plant extinctions being caused by reduced evenness under a controlled setting. Understanding what causes species extinctions at the neighborhood scale is important because it is the scale at which species directly interact and at which the physiological processes underlying primary productivity operate. Our results support the hypothesis that extinctions at the plant neighborhood scale are not random, as has been assumed in assembling species mixtures in most richness–productivity experiments. Rather, extinctions were greater among rare species, and among species with reduced aboveground growth rate. Thus, species evenness can affect grassland ecosystem processes indirectly by affecting species richness, and it will be imperative to understand how nonrandom extinctions affect NPP in future studies (Gonzalez and Chaneton

2002, Smith and Knapp 2003). Future studies with experimental designs that remove the species that are most likely to go locally extinct (e.g., species with low aboveground productivity in this system) will be important in furthering our understanding of species loss on ecosystem processes. Our findings indicate that richness studies may not be biased by using mixtures with artificially high evenness levels, but that results from these studies are directly applicable only to communities in which plant extinctions are random.

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APPENDIX

Additional figures showing gross primary productivity and net biodiversity effect are available in ESA's Electronic Data Archive: *Ecological Archives* E085-083-A1.