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Species richness and evenness respond in a different manner to propagule density in developing prairie microcosm communities

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Abstract Diversity has two basic components: richness, or number of species in a given area, and evenness, or how relative abundance or biomass is distributed among species. Previously, we found that richness and evenness can be negatively related across plant communities and that evenness can account for more variation in Shannon's diversity index (H') than richness, which suggests that relationships among diversity components can be complex. Non-positive relationships between evenness and richness could arise due to the effects of migration rate or local species interactions, and relationships could vary depending on how these two processes structure local communities. Here we test whether diversity components are equally or differentially affected over time by changes in seed density (and associated effects on established plant density and competition) in greenhouse communities during the very early stages of community establishment. In our greenhouse experiment, we seeded prairie microcosms filled with bare field soil at three densities with draws from a mix of 22 grass and forb species to test if increased competition intensity or seedling density would affect the relationships among diversity components during early community establishment. Increased seed density treatments caused diversity components to respond in a different manner and to have different relationships with time. Richness increased linearly with seed density early in the experiment when seedling emergence was high, but was unrelated to density later in the experiment. Evenness decreased log-linearly with seed densities on all sampling dates due to a greater dominance by *Rudbeckia hirta* with higher densities. Early in the experiment, diversity indices weakly reflected differences in richness, but later, after the competitive effects of *Rudbeckia hirta* became more intense, diversity indices more strongly reflected differences in evenness. This suggests that species evenness and diversity indices do not always positively covary with richness. Based on these results, we suggest that evenness and richness can be influenced by different processes, with richness being more influenced by the number of emerging seedlings and evenness more by species interactions like competition. These results suggest that both diversity components should be measured in plant diversity studies whenever it is possible.

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Introduction

Species diversity has two basic components: richness, or number of species in a given area, and evenness, or how relative abundance or biomass is distributed among species (Huston 1994; Purvis and Hector 2000; Magurran 2004). These components are combined in diversity indices (e.g., Shannon's H' and Simpson's diversity). Evenness indices standardize abundance and range from near 0 when most individuals belong to a few species, to close to 1, when species are nearly equally abundant (Smith and Wilson 1996). A better understanding of how diversity components are related empirically should be useful in interpreting measurements from a wide variety of studies on organisms with divergent ecological and evolutionary backgrounds (Buzas and Hayek 1996; Bell 2000; Stirling and Wilsey 2001; Mouillot et al. 2005; Wilsey et al. 2005).

Hill (1973) hypothesized that richness fundamentally regulates variation in evenness and diversity statistics. In this case, richness, evenness, and diversity indices should be strongly and positively correlated, and richness should predict a large proportion of their covariance. Neutral diversity theories predict that species number and immigration rates are sufficient to predict animal and plant community abundance distributions (Caswell 1976; Bell 2000; Hubbel 2001), and Caswell's model makes explicit predictions that evenness and richness will be positively correlated in the absence of species interactions. Stirling and Wilsey (2001) found that species richness and evenness were positively correlated in vertebrate communities, and that a neutral model largely predicted the strong positive relationships among invertebrate richness, evenness, and diversity. However, in plant communities, richness and evenness were negatively correlated and evenness accounted for more variation in Shannon's diversity index than richness (Stirling and Wilsey 2001).

The empirical review by Stirling and Wilsey (2001) also indicated that there can be important deviations from the expectation of a strong positive relationship between richness and evenness. For example, they found that richness and evenness were negatively correlated, and that evenness can account for more variation in diversity indices than richness in plant communities (Stirling and Wilsey 2001). Negative relationships between plant richness and evenness were also found by Weiher and Keddy (1999), Bell (2003), and Wilsey et al. (2005). Manier and Hobbs (2006) found a positive relationship between species richness and evenness among non-grazed exclosures, but found a negative relationship among grazed plots. They hypothesized that increased dominance by shrubs due to grazing may have led to facilitative interactions with herbaceous species and increases in richness. Experimentally reduced evenness (or higher dominance) was found to significantly affect the number of individuals entering grassland plots (Foster et al. 2002; Wilsey and Polley 2002; Smith et al. 2004), and was found to be highly correlated with H' in restoration plots (Baer et al. 2004). Ma (2005) found that richness and evenness were correlated with different edaphic factors in a field study: richness was negatively correlated with soil P, whereas evenness was negatively correlated with soil organic C:N ratio. These results suggest that simple positive, linear relationships between richness and evenness are not necessarily the norm, and the ecological causes of these deviations from positive relationships deserve further study.

Whether richness or evenness has a larger influence on diversity, and how they might be related to each other, may come down to whether species assemblages are (1) structured more by interactions such as competition, or (2) regulated by dispersal and migration, where migration is defined as the movement of individuals or propagules into and out of patches. In situations where communities are regulated by dispersal and migration, evenness should be reduced with each new species detected as long as it remains rare. Alternatively, if rare species are more likely to go locally extinct (Duncan and Young 2000; Gonzalez and Chaneton 2002; Wilsey and Polley 2004), then evenness of the remaining species would increase slightly in concert with each decrease in

richness due to local extinction. However, in situations where communities are regulated by competition or other species interactions, there could be a greater effect on evenness due to large changes in relative abundances of common species. These changes in relative abundance could occur without changes in local extinction. Thus, evenness could be reduced without having any change in richness. Evenness and richness would be weakly related and the change in diversity and possibly the level of diversity would be governed by evenness. These issues are most easily addressed experimentally by regulating the level of propagule pressure and asking about the average percent change in diversity as species interactions progress over time, which we do here.

We test these two alternate mechanisms over one growing season in a greenhouse experiment with prairie microcosms filled with field soil. We recognize that longer-term and larger-scale processes are not included in short-term greenhouse experiments using microcosms. However, we focus here on local communities at the very early stages of community development (i.e., a single extended growing season), starting with seedling emergence in controlled microcosms, because it is an important stage of development in establishing plant communities (Bazzaz 1996). Three levels of seed density were experimentally applied to very large pots to vary the number of propagules that would be arriving at a ''patch'' (pot), as well as the competitive intensity among established individuals. Increasing seed density simultaneously affects the number of emerging plants in microcosms (which increased with density) and the density of interacting individuals (which caused competition intensity to increase with density). After plants had established, bimonthly defoliation to 5 cm and a second seed addition were used as a second test of competition intensity. However, defoliation had unexpectedly (and non-significantly) small effects on diversity possibly due to the long evolutionary history of grazing in prairie systems. As a result, we will emphasize seed density effects here. Indices of diversity (richness, evenness, and combined heterogeneity measures) were monitored over the length of the experiment to determine if all indices would increase with initial seed density as

predicted by the null model of Caswell (1976), or if they would be differentially effected.

Methods

Experimental design

The experiment was conducted in a greenhouse in Ames, Iowa, using 60 large pots (27.5 cm diameter × 30 cm deep) filled with field soil. It was particularly important to control the seed bank (Goldberg and Estabrook 1998) and this was most easily accomplished in a controlled greenhouse setting. A seed mix of 22 species of mixed grass prairie grasses and forbs was prepared by mixing together the same number of seeds of each species into an experimental seed mix, and then seed draws for each pot were weighed out from this common mix at the appropriate densities. Thus, it is important to note that the same exact mixture of species compositions was not used in each pot. This approach was used to introduce some stochasticity into seed additions, which more realistically simulates the early community establishment phase and assures replicate independence. Seeds were bought from an Iowa seed company (Ion Exchange).

Seed densities were varied from those that were found in a typical seed rain in a Missouri prairie (Rabinowitz and Rapp 1980). Based on estimates from Rabinowitz and Rapp (1980), we used 895 seeds per species/m^2, and 19,700 seeds total/m^2 (895 × 22). This worked out to be 1,180 seeds per pot for ambient seed density (1.0×). However, because of the high cost and large seed size, fewer *Silphium laciniatum* seeds (60 per m^2) were added into the mix than other species. *Silphium* was not a major component of communities in this experiment, however. All other species had equal abundance. Out of this larger mix of seeds, we weighed out appropriate amounts so that seeds were added to pots at 1.0× (full density), 0.2× full (reduced density), and 2.0× full (increased density) with two seed additions: on day 0 (pre-plant establishment), and on day 147 (post-plant establishment) of the experiment. Seeds were added in two additions to test whether relationships with seed density would change

depending on whether established plants were present or not.

The seed suppliers promise of high germination rates for all but one species (*Penstemon grandiflorus*) were qualitatively verified in greenhouse flats prior to the start of the experiment for each species. These seedlings were then used as reference material for seedling identifications during sampling periods. The pots were 80% full of soil collected from an occasionally grazed pasture dominated by *Bromus inermis* Leysser in the western Iowa Loess Hills region. Using field soil provided a more realistic growing environment than is normally found in greenhouse experiments. The pots were large enough to encompass the small-scale (20–30 cm) spatial heterogeneity effects on fitness that have reported in natural populations (Stratton 1995; Verhoef 1996; Cahill and Casper 2002). For example, soils are often disturbed by gophers and other rodents in this system (e.g., Platt and Weiss 1985; Klaas et al. 2000). Gophers create bare soil spots that can be three times larger (0.18 m^2, Klaas et al. 2000) than the area encompassing our pots (0.06 m^2). Thus, aside from the general issues of diversity measurement, our microcosm communities were relevant to those developing on gopher mounds or on other bare ground situations.

Species used in the seed mix were species that grow in dry tall grass prairie/mixed grass prairie communities of western Iowa, US (Novecek et al. 1985), and were not present in the soil seed bank. Most species are short-statured with shallow rooting depths (Sun et al. 1997; Craine et al. 2003), which makes them easy to accommodate in a greenhouse experiment. Species included in the experiment were: the C$_4$ grasses *Sporobolus asper* (Michx.) Kunth, *Schizachyrium scoparium* (Michx.) Nash, *Bouteloua curtipendula* (Michx.) Torrey and *B. gracilis* (Willd. ex HBK.) Lar. ex Stuedel, the C$_3$ grass *Stipa spartea* Trin., the leguminous forbs *Dalea purpurea* Vent. and *D. candida* Willd., *Chamaecrista fasciculata* (L.) Moench, *Lespedeza capitata* Michx., and the small shrub *Amorpha canescens* Pursh, and the non-leguminous forbs *Silphium lacinatum* L., *Solidago nemoralis* Aiton, *S. rigida* L., *S. speciosa* Nutt., *Rudbeckia hirta* L., *Asclepias tuberosa* L., *Heliopsis helianthoides* L., *Verbena stricta* Vent.,

Penstemon grandiflorus Nutt., *Liatris aspera* Michx., *Echinacea pallida* Nutt., and *Ratibida pinnata* (Vent.) Barnh. (taxonomy follows Eilers and Roosa 1994).

Plant relative abundances typically vary greatly among species in a community (Grime 1998; Hubbell 2001; Magurran 2004; Wilsey and Polley 2004), and species can vary in their reproduction and colonization rates. In this experiment however, we kept all species relative abundances equal in the "seed rain" by controlling the species pool and species proportions in the seed mix. This protocol was done to maximize initial species diversity.

Defoliation treatments started on day 59 after plants had emerged and established. Plants in each pot were either defoliated to 5 cm, or left undefoliated (control). Plants in pots were defoliated bimonthly thereafter (Wilsey 2002). This gave us six treatments with 10 pots per treatment or 60 pots total.

Pots were watered weekly in a way that was meant to fall within the range of average rainfall amounts and frequencies, at a rate of 1 cm/week during winter (520 mm/year), 1.26 cm/week during March, April, and early October (657 mm/year), 1.51 during May and late October (788 mm/year), and 2.02 cm/week during June through September (1,040 mm/year). Pots received supplemental lighting during winter and early spring months. Weed seedlings were removed from the soil seed bank by watering pots for 3 weeks before the experimental seeds were sown and removing emerging seedlings. Almost all of the weed seedlings emerged during this initial period. The few that emerged during the experiment were removed before they affected experimental seedlings.

Estimation of diversity measures

Beginning 6 weeks after seeds were sown (i.e., after plants had begun to establish), all plants were counted in each pot and identified to species, and then were counted bimonthly for a total of 10 months. We used the Shannon index ($H' = -\Sigma \ln(p_i)p_i$) and the Simpson's index ($1/D = 1/\Sigma p_i^2$), where p_i is the relative abundance of each species (n/N), because they are the most

commonly used diversity indices. The Simpson's diversity index is less commonly used than the Shannon's index, but was used here because it has desirable statistical properties (Hurlbert 1971; May 1981; Lande 1996; Bell 2000), and produces an evenness index that is mathematically independent from richness across its range of values (Smith and Wilson 1996). Abbreviations will be used in the text as follows: species richness (S_a), evenness based on the Simpson's index ($E_a = [1/D]/S$) and the Shannon's index ($J'_a = H'/\ln S$), and Simpson's ($1/D_a$) and Shannon's diversity (H'_a) indices were all calculated, with the subscript 'a' denoting 'abundance' in this case, or 'b' for 'biomass' in the case of harvest data.

Relative biomass was also used to calculate the same diversity indices (denoted S_b, E_b, J'_b, $1/D_b$, H'_b with 'b' denoting 'biomass') at the end of the experiment. Half of the pots were harvested after 10 months (at the end of summer) and the other half were harvested after 14 months in order to extend the length of the experiment (to the end of fall). Aboveground biomass was collected by cutting plants at the soil surface and sorting by species. Litter (shed dead leaves and stems) was also collected at the soil surface. Biomass and litter samples were dried to constant mass and weighed. Belowground biomass was hand picked (dry) from a centrally located 5 cm diameter soil core taken to the bottom of the pot, separated into course (rhizomes and taproots) and fine belowground components (i.e., fine roots), washed, dried, weighed, and then converted into grams biomass per pot.

Data analysis

We compared S, E, J', $1/D$, and H' across treatments with 2-way (seed densities and defoliation regimes) repeated measures ANOVA for abundance data and with 3-way (seed densities, defoliation regimes, and harvest dates) ANOVA for biomass data. Species composition was compared among seed density treatments and among time periods with multi-response permutation procedures (MRPP), which is a non-parametric multivariate procedure for testing among groups (Biondini et al. 1985; McCune and Grace 2002).

A non-parametric test was used because data were not normally distributed and had many zeroes. Euclidean distance was used as the distance measure. Tests were done across times for each seed density with PCORD software (MjM Software, Glendedon Beach, OR, USA), and across seed densities at each time because MRPP can only be used to compare simple groupings without interactions (McCune and Grace 2002). A measure of chance-corrected within-group agreement (A), which measures the amount of clustering and grows larger as differences in species composition among groups increases, is reported along with p values (McCune and Grace 2002).

Results

Species composition

There were large changes in species composition over time in all three seed density treatments, but these changes were larger in higher density treatments (Table 1). All 22 species were equally abundant in the seed mix (with the minor exception of compass plant), and 21 species were observed in at least a few pots as seedlings. However, species composition changed significantly between week 6 and week 15 (Table 1) when seedling mortality was high (Fig. 2a), which suggest that species sorting had occurred. We found significant differences in species composition over time in all density treatments as indicated by the agreement index A, but the amount of change grew from low seed density (0.2×, $A = 0.038$, $p < 0.001$), to ambient seed density (1×, $A = 0.109$, $p < 0.001$), to high seed density (2×) pots ($A = 0.168$, $p < 0.001$).

Differences in species composition were associated with changes in relative abundance and biomass of *Rudbeckia hirta*. *Rudbeckia hirta* was more abundant in the higher seed density treatments, and this difference showed up as early as 6 weeks into the experiment (Table 1). Relative abundance of *Rudbeckia* during week 6 was 7.3%, 20.9%, and 15.6% at 0.2×, 1×, and 2× seed densities, respectively, and these differences were

Table 1 Mean (median in parentheses) percent relative abundances from week 0 to week 40, and percent relative biomass at harvest in prairie microcosms with three densities of seed (0.2×, 1.0×, and 2.0× the number of seeds in seed rain estimates of Rabinowitz and Rapp 1980) taken from a mix of 22 species

Seed density, species	Mix	Week 6	Week 15	Week 25	Week 34	Week 40	Biomass at harvest
0.2×							
Rudbeckia hirta	4.75	7.3 (0)	11.4 (0)	21.5 (7.1)	22.2 (9.3)	20.5 (11.8)	39.6 (25.1)
Heliopsis helianthoides	4.75	12.8 (13.7)	16.7 (16.7)	13.3 (14.0)	13.5 (12.8)	19.6 (16.6)	26.4 (14.9)
Bouteloua gracilis	4.75	0.2 (0)	7.4 (7.5)	8.9 (7.6)	10.6 (10.3)	10.3 (11.0)	14.9 (3.9)
Ratibida pinnata	4.75	2.0 (0)	3.0 (0)	2.6 (0)	3.5 (0)	3.1 (0)	7.6 (0.3)
Echinacea augustifolia	4.75	0 (0)	5.4 (5.1)	4.8 (5.3)	4.8 (4.4)	2.9 (0)	4.8 (0)
Stipa spartea	4.75	4.8 (1.9)	5.7 (2.2)	10.4 9.2)	8.0 (6.9)	7.1 (6.5)	1.8 0.03)
Bouteloua curtipendula	4.75	1.0 (0)	7.4 (7.5)	2.0 (0)	1.8 (0)	2.7 (0)	1.3 (0)
Chamaecrista fasciculata	4.75	0.2 (0)	1.0 (0)	1.3 (0)	0.9 (0)	0.9 (0)	1.3 (0)
Asclepias tuberosa	4.75	13.8 (13.5)	11.1 (11.4)	12.9 (10.2)	14.7 (14.6)	13.9 (13.5)	1.0 (0.1)
Sporobolus asper	4.75	6.6 (6.5)	4.2 (2.3)	1.1 (0)	0.5 (0)	1.7 (0)	0.7 (0)
Schizachyrium scoparium	4.75	23.6 (22.4)	13.6 (10.8)	9.0 (6.7)	9.1 (5.5)	9.7 (7.7)	0.6 (0.3)
Amorpha canescens	4.75	5.7 (4.8)	4.5 (2.2)	0.8 (0)	1.8 (0)	1.6 (0)	0.04 (0)
Lespedeza capitata	4.75	8.0 (4.8)	6.1 (5.1)	4.1 (0)	4.2 (5.1)	3.6 (4.2)	0.02 (0)
Dalea purpurea	4.75	1.4 (0)	1.4 (0)	1.7 (0)	1.4 (0)	0.9 (0)	0.01 (0)
Silphium laciniatum[a]	0.32	4.6 (4.1)	0.4 (0)	0.3 (0)	0.2 (0)	0 (0)	0 (0)
1.0×							
Rudbeckia hirta	4.75	20.9 (17.4)	36.7 (32.1)	45.3 (49.)	47.1 (52.2)	42.5 (47.6)	82.1 (91.8)
Heliopsis helianthoides	4.75	10.5 (11.3)	11.3 (10.6)	10.2 (11.1)	13.7 (12.5)	15.6 (15.7)	12.0 (2.8)
Bouteloua gracilis	4.75	0.3 (0)	9.9 (10.4)	5.5 (6.1)	8.2 (9.6)	9.4 (7.7)	1.6 (0.5)
Asclepias tuberosa	4.75	18.1 (18.3)	9.0 (6.6)	13.0 (12.3)	15.2 (14.6)	19.4 (17.6)	1.5 (0.3)
Bouteloua curtipendula	4.75	0.8 (0)	1.0 (0)	2.0 (0)	1.4 (0)	1.4 (0)	1.1 (0)
Stipa spartea	4.75	3.2 (1.9)	4.0 (0)	6.1 (4.5)	3.7 (3.4)	3.9 (3.6)	0.6 (0.1)
Sporobolus asper	4.75	3.9 (6.5)	3.4 (3.4)	3.2 (3.5)	1.7 (0)	1.7 (0)	0.4 (0.3)
Echinacea augustifolia	4.75	0 (0)	4.0 (3.9)	1.7 (0)	2.1 (0)	1.1 (0)	0.4 (0.02)
Schizachyrium scoparium	4.75	18.2 (22.4)	4.5 (3.9)	5.9 (5.5)	2.8 (3.7)	1.1 (0)	0.1 (0.001)
Ratibida pinnata	4.75	1.2 (1.2)	1.7 (0)	1.0 (0)	0.8 (0)	0.6 (0)	0.1 (0)
Lespedeza capitata	4.75	8.6 (4.8)	5.2 (5.2)	0.8 (0)	0.9 (0)	1.3 (0)	0.05 (0)
Amorpha canescens	4.75	4.7 (4.8)	3.5 (3.6)	0.7 (0)	0.5 (0)	1.1 (0)	0.02 (0)
Chamaecrista fasciculata	4.75	0.1 (0)	0.6 (0)	0.8 (0)	0.8 (0)	0.3 (0)	0.01 (0)
Dalea purpurea	4.75	1.8 (0)	1.2 (0)	1.7 (0)	0.2 (0)	0.2 (0)	0.01 (0)
Silphium laciniatum	0.32	4.1 (4.1)	0.5 (0)	0.1 (0)	0 (0)	0 (0)	0 (0)
2.0×							
Rudbeckia hirta	4.75	15.6 (15.4)	34.9 (32.1)	39.8 (42.4)	42.6 (40.0)	38.5 (41.0)	81.5 (83.0)
Heliopsis helianthoides	4.75	12.4 (12.8)	13.5 (10.6)	11.7 (10.3)	18.1 (16.9)	19.4 (18.6)	11.9 (9.2)
Bouteloua gracilis	4.75	0.2 (0)	11.6 (10.4)	4.9 (3.8)	8.1 (8.9)	8.0 (8.1)	2.6 (1.0)
Asclepias tuberosa	4.75	16.6 (16.2)	6.3 (6.6)	13.7 (12.3)	14.5 (14.0)	20.8 (21.7)	1.5 (1.1)
Bouteloua curtipendula	4.75	0.1 (0)	0.8 (0)	1.4 (0)	0.6 (0)	0.7 (0)	0.6 (0.01)
Ratibida pinnata	4.75	1.5 (1.2)	1.8 (0)	1.5 (0)	2.2 (0)	1.1 (0)	0.6 (0)
Stipa spartea	4.75	2.4 (2.2)	2.0 (0)	3.9 (4.1)	4.1 (3.5)	3.4 (2.8)	0.5 (0.09)
Echinacea augustifolia	4.75	0 (0)	3.9 (3.9)	2.6 (2.6)	1.7 (0)	0.8 (0)	0.3 (0)
Schizachyrium scoparium	4.75	21.9 (21.7)	4.3 (3.9)	6.1 (5.4)	2.5 (0)	1.9 (0)	0.1 (0.003)
Chamaecrista fasciculata	4.75	0.6 (0.9)	1.6 (0)	2.0 (0)	2.0 (0)	1.4 (0)	0.1 (0)
Sporobolus asper	4.75	3.7 (3.3)	3.5 (3.4)	2.5 (2.3)	0.7 (0)	0.9 (0)	0.03 (0.009)
Lespedeza capitata	4.75	12.9 (13.1)	6.8 (5.2)	2.1 (0)	1.2 (0)	1.5 (0)	0.002 (0)
Amorpha canescens	4.75	3.1 (3.2)	3.2 (3.6)	0.5 (0)	0.4 (0)	0.1 (0)	0 (0)
Dalea purpurea	4.75	2.2 (2.2)	1.7 (0)	0.5 (0)	0 (0)	0.3 (0)	0 (0)
Silphium laciniatum	0.32	3.9 (3.3)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)

[a] Fewer seeds were added for this species because of very high cost

significantly different ($F_{2,54} = 6.2$, $p < 0.01$). However, *Rudbeckia* was not initially (e.g., at week 6) more abundant than other species. For

example, *Schizachyrium scoparium*, which commonly dominates field plots in the Iowa Loess Hills, had the highest relative abundance in week

6. However, between week 6 and week 15, relative abundance of *Rudbeckia* increased dramatically compared to this and other species. Other species that decreased in abundance to near zero while *Rudbeckia* developed strong dominance were the grasses *Sporobolus asper* and *Bouteloua curtipendula*, and the forbs *Amorpha canescens* and *Silphium laciniatum*. The dominance by *Rudbeckia* was even more dramatic when estimated with relative biomass data, with *Rudbeckia* making up 40%, 82%, and 81% percent of relative biomass in 0.2×, 1×, and 2× density treatments, respectively. There were relatively few species that became abundant out of the initial mix of 22 species, and only 8 that made up > 1% of mean relative biomass by the end of the experiment (all pots combined, Table 1).

Seed density and competition intensity

By definition biomass per individual is inversely related to net competition intensity—larger plants occur when competition is not as intense. Thus, we used biomass per individual (total biomass/total number of seedlings in each pot at the end of the experiment) as a surrogate for net competition intensity. Both above and belowground biomass per individual were higher when migrant seed densities were lower than the full density treatment (Fig. 1). Thus, competition intensity was lower at 0.2× than at 1× and 2× densities (above: density $F_{2,48} = 17.4$, $p < 0.0001$, below: $F_{2,48} = 8.8$, $p < 0.001$). Mean aboveground biomass/individual was 1.00 g (0.07 least square means and SE) at 0.2× densities, 0.56 (0.07) at 1× density, and 0.47 (0.07) at 2× density. Mean belowground biomass/individual was 0.23 g (0.03 SE), 0.10 (0.03), and 0.08 (0.03) for 0.2×, 1×, and 2× densities, respectively (Fig. 1). Aboveground biomass/individual was lower in defoliated plants than in plants that were not defoliated ($F_{1,48} = 10.9$, $p < 0.002$). However, belowground biomass/individual did not differ consistently due to defoliation. Belowground biomass/individual was higher in defoliated pots at harvest 1, but was lower in defoliated pots in harvest 2 (defoliation × date interaction, $p < 0.05$). There were no other interactions among seed density and defoliation treatments ($p > 0.45$). Taken together,

these results suggest that (1) competition intensity increased both above and belowground with increased seed densities, and (2) competition intensity was not consistently affected by defoliation. Seedling mortality was much higher in 1× and 2× than it was in 0.2× pots (Fig. 2a), which also suggests that competition intensity was higher in these pots.

Seed density and total community biomass

Total aboveground biomass (biomass summed across species in a pot) did not change significantly in response to seed densities (means 0.2×: 17.7 g/pot, 1.0×: 18.9 g/pot, 2×: 21.0 g/pot, least squares mean SE = 1.3). There were also no significant interactions with density for total aboveground biomass ($p > 0.13$). Thus, individual biomass varied with density treatments but total
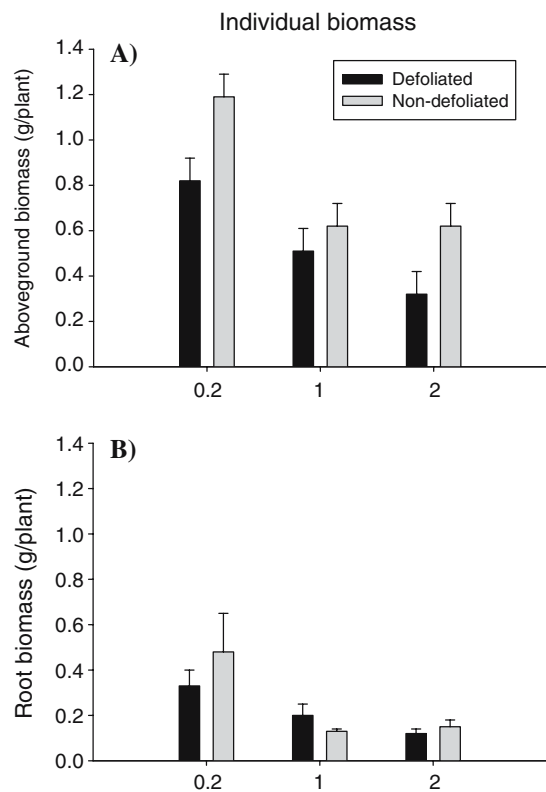

Fig. 1 Aboveground (**a**) and belowground (**b**) biomass per individual (biomass/*N*) in prairie microcosms that were seeded with 0.2×, 1×, and 2× ambient seed densities, and that were either defoliated or not defoliated

biomass did not. This indicates that pots had a common overall biomass, but that seed density affected competition among individuals for limited resources in the pots.

Defoliating plants had a significant effect on total aboveground biomass and litter, but not on belowground biomass. Aboveground biomass (not including off-take) was significantly lower in clipped plots than in non-clipped pots ($F_{1,48} = 14.7$, $p < 0.01$). Total aboveground biomass was greater during the first harvest than the second ($F_{1,48} = 10.6$, $p < 0.01$). Litter production increased as seed densities increased ($F_{2,48} = 10.3$, $p < 0.001$), and was higher in pots that were not clipped ($F_{1,48} = 18.0$, $p < 0.001$). There were no other significant effects and interactions among treatments for total aboveground biomass ($p > 0.13$).

Both fine and course belowground biomass were unaffected by seed densities (main effect $p = 0.78$ [fine] and $p = 0.88$ [course], interaction $p > 0.07$). Fine root mass was greater in defoliated pots than in non-defoliated pots during the first harvest. During the second harvest, fine root mass was higher in non-defoliated pots (defoliation × date interaction, $p < 0.02$).

Seed density effects on species richness, evenness, and diversity: the time course

Over the length of the experiment, species richness and evenness responded in a different manner to seed density treatments (Table 2). There was a significant decline in species richness (S_a) during the length of the experiment indicating the process of extinction from competitive exclusion during the thinning process (Fig. 2, Table 2). Although 21 out of the 22 species from the seed mix were observed at least occasionally, mean S_a declined to a mean of about 11 species per pot by week 5, and to 7 species per pot by the end of the experiment (Fig. 2b). This decline was due to high levels of species sorting and seedling mortality (Fig. 2a). During the early part of this decline (up to 25 weeks), S_a was greater with greater initial seed densities (contrast, $p < 0.01$). This was associated with a very large increase in the number of individuals in each pot with initial seed density (Fig. 2a). In other words, initial differences (first 25 weeks) in S_a were due to differ-

ences in the number of individuals emerging in the pots. From week 25 to the end of the experiment, the differences in S_a between the three density treatments were not significant (Fig. 2b). The second seed addition during week 21 had no effect on S or density (Fig. 2b), and S–density relationships that had developed before week 21 did not change in response to this second addition. Thus, S_a during later periods (after week 25) was unrelated to seed density.

Contrary to the simple expectation of a positive relationship between richness and evenness, we found the highest evenness in the low seed density treatment (Fig. 2c, d). Differences in evenness occurred as early as the first sampling date, and these differences were associated with differences in *Rudbeckia* abundance. Evenness fluctuated among time periods (Table 2), but unlike richness, there was no directional change from the beginning to the end of the experiment (Fig. 2c, d). Furthermore, unlike richness, the differences in evenness between the 0.2×, 1×, and 2× treatments persisted throughout the experiment (Fig. 2c, d).

The diversity indices H'_a, $1/D_a$ also changed significantly over the length of the experiment (Table 1, Fig. 2e, f). Both diversity indices declined until week 25, and this decline was steeper in high seed density pots (Fig. 2, time × treatment interaction). Unlike richness or evenness during this initial period, diversity indices did not differ as greatly among seed density treatments (Fig. 2e, f), suggesting that the divergent effects of evenness and richness on the low seed density treatment had offset each other. After 25 weeks, however, diversity followed trends in evenness and was significantly higher in the low seed density treatment (Fig. 2). (The difference between H'_a and $1/D_a$ may indicate the importance of dominance by relatively few species in the low seed density treatment.) Furthermore, after 25 weeks, both diversity indices declined slightly over time, but in high seed density pots only.

Seed density and species diversity based on relative biomass

At the end of the experiment, relative biomass-based diversity relationships with seed density treatments were similar to corresponding
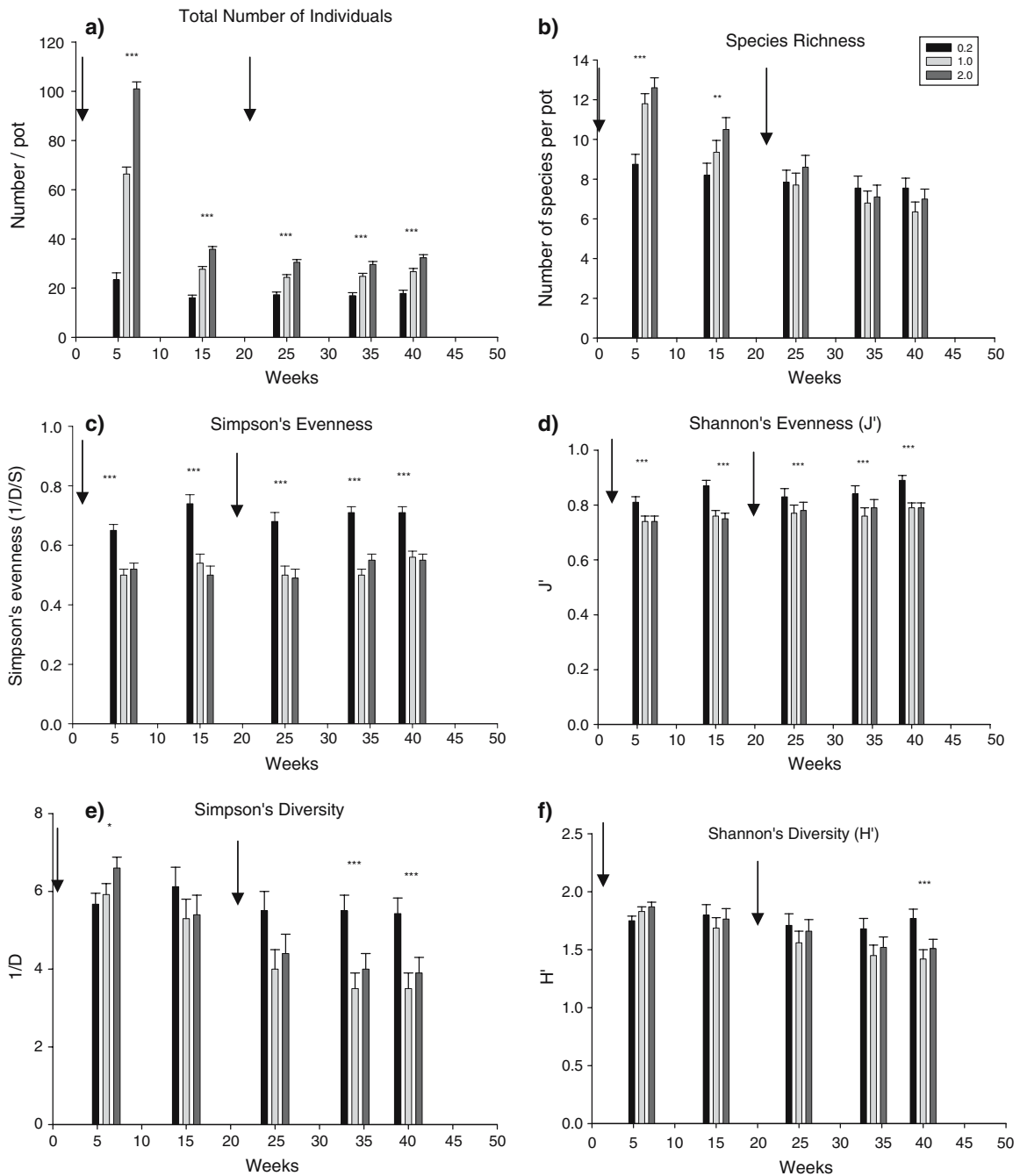
Fig. 2 Total number of individuals (#/microcosm), species richness (#/microcosm), evenness (Simpson's and Shannon's), and diversity (1/D and H′) based on relative abundance data in prairie microcosms that had been seeded with 22 species at 0.2×, 1×, and 2× ambient seed densities. Thus, species richness was 22, evenness was close to 1.0, H′ was 3.1 and 1/D was 22 at time 0. Seeds were added at the beginning of the experiment and after 21 weeks in half increments (denoted by *arrows*). Significant relationships are denoted as *(p < 0.10), **(p < 0.05), and ***(p < 0.01), and are from ANOVA's from each time period for variables where a significant time × density interaction was observed in the repeated measures ANOVA, and from the density main effect from the repeated measures ANOVA for variables without a significant time × density interaction

Table 2 Results of ANOVA (*F* values) for diversity components[a,b] measured with relative biomass and abundance in a prairie mesocosm experiment

Source	d.f.	S_a	E_a	J'_a	$1/D_a$	H'_a
Abundance						
Density	2	2.57*	24.94***	6.31***	3.14**	1.08
Defoliation	1	0.55	0.12	0.43	0.10	0.01
Defoliation × density	2	0.26	1.65	2.25	0.76	1.31
Error	54					
Time	4	55.70***	2.79**	5.00***	24.25***	13.67***
Time × defoliation	4	1.79	0.47	1.28	0.98	1.45
Time × defoliation	8	7.04***	1.38	1.02	4.03***	2.62***
Time × defoliation × density	8	0.57	0.94	1.24	0.39	0.68
Error	216					
Biomass[a]		S_b	E_b	J'_b	$1/D_b$	H'_b
Density	2	0.08	5.34***	9.41***	10.94***	7.59***
Defoliation	1	2.64	0.40	0.16	1.34	0.97
Defoliation × density	2	0.78	0.36	1.91	1.74	2.06
Harvest date	1	21.63***	18.23***	0.55	0.00	0.33
Error	55					

Pots filled with field soil were seeded with 0.2 ×, 1 ×, or 2× ambient seed densities (Rabinowitz and Rapp 1980) which led to variation in competition intensity, and with and without aboveground bimonthly defoliation to 5 cm (Def.). Aboveground biomass was harvested after 10 and 14 months, and abundance was measured bimonthly for the first 10 months of the experiment

[a] *S* = species richness, or number of species; *E* = evenness based on the simpson's index/*S*; *J*′ = evenness based on the Shannon's index *H*′/log *S*; 1/*D* is the diversity form of the Simpson's index ($1/\Sigma\, p_i^2$); *H*′ is the Shannon's index ($-\Sigma\, p_i\, \{\ln p_i\}$)

[b] Subscripts denote abundance (a) or biomass (b)

*$0.05 < p < 0.1$

**$0.01 < p < 0.05$

***$p < 0.01$

abundance measures, although biomass values were lower overall. We found no relationship between S_b and seed density at harvest (Fig. 3a), similar to the abundance data from week 34 to week 40 (Fig. 2b). Both measures of evenness, E_b and J'_b, were significantly higher in low-density pots (0.2×) than in the two higher density treatments (1× and 2×) with no difference between the 1× and 2× treatments (log-linear contrast, $p < 0.01$) (Fig. 3b, c). H'_b and $1/D_b$ were lower with lower seed density in a manner that was similar to evenness measures (Fig. 3d, e). There were no significant 2-way or 3-way interactions observed (all $p > 0.15$), so these interactions were pooled into the error term for presentation (Table 2).

Discussion

We experimentally tested how early colonizer density and an ecological interaction (competi-

tion) affect species diversity components, and whether the relationship among diversity components is in the direction predicted by the literature review analyses of Stirling and Wilsey (2001). In our experiment, which simulated the early development of local grassland communities in microcosms, richness and evenness were found to initially respond in opposite directions to seed density and associated abundances of *Rudbeckia hirta*. Increased seed density led to a greater number of individuals emerging in pots (especially early on) but also to a greater competition intensity among established individuals. Richness and evenness had opposite relationships with seed density treatments because richness and evenness measures responded differently to emergence rate and competition. Richness declined as plants failed to establish, and relationships between richness and density disappeared after 15 weeks, whereas the differences in evenness with initial seed density persisted through to the end of the
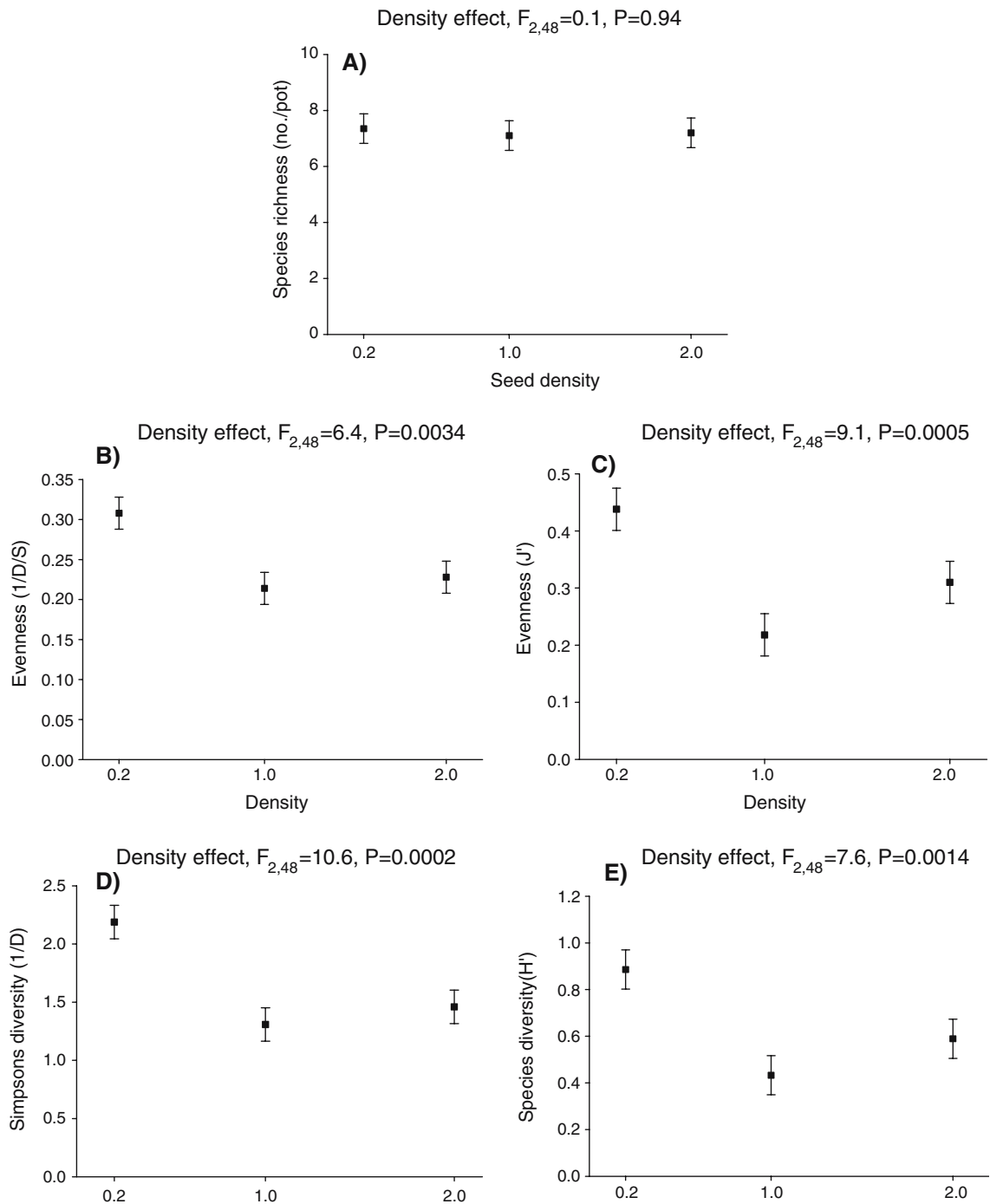
Fig. 3 Species richness (# species/microcosm, **a**), evenness (Simpson's, **b**, and Shannon's, **c**), and diversity (1/*D*, **d**, and *H*′, **e**) based on relative biomass data in prairie microcosms that had been seeded with 0.2×, 1×, and 2× ambient seed densities

experiment. This happened because richness was heavily influenced by very small and ephemeral populations of seedlings, similar in nature to the "transients" described by Grime (1998). Correlations between species richness and the number of individuals are frequently reported, and pro-

vide the rationale for rarefaction curves (reviewed by Magurran 2004). However, our finding that evenness and richness may respond to different ecological processes is novel and supports the hypotheses of Stirling and Wilsey (2001), and the empirical findings of Ma (2005) and Manier and Hobbs (2006). The richness component was more sensitive to migration rates and the evenness component was more sensitive to biotic interactions; specifically, changes in competition intensity. In other words, the individual diversity components were found to respond independently to different ecological factors (Ma 2005), in our case, over time in response to changes in seed densities.

The hypothesis that diversity in developing communities is regulated by local seed density (see Bell 2000; Hubbel 2001) was not supported here, although this experiment was admittedly short-term and only covered the early stages of community development. By the latter half of the experiment, the community was only weakly influenced by seed density, and the species composition of the community was very different from the composition of the seed mix. When seedling emergence rates were high early in the experiment, we found that both richness and diversity indices increased with seed density, suggesting that seed density was initially regulating diversity. However, seed density had no effect after this initial period. After individual plants grew large and *Rudbeckia hirta* began to displace other species during the latter part of the experiment, species evenness and diversity indices decreased with seed density, whereas richness was unrelated to seed density treatments. A second seed addition 21 weeks into the experiment simulated another seed addition event, *but it did not affect these relationships* (Fig. 2). This suggests that seed availability had a diminishing effect on diversity with community development. During the later periods, there were changes in diversity that were largely independent of richness and were apparently regulated by variation in evenness and competition. Thus, our experiment indicates that variation in richness and evenness may independently regulate diversity under different ecological conditions. This hypothesis should be tested in other systems, and in longer-term studies conducted over multiple years and generations.

We further hypothesize that variation in richness may regulate diversity when seed availability and disperal are the factors regulating diversity (e.g., Tilman 1997; Altesor et al. 1998; Zobel et al. 2000; Martin et al. 2005) because richness is highly influenced by the number of individuals (Hayek and Buzas 1996; Gotelli and Colwell 2001). Variation in evenness may regulate diversity in sites with moderate disturbance like grazing (McNaughton 1977; King and Pimm 1983; Shaffers 2002; Schmitz 2003; Martin and Wilsey 2006), when grazing lowers the amount of dominance by common species but no new migrants are gained or lost.

Various indices of diversity are used for estimating the amount of environmental change. For an index to be useful, it should be applicable to a variety of situations and at multiple temporal and spatial scales. The literature is mixed on whether richness, evenness or diversity indices are more sensitive to changes in the environment such as nutrient enrichment or pollution. For example, Kevan et al. (1997), Garcia-Creado et al. (1999), and Magurran and Philip (2001) found that richness is more sensitive than diversity measures, whereas, Cottingham and Carpenter (1998), Gydedu-Ababio et al. (1999), Spurgeon and Hopkin (1999), and Bowman et al. (2006) found that evenness or diversity indices are more sensitive than richness. Studies that tended to find that richness is more sensitive than diversity measures used aquatic invertebrates (Garcia-Criado et al. 1999), fish (Magurran and Philip 2001), and insects (Kevan et al. 1997). These are the taxa where positive relationships among indices corresponded more to Caswell's (1976) null model that only included migration (Stirling and Wilsey 2001). Studies that tended to find that diversity and evenness measures were as sensitive or more sensitive than richness were done on nematodes (Gyedu-Ababio et al. 1999), worms (Spurgeon and Hopkin 1999), phytoplankton (Cottingham and Carpenter 1998), and plants (Bowman et al. 2006), which are taxa where migration is expected to be less important. Cottingham and Carpenter (1998) concluded that the best environmental indicators may be different

for plants and phytoplankton than for animals, which is consistent with the across taxa differences of Stirling and Wilsey (2001). Because species evenness and richness may respond differently to different ecological processes, we hypothesize that answering the question of ''which index is most sensitive'' will come down to whether the taxa and system under investigation is regulated more by dispersal and migration (with richness being more sensitive) or ecological interactions (with evenness being more sensitive).

We found it remarkable that individual species had differential effects on diversity. Even though 22 species were included in the seed mix, only a few species affected diversity, and the abundance of one species, *Rudbeckia hirta*, significantly affected diversity all by itself. These effects were not found because the propagule pressure of this particular species was higher (e.g., Hubbel 2001), because species had roughly the same number of seeds in the species pool. Rather, *Rudbeckia* has characteristics (small, quickly germinating seeds, rosette growth form, dense stature and high litter production) that enabled it to dominate plots, especially in high seed density pots where it was able to establish more individuals. This effect has also been anecdotally noted about prairie restorations, where the *Rudbeckia* 'stage' has low diversity for the first several years of establishment (e.g., Howe 1995). In this respect, a key interaction structures these local communities initially, but they are expected to change in ways that need to be measured over longer time frames. Once key community interactions are established, variation in abundant species may regulate community diversity overall (Baer et al. 2004). However, disturbances such as gopher holes or fire (e.g., Allen and Wileyto 1983), hurricane or anthropogenic effects (e.g., Hughes and Connell 1999) may allow changes in species richness to temporarily govern local community diversity in prairies.

Conclusions

Similar to our comparative literature review (Stirling and Wilsey 2001), and comparisons of quadrat-scale ungrazed (Wieher and Keddy 1999;

Wilsey et al. 2005), and grazed field plots (Manier and Hobbs 2006), this experiment showed that there can be negative relationships between richness and evenness, and that they can respond in a different manner to an ecological factor (seed density). It also demonstrated a possible causal mechanism: changing seedling emergence rates early in the experiment due to initial seed densities, later competition effects, and the changing time-course of species interactions. When seedling emergence was highest (early in the experiment), diversity (heterogeneity) indices weakly reflected differences in richness. Later in the experiment, when competition intensity was high, then diversity indices strongly reflected differences in evenness. Thus, evenness and diversity indices were not consistently regulated by richness. The richness component was more sensitive to migration rates and the evenness component was more sensitive to biotic interactions; specifically, changes in competition intensity. Because diversity depends on both migration and species interaction effects, these results suggest that both diversity components should be measured in plant diversity studies whenever it is possible (Buzas and Hayek 1996; Hayek and Buzas 1996; Stirling and Wilsey 2001; Ma 2005; Wilsey et al. 2005).

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