



## Diversity–productivity relationships in two ecologically realistic rarity–extinction scenarios

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To develop a better understanding of how biodiversity loss and productivity are related, we need to consider ecologically realistic rarity (i.e. reduced evenness and increased dominance) and extinction (i.e. reduced richness) scenarios. Furthermore, we need to identify and better understand the factors that influence species and community yielding behaviors because the general conditions for overyielding are the same as those for coexistence. We established experimental tallgrass prairie plots in Iowa to determine how two ecologically realistic rarity–extinction scenarios influenced aboveground net primary productivity (ANPP) and disassembly. Equal-mass seedlings of six tallgrass prairie species were transplanted into field plots to establish realistic declining species evenness (high, medium, low) and richness (4, 1) treatments. Across declining evenness treatments, the relative abundance of the ubiquitous tall species *Andropogon gerardii* increased, the relative abundance of the tall species *Salvia azurea* was constant, and the relative abundance of two short (dissimilar height scenario) or two tall species (tall scenario) decreased. Monocultures of *Andropogon* represented a continuation of this trend until there was complete dominance by *Andropogon* and extinction of all other species. Our treatments also allowed us to test if variation in plant height contributes to the complementarity effect. Niche partitioning in plant height was not positively related to complementarity. The effects of declining species evenness and richness on the diversity–productivity relationship were different for these two ecologically realistic rarity–extinction scenarios. Specifically, as diversity declined across treatments, ANPP and the selection effects decreased in tall communities, but not in dissimilar communities. Additionally, differences between these two scenarios revealed that decreased species yielding behavior is associated with two tallgrass prairie extinction risk factors, rarity and short height. The differences between these scenarios demonstrate the importance of incorporating the known patterns of diversity declines into future studies.

Species diversity is rapidly declining worldwide (Pimm et al. 1995, Chapin et al. 2000). Declines in diversity are predicted to result in subsequent declines in the magnitude and stability of productivity (Loreau et al. 2001, Hooper et al. 2005, Tilman et al. 2006). To further advance our mechanistic understanding of these diversity–productivity relationships, both components of diversity, richness (number of species) and evenness (equity of biomass or abundance among species), should be considered. Ma (2005) found that different environmental factors influenced richness and evenness. Additionally, declines in species evenness can sometimes ‘pave the way’ for subsequent declines in species richness (Chapin et al. 2000, Wilsey and Polley 2004). In part, this is because rare species, which by definition occur in communities with low evenness, are usually at greater risk for extinction (MacArthur and Wilson 1967, Pimm et al. 1988, Fischer and Stocklin 1997, Duncan and Young 2000, Wilsey and Polley 2004). Thus, declines in evenness could directly decrease productivity (Wilsey and Potvin 2000, Mattingly

et al. 2007), or indirectly decrease productivity by decreasing richness (Wilsey and Polley 2004).

The designs of numerous neighborhood scale biodiversity–ecosystem functioning experiments have been criticized (Huston 1997, Wardle 1999, Huston et al. 2000), and several techniques have been developed to address criticisms (Losure et al. 2007). In this experiment we transplanted seedlings, rather than sowing seeds, to control the assembly process (e.g. propagule success). This allowed more direct measurement of the temporal changes in diversity that characterize the disassembly process (Huston 1997). This technique also allowed us to experimentally vary evenness (Wilsey and Potvin 2000, Loreau et al. 2001, Wilsey and Polley 2004), dominance (which, conceptually, is inversely proportional to evenness), and the coefficient of variation in species height, by manipulating the slope of the species rank–abundance distribution (Table 1). Our experiment was designed to determine the effects of nonrandom changes in diversity on productivity, in a manner consistent with patterns observed

Table 1. Treatment design established by transplanting seedlings into field plots. Evenness was varied by changing the dominance of *Andropogon gerardii* to establish high (H), medium (M), and low (L) evenness treatments for two types of four-species mixtures (i.e. dissimilar and tall). Planted relative abundances of species and coefficients of variation (CV) in plant height are given for each treatment combination and for *Andropogon* monocultures. <sup>D</sup>deep-rooting, <sup>S</sup>shallow-rooting, <sup>C</sup>C<sub>4</sub> grass, <sup>F</sup>nonleguminous forb.

Rarity–extinction scenario	Species height	Evenness treatment			<i>Andropogon</i> Monoculture
		H	M	L	
Dissimilar:					
<sup>D,G</sup> <i>Andropogon gerardii</i>	Tall	0.31	0.53	0.72	1.00
<sup>D,F</sup> <i>Salvia azurea</i>	Tall	0.26	0.27	0.21	
<sup>S,C</sup> <i>Bouteloua gracilis</i>	Short	0.24	0.14	0.06	
<sup>S,F</sup> <i>Liatris punctata</i>	Short	0.19	0.07	0.01	
CV height		0.52	0.42	0.37	0.10
Tall:					
<sup>D,G</sup> <i>Andropogon gerardii</i>	Tall	0.31	0.53	0.72	1.00
<sup>D,F</sup> <i>Salvia azurea</i>	Tall	0.26	0.27	0.21	
<sup>S,C</sup> <i>Schizachyrium scoparium</i>	Tall	0.24	0.14	0.06	
<sup>S,F</sup> <i>Heterotheca villosa</i>	Tall	0.19	0.07	0.01	
CV height		0.21	0.19	0.18	0.10
Simpson's evenness		0.97	0.67	0.44	Undefined
<i>Andropogon</i> dominance		0.31	0.53	0.72	1.00
Rank–abundance slope		–0.06	–0.29	–0.57	

in the field (Leach and Givnish 1996, Craine et al. 2002, Zavaleta and Hulvey 2004), as suggested by Loreau et al. (2001) and Hooper et al. (2005).

Our two ecologically realistic rarity–extinction scenarios were conceptually based on patterns of declines in diversity observed in remnant and restored tallgrass prairies (Losure et al. 2007). Of the many testable realistic extinction scenarios (Bunker et al. 2005), these are two of the most prevalent scenarios in the tallgrass prairie region. As evenness declined across treatments in the first scenario, our ‘dissimilar’ plots, two short species became increasingly rare, and dominance of the tall and ubiquitous tallgrass prairie species *Andropogon gerardii* (big bluestem) increased (Table 1). Monocultures of *Andropogon* represented a continuation of this trend until there was complete dominance by *Andropogon* and extinction of all other species. This trend of losing short species from plots with species of dissimilar (tall and short) heights has been observed in small, isolated tallgrass prairie remnants (Leach and Givnish 1996). In the second scenario, our ‘tall’ plots, the community contained only tall species, two of which became increasingly rare as dominance of *Andropogon* increased (Table 1). Again, *Andropogon* monocultures represented the extinction component of the rarity–extinction scenario. This trend has been observed in numerous restored tallgrass prairies where frequent spring burning (Towne and Owensby 1984) often leads to increased dominance of one (*Andropogon gerardii*), or two, species of warm season grasses (Collins et al. 1998, Howe 2000, Martin et al. 2005).

Two classes of mechanisms have been identified by which plant diversity can influence productivity: 1) the complementarity effect (COM), which is community overyielding due to niche partitioning and/or positive species interactions; and 2) the selection effect (SEL), which is community overyielding due to selection for species with extreme monoculture yields (Loreau and Hector 2001). The sum of the COM and the SEL is the net biodiversity effect (NBE), which is the difference in biomass between

mixtures, and their expected value based on species’ monoculture yields and relative abundances (Loreau and Hector 2001). Monitoring the COM and the SEL across evenness treatments may reveal mechanisms that maintain richness, because the general conditions for overyielding are the same as those for coexistence (Vandermeer 1981, Loreau 2004). For example, a decrease in the COM across declining evenness treatments (Wilsey and Polley 2004, Polley et al. 2007) may indicate reduced opportunities for niche partitioning that could result in competitive exclusion. In addition to knowing how the NBE, COM and SEL will respond to declines in evenness, we need to know how these dynamics will affect productivity.

Determining specific mechanisms contributing to the COM and the SEL may reveal how declines in diversity could lead to declines in productivity. Several specific mechanisms are thought to contribute to the COM, but few have been demonstrated. Facilitation between legumes and perennial grasses has been shown to increase productivity and contribute to the COM (Loreau and Hector 2001). Other mechanisms are thought to contribute as well, because positive species interactions between legumes and perennial grasses have only partially explained the COM (Loreau and Hector 2001, van Ruijven and Berendse 2003). For example, partitioning of niche space in plant height, phenology, and/or rooting depth have been hypothesized to contribute to the COM (Naeem et al. 1994, Spehn et al. 2000, Wilsey and Potvin 2000, Hooper and Dukes 2004, Silvertown 2004); however, these hypothesized mechanisms have not been directly tested (Loreau et al. 2001, Petchey 2003).

Variation in plant height is hypothesized to increase the COM by increasing the amount of light captured. There is considerable evidence that light can be a limiting resource in the lower canopy of highly productive tallgrass prairies (Schimel et al. 1991). Experimental results have suggested that niche partitioning in plant height may be an important mechanism contributing to the COM (Naeem et al. 1994, Spehn et al. 2000, Wilsey and Potvin

2000). For example, Spehn et al. (2000) found that light capture, three-dimensional canopy space filling and biomass increased with diversity. If tall, dominant species do not capture all the photosynthetically active radiation (PAR), then the addition of shorter species may increase the amount of light captured, and thus the COM in the community. Jurik and Kliebenstein (2000) measured light capture in restored prairies dominated by *Andropogon gerardii* in central Iowa, and found that 40% of PAR was available 30 cm above the soil surface in August. This suggests that there is potential for short species to improve light interception, even when the canopy is most dense later in the growing season. Additionally, experiments with sun (alpine) and shade (prairie) ecotypes of *Stellaria longipes* have demonstrated the adaptability of prairie species to shade conditions (Kurepin et al. 2006, 2007). Thus, the COM may be increased in communities where plant height is partitioned because short species can be adapted to capture the significant portion of PAR not absorbed by tall species. This increase in COM as height variation increases may, or may not, compensate for the expected decrease in ANPP due to the replacement of tall species with less productive short species.

Here we test the influence of experimental reductions in species evenness and richness on the diversity–productivity relationship for two ecologically realistic rarity–extinction scenarios. We pay particular attention to the relationship between yielding behaviors (community and species) and diversity because the general conditions for overyielding are the same as those for coexistence (Vandermeer 1981, Loreau 2004). Additionally, differences in plant height dissimilarity among our treatments allowed us to determine if partitioning on this specific niche axis contributes to the COM. Previously we reported on second year plant invasion and light capture for our experimental plant communities (Losure et al. 2007); here we report on ANPP responses during year three.

## Methods

### Experimental design

The study is part of an ongoing experiment being conducted in the loess hills region of Iowa in an abandoned pasture formerly dominated by *Bromus inermis* at Iowa State University's Western Research Farm near Castana, Iowa, USA (42°1'N, 95°8'W). See Losure et al. (2007) for further details on methodology. Here we will briefly describe the experimental design and peak biomass sampling regime.

Six tallgrass prairie plant species native to the region were grown from seed in pots in a greenhouse and transplanted into experimental plots (1 m<sup>2</sup>) during spring of 2003 (trial one), and the entire experiment was repeated in the spring of 2004 (trial two). Plots were composed of monocultures or four-species mixtures. Species used were selected based on the availability of published heights and rooting depths (Sun et al. 1997, Craine et al. 2002). This allowed us to control for rooting depth (Table 1) as we varied plant height (Losure et al. 2007). Each 1 m<sup>2</sup> plot was planted with 72 approximately equal-mass plants (plant

density was determined by sampling a nearby prairie remnant, Losure et al. 2007), which were randomly assigned to a cell in a grid at planting. The evenness treatment values bracketed those observed in high diversity remnant and less diverse restored prairies, and persisted through the second growing season (Losure et al. 2007).

The experimental plots are arranged in six complete blocks of 12 plots, with two blocks on each of three slopes (north, east and southwest) of a hill (Losure et al. 2007). One set of three blocks (one on each slope) was planted as a first trial in May 2003, and the second set of blocks (one on each slope) was planted as a second trial in May 2004. Each block has one of each monoculture (six monocultures) and mixture (two scenarios × three evenness = six mixtures) lot, with the exception of one *Liatris* monoculture, which is missing in the north block of the first trial due to a shortage of transplants.

### Aboveground net primary productivity

We estimated aboveground net primary productivity (ANPP) for each species in all plots by measuring peak aboveground biomass. This is an acceptable method for estimating ANPP in this region because aboveground plant tissues do not survive the winter season. All plant material in all plots was clipped to 2 cm height and sorted by species, or grouped as standing dead. Plant material was dried at 65°C in an oven for 48 h and weighed. Biomass was harvested in September 2005 for trial one and September 2006 for trial two, after the third growing season for each trial in the experiment.

The biomass data was used to calculate and analyze diversity effects among treatments. The COM and the SEL can simultaneously contribute to the NBE ( $\Delta Y$ ), as demonstrated by Loreau and Hector's (2001) additive partition model:

$$\Delta Y = \overline{S\Delta RYM} + \text{Scov}(\Delta RY, M) \quad (1)$$

where  $S$  is species richness,  $M$  is monoculture yield, and the change in relative yield ( $\Delta RY$ ) is the difference between the observed relative yield ( $RY_O$ ; mixture yield divided by monoculture yield) and the expected relative yield ( $RY_E$ ; the planted relative abundance). The mean term is the COM and the covariance term is the SEL (Loreau and Hector 2001). Fox (2005) extracted another component of complementarity from the SEL to produce:

$$\Delta Y = \overline{S\Delta RYM} + \text{Scov}\left(RY_O - \frac{RY_O}{RYT_O}, M\right) + \text{Scov}\left(\frac{RY_O}{RYT_O} - RY_E, M\right) \quad (2)$$

where  $RYT_O$  is the observed relative yield total (i.e. the sum of the observed relative yields). Fox (2005) called the first term 'trait-independent complementarity', the second term 'trait-dependent complementarity', and the third term 'dominance'. The dominance term in the tripartite partition more truly reflects the process of natural selection because the frequency ratio quantifies the extent to which species' yielding behaviors operate as a zero sum game. Following the suggestion of Hector (2006), we combined the two

complementarity terms, and used Fox's (2005) tripartite partition as a correction factor for the original partition. We calculated and analyzed these effects for all mixture treatment combinations. For dissimilar mixture plots in the north block of the first trial, where the *Liatrix* monoculture was missing, the  $RY_O$  was calculated using the average of the other two *Liatrix* monocultures in this trial.

### Species relative yields

Calculating diversity effects allowed us to determine the relationship between community yielding behavior and coexistence, but did not allow us to consider the relationship between species yielding behaviors and coexistence. We calculated species relative yields to determine how population-level yielding behaviors were related to: 1) the COM and the SEL, 2) our evenness and scenario treatment combinations, and 3) temporal changes in diversity. The species relative yields ( $RY_i$ ) were calculated for each species (i) as follows:

$$RY_i = \frac{(Y_{Oi} - Y_{Ei})}{Y_{Ei}} \quad (3)$$

where  $Y_{Oi}$  is the observed yield, and  $Y_{Ei}$  is the expected yield, which is the product of the monoculture yield and the expected relative yield (i.e. the proportion of individuals planted).

### Changes in species diversity

The use of transplants rather than seeds in our experimental plots allowed more direct observation of the disassembly processes. We monitored changes in diversity during the first three years of the study by calculating Simpson's diversity index (1/D) for mixture plots using planted (i.e. initial) and harvested data, where  $D = \sum p_i^2$  and  $p_i$  is the relative biomass of species  $i$ . This diversity index was then decomposed into species richness (S), and evenness (E) components where:

$$E = \frac{\left(\frac{1}{D}\right)}{S} \quad (4)$$

Simpson's diversity was used because it is an unbiased estimator that performs well at low sample size (Lande 1996, Lande et al. 2000), and its evenness measure is mathematically independent of species richness (Smith and Wilson 1996). Diversity can be calculated with abundance or biomass; we used biomass because this measure is most closely related to resource use.

### Statistical analyses

Peak biomass, species relative yields, the NBE, the COM, the SEL and diversity were analyzed with ANOVA using PROC GLM (SAS Inst.), with a priori contrasts between rarity-extinction scenarios and among evenness treatments (Losure et al. 2007). The SEL was regressed on the relative biomass of the most productive species, *Heterotheca*, to

determine if this species contributed to the SEL. The COM was regressed on the coefficient of variation in plant height for all plots to determine if height variation contributed to the COM. For mixtures, the coefficients of variation in plant height were calculated by dividing the standard deviation (SD) of measured heights among species in each plot by the mean measured heights of each species, weighted by its relative abundance in high, medium and low evenness treatments. For the *Andropogon* monoculture, the coefficient of variation was calculated by dividing the SD of the measured heights by the mean measured height of *Andropogon* individuals. See Losure et al. (2007) for details about height sampling. Pairwise least square means (LS-means) comparisons for ln-transformed monoculture biomass values were made with a Tukey-test.

Contrast coefficients were based on planted rank-abundance slopes and *Andropogon* dominance, and were calculated with PROC IML (SAS Inst., Losure et al. 2007). In evenness contrasts, the coefficient values were  $-0.73$ ,  $0.06$  and  $0.68$  for low, medium and high evenness mixture plots, respectively. *Andropogon* dominance contrasts included the *Andropogon* monocultures, in addition to the three evenness treatments in mixture (Table 1). In *Andropogon* dominance contrasts the coefficient values were  $0.71$  in the *Andropogon* monocultures and  $0.16$ ,  $-0.21$ , and  $-0.65$  in the low, medium and high evenness mixture plots, respectively. Lack of fit for linear contrasts was tested with a quadratic term (Petersen 1985), which was then removed if it was not significant. Type IV sums of squares were used for all analyses because data were unbalanced due to lack of data resulting from a recording error for one of the medium evenness, dissimilar plots in trial one, and the missing *Liatrix* monoculture.

## Results

### Aboveground net primary productivity

As dominance of *Andropogon* increased across treatments, ANPP decreased linearly in tall plots (Table 2, Fig. 1). In

Table 2. Results from ANOVA of peak biomass in experimental plant community monocultures and mixtures for two realistic rarity-extinction scenarios (i.e. dissimilar or tall plots) across three evenness treatments. F-values are for type IV SS. Biomass data ( $g\ m^{-2}$ ) were ln-transformed to meet assumptions of analyses. Dominance contrast coefficients were based on relative abundance of *Andropogon gerardii*, and included its monoculture (\*for  $p \leq 0.05$ , \*\*for  $p \leq 0.01$ , \*\*\*for  $p \leq 0.001$ ).

Source	DF	Biomass F
Trial	1	32.04***
Block	2	4.72*
Plot	11	11.16***
Error	55	
A priori linear contrasts		
Species richness	1	29.95***
Rarity-extinction scenario	1	6.01*
Overall evenness	1	1.08
Evenness in Tall	1	2.97
Evenness in Dissimilar	1	0.06
Dominance in Tall	1	10.94**
Dominance in Dissimilar	1	0.64

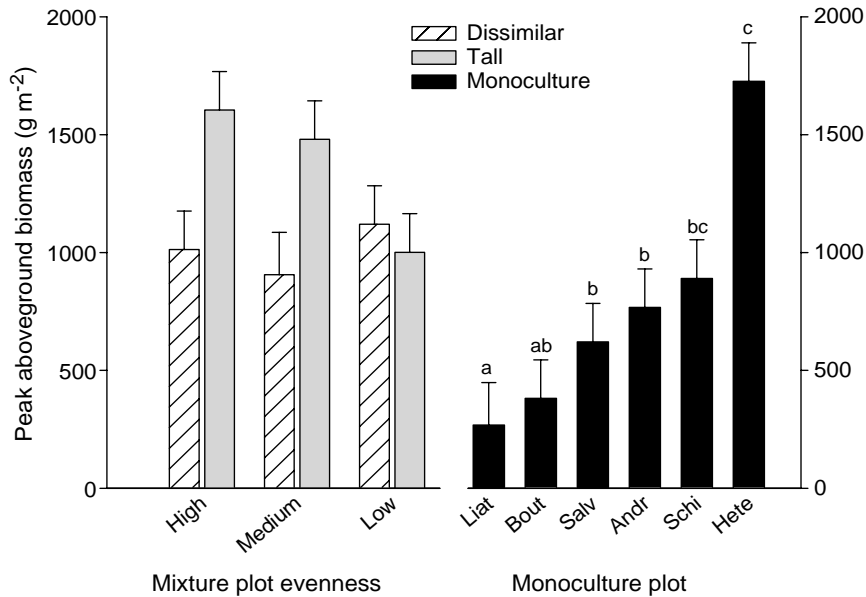


Figure 1. Peak biomass for mixture plots (by evenness and species composition treatments) and monoculture plots (by species) during year three of our field experiment in western Iowa. Plot biomass (LS-means + 1 SE) did not differ among evenness treatments in dissimilar plots, but decreased with declining evenness in tall plots. Monoculture means with the same letter are not significantly different (Tukey's test on ln-transformed data). Species abbreviations: Andr = *Andropogon gerardii*, Salv = *Salvia azurea*, Bout = *Bouteloua gracilis*, Liat = *Liatris punctata*, Schi = *Schizachyrium scoparium*, Hete = *Heterotheca villosa*.

contrast, ANPP did not change with increased *Andropogon* dominance in dissimilar plots (Table 2, Fig. 1). When only mixtures were considered, ANPP did not vary significantly across evenness treatments in dissimilar plots (Table 2, Fig. 1). However, there was a marginally significant linear decrease in ANPP across declining evenness treatments in tall plots ( $F_{1,55} = 2.97$ ,  $p = 0.09$ ). Mean ANPP was greater in tall plots than in dissimilar plots (Table 2), but only in high and medium evenness treatments (Fig. 1). There were also significant differences in ANPP among species in monocultures (Fig. 1).

Increasing species richness from one to four species increased productivity by mechanisms associated with the COM and the SEL in both rarity-extinction scenarios (i.e. COM and SEL grand means significantly greater than zero;

Table 3, Fig. 2). Contrary to our prediction, the COM was not positively associated with height dissimilarity. The magnitude of the COM and the NBE did not differ between rarity-extinction scenarios or across evenness treatments (Table 3, Fig. 2), and the slope of the regression of the COM on the coefficient of variation in plant height was not different from zero ( $t = 0.32$ ,  $p = 0.75$ ,  $DF = 1$ ,  $R^2 = 0.003$ ). The SEL was greater in tall plots (LS-mean  $\pm$  SE:  $113 \pm 3.1 \text{ g m}^{-2}$ ) than dissimilar plots ( $13 \pm 3.3 \text{ g m}^{-2}$ ; Table 3, Fig. 2). The SEL did not vary across evenness treatments in dissimilar plots, but decreased linearly across declining evenness treatments in tall plots (Table 3, Fig. 2). About 73% of the variation in the SEL in tall plots was explained by the linear regression on the relative biomass of *Heterotheca*. The SEL increased as the

Table 3. Summary of ANOVA tests using biomass data from experimental plant community mixtures representing two rarity-extinction scenarios (i.e. dissimilar height and tall plots) across three evenness treatments. Tests are shown for the net biodiversity effect (NBE), and its two components: the complementarity effect (COM) and the selection effect (SEL); tests are also shown for changes in Simpson's diversity and its two components: richness and evenness. F-values are for type IV SS. Diversity effect values ( $\text{g m}^{-2}$ ) were square-root transformed to meet assumptions of analyses, but retain original positive or negative signs (\*for  $p \leq 0.05$ , \*\*for  $p \leq 0.01$ , \*\*\*for  $p \leq 0.001$ ).

Source	DF	NBE F	COM F	SEL F	Change in diversity F	Change in richness F	Change in evenness F
Grand mean	1	70.80***	46.28***	31.84***	183.36***	17.32***	97.33***
Trial	1	3.58	1.32	10.22**	4.12	0.73	4.97*
Block	2	3.37*	3.05	2.05	1.43	0.12	0.74
Species evenness	2	0.75	0.25	9.84***	84.34***	7.17**	80.23***
Rarity-extinction scenario	1	0.50	0.17	7.73**	3.89	9.98**	0.07
Evenness $\times$ Scenario	2	1.37	1.07	4.12*	6.43**	3.15	4.73*
Error	26						
A priori contrasts							
Overall evenness	1	1.47	0.43	18.99***	151.87***	14.26***	148.72***
Evenness in Tall (linear)	1	1.81	0.20	23.25***	80.32***	0.83	64.24***
Evenness in Tall (quadratic)	1				31.16***		21.52**
Evenness in Dissimilar (linear)	1	0.14	0.23	1.80	71.68***	19.60***	85.22***

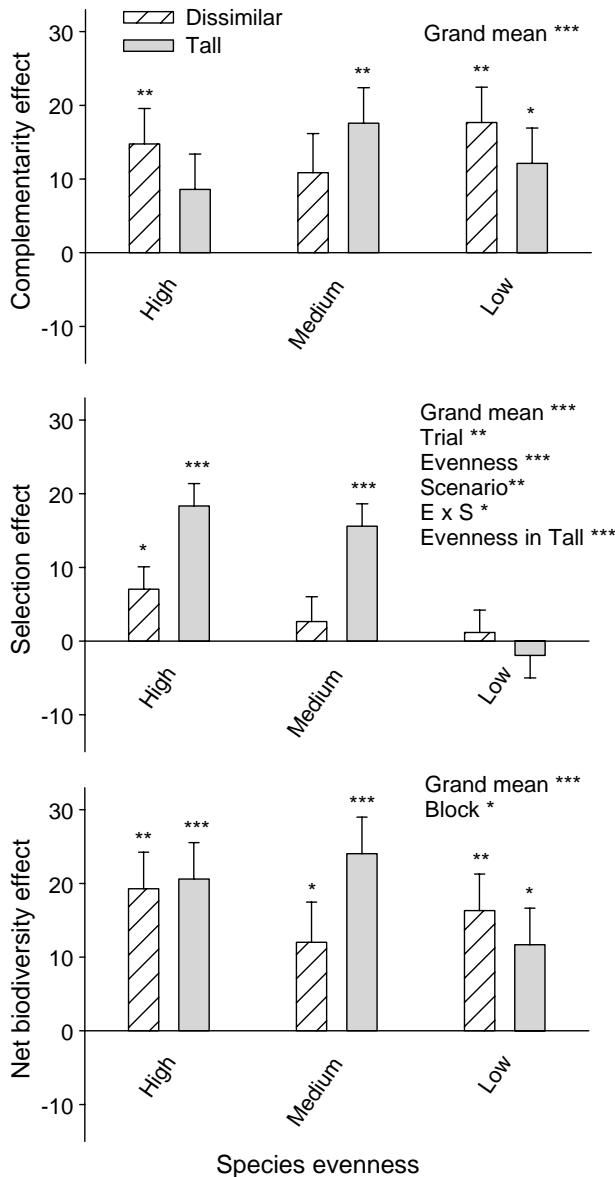


Figure 2. Diversity effects (LS-means  $\pm$  1 SE) vs declining evenness for two rarity–extinction scenarios (i.e. dissimilar or tall plots). Diversity effect values ( $\text{g m}^{-2}$ ) were square-root transformed to meet assumptions of analyses, but retain original positive or negative signs. Abbreviation: E  $\times$  S = evenness  $\times$  scenario. (asterisks above bars denote significant difference from zero: \* for  $p \leq 0.05$ , \*\* for  $p \leq 0.01$ , \*\*\* for  $p \leq 0.001$ ).

relative biomass of this rare species increased ( $t = 6.53$ ,  $p < 0.0001$ ,  $DF = 1$ ,  $R^2 = 0.727$ ).

### Species relative yields

Species relative yields did not differ across evenness treatments for any species except *Heterotheca* (Fig. 3). The relative yield of *Heterotheca* decreased with declining evenness ( $F_{2,17} = 8.33$ ,  $p < 0.01$ ). Species relative yields were lower in tall plots than in dissimilar plots for the two species that were in both rarity–extinction scenarios: *Andropogon* ( $F_{1,26} = 6.40$ ,  $p < 0.05$ ) and *Salvia* ( $F_{1,26} = 21.85$ ,  $p < 0.0001$ ). Specifically, the two most abundant

species, *Andropogon* and *Salvia*, did not have a relative yield significantly different from zero in tall plots, but overyielded in dissimilar plots (Fig. 3). The two rarest species in tall plots (*Schizachyrium* and *Heterotheca*) overyielded, but the two rarest species in dissimilar plots (*Bouteloua* and *Liatris*) underyielded (Fig. 3). In other words, the two species with the highest monoculture yields in each scenario overyielded, and the other two species did not (Fig. 1, 3). Species yielding behavior did not vary significantly between the two trials or among the three blocks for any species (all  $p > 0.15$ ).

### Changes in species diversity

Differences in yielding behaviors of rare and abundant species were related to declines in richness during the first three years of the study. By the end of the third growing season, local extinctions had occurred only for the rarest species in each rarity–extinction scenario (*Liatris* in dissimilar plots and *Heterotheca* in tall plots). *Heterotheca* only became locally extinct once, in one of the six low evenness plots. *Liatris* became locally extinct in five of six low evenness plots and two of five medium evenness plots. No species were lost from high evenness plots.

Diversity declined from initial planted values in some treatments, but the richness and evenness components varied independently (Table 3, Fig. 4). The greatest declines in species richness occurred in the low evenness treatment plots, but the greatest declines in species evenness and Simpson's diversity occurred in high evenness treatment plots (Fig. 4). A decline in richness ( $p < 0.0001$ ) in dissimilar, low evenness treatment plots was nullified by an increase in species evenness ( $p < 0.05$ ) so that Simpson's diversity did not differ from the initial value ( $p = 0.69$ ; Fig. 4). Dissimilar plots had greater declines in species richness than tall plots, but had equal declines in species evenness and Simpson's diversity (Table 3, Fig. 4).

### Discussion

The effects of declining species evenness and richness on the diversity–productivity relationship were different for these two ecologically realistic rarity–extinction scenarios, with this pool of species. Specifically, as diversity declined across treatments, ANPP and the SEL decreased in tall communities, but not in dissimilar communities. Additionally, differences in disassembly between these two scenarios revealed that decreased species yielding behavior is associated with two tallgrass prairie local extinction risk factors, rarity and short height. Niche partitioning in plant height was not positively related to complementarity in these scenarios.

In tall plots, ANPP decreased linearly as *Andropogon* dominance increased and other species became increasingly rare, and then extinct, across treatments. This result was surprising because *Andropogon* is a tall, productive,  $C_4$  grass. This trend can be understood by realizing that the relative abundance of an even more productive species, *Heterotheca*, decreased as *Andropogon* dominance increased. Thus, management practices homogenizing tallgrass prairies and

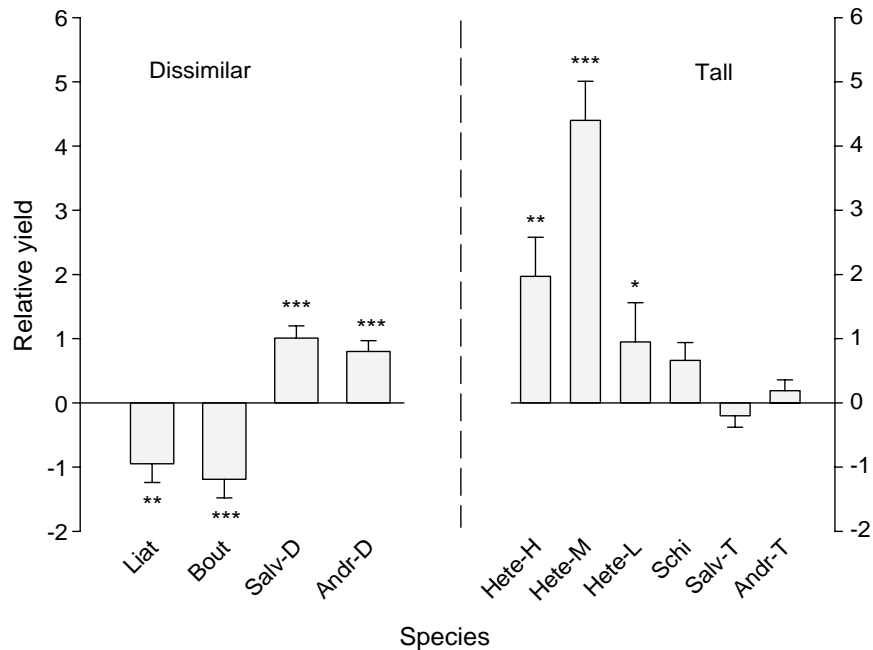


Figure 3. Species relative yields (LS-means  $\pm$  1 SE) for species ordered from least (Liat or Hete) to most (Andr) abundant in each rarity-extinction scenario. Species relative yields did not differ among evenness treatments, except for *Heterotheca*. See Fig. 1 for species abbreviations. Abbreviations: D = dissimilar plot; T = tall plot; H = high evenness; M = medium evenness; L = low evenness (asterisks denote significant difference from zero: \*for  $p \leq 0.05$ , \*\*for  $p \leq 0.01$ , \*\*\*for  $p \leq 0.001$ ).

increasing the dominance of one, or two, species of warm season grasses (Collins et al. 1998, Howe 2000, Martin et al. 2005) may be, in some cases, indirectly decreasing productivity. This outcome would be most likely when the dominant species are not the most productive species.

It was also surprising to us that ANPP did not vary across *Andropogon* dominance treatments in dissimilar plots. One might expect that the replacement of short individuals with tall individuals as *Andropogon* dominance increased across treatments would result in an increase in ANPP. The absence of this trend suggests that ANPP is significantly influenced by species interactions in mixture, and the positive NBE confirms this logical explanation. Diverse prairie systems with variation in plant height may have feedback mechanisms that prevent declines in productivity over time as dominance increases. This deserves further study.

The NBE and COM did not change across species evenness treatments in either scenario. These results agree with, and are comparable to, the second year results of Wilsey and Polley (2004) because in both cases there was no difference in evenness among the evenness treatments (i.e. initial treatment differences had collapsed; Fig. 4). In contrast, results from studies that have experimentally varied evenness and measured diversity effects after only one growing season suggest that the NBE (Polley et al. 2007) and the COM (first year results of Wilsey and Polley 2004, Polley et al. 2007) decrease across declining evenness treatments. Other studies have found a positive relationship between species richness and the COM (Loreau and Hector 2001, Tilman et al. 2001). Thus, our results do not conflict with the developing consensus that declines in evenness and richness may result in a decrease in niche partitioning and positive species interactions.

It was not surprising that tall plots had greater ANPP than dissimilar plots because tall species produce more biomass than short species. However, we were surprised that the COM was not related to variation in plant height between scenarios or across evenness treatments. Note that if there were differences in the COM between these two scenarios, they would be due to differences in height variation, and not height itself, because mixture biomass is divided by monoculture biomass when the  $RY_O$  is calculated. Directly comparing ANPP between these two scenarios confounds differences due to height variation with differences due to mean height. We originally predicted that dissimilar plots would have a larger COM than tall plots due to increased light capture, but found no evidence for differences in the COM or light capture (Losure et al. 2007) between these scenarios. Therefore, our results suggest that variation in plant height does not contribute to the COM in tallgrass prairie. Instead, the positive COM we observed for all of our mixture treatments was possibly the result of niche partitioning from traits that were controlled in our experiment (e.g. rooting depth, Craine et al. 2002, Silvertown 2004), and phenological differences among species (Hooper and Dukes 2004, Losure et al. 2007).

It is important to have a better ecological understanding of the SEL, because it could impact long-term ecosystem stability. The SEL, which tended to be positive to neutral, responded differently to evenness treatments in these two rarity-extinction scenarios. The SEL did not change across evenness treatments in dissimilar plots. However, the SEL decreased as evenness declined across treatments in tall plots. This decrease could have resulted from a change in the yielding behavior of the less productive species, or a change in the yielding behavior of the most productive species; we observed the latter. Previously we showed that

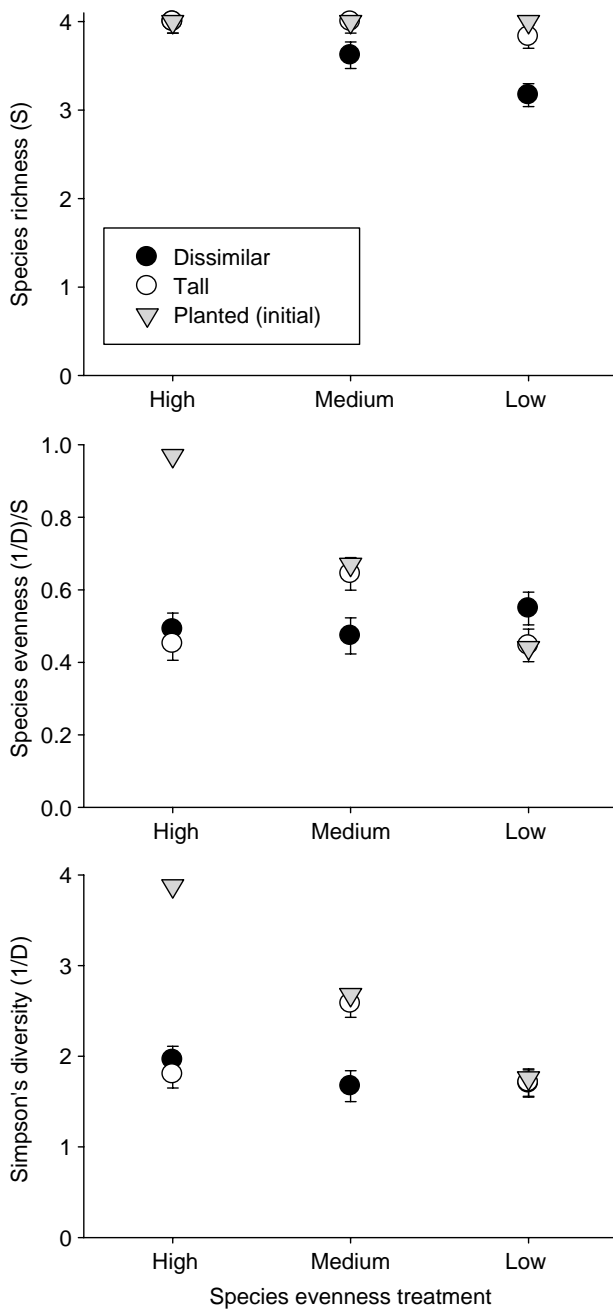


Figure 4. Species richness, Simpson's evenness, and Simpson's diversity are shown for tall (open circles) and dissimilar (filled circles) plots three growing seasons after planted values (triangles). Values are LS-means  $\pm 1$  SE.

treatments with high abundance of *Heterotheca* captured light early in the growing season and helped to decrease invasion (Losure et al. 2007). Our data here suggest that *Heterotheca* increased ANPP by contributing to the SEL.

Our experimental design hints at a potentially important relationship between selective disturbance and the SEL that may increase our understanding of the intermediate disturbance hypothesis (Grime 1973, Huston 1979). In our study, the planted relative abundance of the most productive species (i.e. *Heterotheca*) decreased as evenness declined across treatments. Furthermore, a considerable reduction in the relative abundance of this highly productive

species decreased its ability to overyield, and consequently decreased the SEL. This is an important result because a positive SEL is predicted to lead to competitive exclusion (Fox 2005). Thus, a reduction like this in the SEL may facilitate maintenance of diversity. Chesson and Huntly (1997) showed that harsh conditions, which may result in a reduction in biomass, promote coexistence by influencing species interactions. Our experimental results complement these theoretical conclusions, and we hypothesize that disturbance can oppose competitive exclusion by decreasing the SEL. For example, we suggest that selective grazing may be maintaining diversity in tallgrass prairies (Howe 1994, Collins et al. 1998) because it decreases the SEL by reducing the yielding behavior of highly productive species. Unfortunately, as is the case in most studies, our design does not allow us to determine if these yielding behavior dynamics are unique to the species that we used, or are exhibited by many highly productive species.

If overyielding promotes coexistence (Vandermeer 1981, Loreau 2004), then it is important to determine factors that influence species yielding behaviors. Species interactions influenced the yielding behavior of the two species that were in both rarity-extinction scenarios: *Andropogon* and *Salvia*. Both overyielded in dissimilar plots, where the other species were less productive and underyielded, but were not able to overyield in tall plots, where the other species were more productive and overyielded. Additionally, species' yielding behaviors were consistent across evenness treatments for all species but *Heterotheca*. Thus, for most species, yielding behavior was influenced more by the identity than the relative abundance of neighbors. Temporal variability between trials and spatial variability among blocks resulted in differences in ANPP, but not in differences in species yielding behaviors. Thus, for all species, yielding behavior was influenced more by species interactions than by spatial and temporal variability. Therefore, our data suggest that species overyielding, and its potential contribution to coexistence, depends more on species composition and species interactions than on variability in time (between years), space (among slopes and aspects), and species abundances.

Disassembly in our plots during the first three growing seasons also suggests that yielding behaviors may influence rarity and extinction. No species were lost from high evenness treatment plots, and most local extinctions (7 of 8) were associated with a combination of short height, rarity and underyielding. Our results suggest that short species may be at greater risk for local extinction in tallgrass prairie because they are underyielding. If all rare species were at equal risk for local extinction, then *Heterotheca* would have become locally extinct as frequently as *Liatis*. Instead, our data indicated that a short, rare, underyielding species (i.e. *Liatis*) was at higher risk for local extinction than a tall, rare, overyielding species (i.e. *Heterotheca*). Our experimental results complement other studies showing that short (Leach and Givnish 1996) and rare (Pimm et al. 1988, Fischer and Stocklin 1997, Duncan and Young 2000, Wilsey and Polley 2004) species are at greater risk for extinction, and additionally suggest that underyielding is an associated risk factor. Further work is needed to elucidate the influence of underyielding on rarity and extinction.



In conclusion, although our study included only six tallgrass prairie species, our results suggest that we can better understand diversity–productivity relationships by incorporating the known nonrandom patterns of declines in diversity into experimental designs, and by considering how community and species yielding behaviors influence and respond to diversity. Specifically, we found that ANPP and the SEL can decrease as diversity declines in communities where the abundant species are not the most productive species. In contrast, ANPP and diversity effects did not change as tall species became more dominant in communities with considerable variation in plant height. Community overyielding did not differ between dissimilar and tall plots, but coexistence did. Consideration of species yielding behaviors revealed that the rare, short species that frequently went locally extinct in dissimilar plots underyielded. We suggest future studies incorporate nonrandom patterns of declines in diversity and consider the relationship between yielding behaviors (community and species) and diversity.

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