

REPORT

## Dominant species maintain ecosystem function with non-random species loss

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### Abstract

Loss of species caused by widespread stressors, such as drought and fragmentation, is likely to be non-random depending on species abundance in the community. We experimentally reduced the number of rare and uncommon plant species while independently reducing only the abundance of dominant grass species in intact, native grassland. This allowed us to simulate a non-random pattern of species loss, based on species abundances, from communities shaped by natural ecological interactions and characterized by uneven species abundance distributions. Over two growing seasons, total above-ground net primary productivity (ANPP) declined with reductions in abundance of the dominant species but was unaffected by a threefold decline in richness of less common species. In contrast, productivity of the remaining rare and uncommon species decreased with declining richness, in part due to loss of complementary interactions among these species. However, increased production of the dominant grasses offset the negative effects of species loss. We conclude that the dominant species, as controllers of ecosystem function, can provide short-term resistance to reductions in ecosystem function when species loss is nonrandom. However, the concurrent loss of complementary interactions among rare and uncommon species, the most diverse component of communities, may contribute to additional species loss and portends erosion of ecosystem function in the long term.

### Keywords

Above-ground productivity, complementary interactions, dominant species, grassland, rare species loss, subordinate species, tallgrass prairie.

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### INTRODUCTION

The rapid loss of biota from communities (Lawton & May 1995; Pimm *et al.* 1995; Gibbs 2001; Regan *et al.* 2001) has prompted ecologists to examine the consequences of reduced biodiversity for ecosystems (Chapin *et al.* 2000; Loreau *et al.* 2002). Recent experimental and theoretical studies have demonstrated that random loss of species leads to declines in productivity, nutrient retention, resistance to invasion, and other processes critical to the functioning of ecosystems (Naeem *et al.* 1994, 2000; Tilman *et al.* 1996, 1997a,b, 2001; Symstad *et al.* 1998, Van der Heijden *et al.* 1998; Hector *et al.* 1999; Loreau 2000; Lyons and Schwartz 2001; Kennedy *et al.* 2002; Mouquet *et al.* 2002). Such patterns of loss, however, do not reflect those in natural communities (Wardle 1999; Huston *et al.* 2000; Schwartz *et al.* 2000) where major drivers of species loss are

widespread stressors, such as land-use change, fragmentation, biotic invasions, and climate change (Chapin *et al.* 1997). These drivers of change, rather than extinguishing species in a random fashion, cause non-random species loss or shifts in species composition (Vitousek *et al.* 1997; Loreau *et al.* 2001; Grime 2002).

Indeed, all else being equal, rare and uncommon species, that collectively are the most diverse component of communities (Whittaker 1965; Grime 1998), are generally at greater risk for extinction due to their small population sizes (MacArthur & Wilson 1967; Pimm *et al.* 1988, 1995; Hubble 2001). In contrast, common or dominant species, which garner a disproportionate share of resources and contribute most to productivity (Whittaker 1965; Grime 1998; Geider *et al.* 2001), are less likely to be lost from communities unless they are, for example, particularly vulnerable to catastrophic events (e.g. pathogen outbreaks)

or are targets of selective harvesting (Vitousek *et al.* 1997; Grime 1998). Under this scenario of non-random species loss, ecosystem responses – at least in the short term – should largely be influenced by persistent common or dominant species (Geider *et al.* 2001). In contrast, for studies that simulate random loss of species, dominant and rare species have an equal probability of being lost, and therefore ecosystem responses depend disproportionately on the identity of species selected for inclusion in or exclusion from the community (Huston 1997; Wardle 1999). Experiments that simulate non-random species loss from natural ecosystems and that are coupled to extinction scenarios documented in the field have been called for as part of the next generation of biodiversity experiments (Grime 2002; Loreau *et al.* 2002). These also provide a fundamentally different template from which to evaluate the impacts of species loss and the mechanisms by which altered species richness affects ecosystem functioning.

We conducted a 2-year (2000–2001) field experiment to examine the consequences of nonrandom species loss on productivity of a grassland ecosystem. To simulate non-random loss, plant species were eliminated from intact, native tallgrass prairie plots based on their probability of occurrence and abundance in the community, so that rare and uncommon (subordinate) species were lost first and the most abundant species were rarely lost. The capacity of tallgrass prairie communities to respond rapidly to a variety of perturbations (Tilman & El Haddi 1992; Steinauer & Collins 1995; Turner & Knapp 1996) makes it an excellent system to examine the immediate consequences of species loss on above-ground net primary productivity (ANPP), an integrative measure of ecosystem function in this system (Briggs & Knapp 1995).

We chose this pattern of nonrandom loss because environmental changes that impact grasslands, such as drought, fragmentation or altered disturbance regimes (i.e. exclusion of fire or grazing), have been shown to cause loss of rare and uncommon species only (e.g. Weaver & Albertson 1944; Tilman & El Haddi 1992; Leach & Givnish 1996; Collins & Steinauer 1998). We also reduced densities of the most abundant and productive species (i.e.  $C_4$  dominant grasses) separately, because those drivers of change that cause loss of rare and uncommon species reduce the abundance of common species long before their frequency of occurrence is affected. We recognize that other widespread stressors (e.g. climate change, eutrophication) may result in different patterns of species loss, such as shifts in functional composition or increased abundance of dominant species (e.g. Harte and Shaw 1995; Tilman 1996). However, we chose a pattern of species loss that is arguably more likely than the random loss simulated in other studies (Wardle 1999; Huston *et al.* 2000; Schwartz *et al.* 2000). These latter studies, which often use

synthetic model communities, are most useful for identifying potential relationships between diversity and ecological patterns and processes (Loreau *et al.* 2001). Our approach allowed us to not only to simulate a more realistic extinction scenario in natural communities with uneven species abundance patterns (Schwartz *et al.* 2000), but also to examine the underlying mechanisms by which diversity may alter productivity. Finally, maintaining the dominant species at all richness levels allowed us to decouple diversity effects, such as niche complementarity (Tilman *et al.* 1997a; Loreau 2000; Loreau & Hector 2001; Mulder *et al.* 2001; Cardinale *et al.* 2002) from those of the dominant species (i.e. the sampling effect, Aarssen 1997; Huston 1997; Tilman *et al.* 1997a).

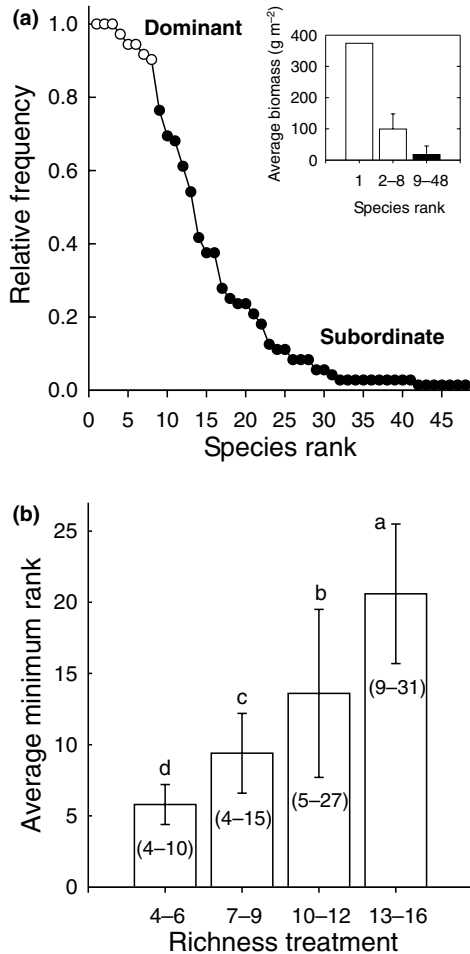
## METHODS

### Study site

The study was conducted on Konza Prairie Biological Station, a 3487 ha tallgrass prairie preserve located in the Flint Hills region of Northeastern Kansas (39°5′N, 96°35′W). Grassland vegetation at Konza Prairie is typical of the tallgrass prairie biome (see Freeman 1998) and is dominated by a few  $C_4$  grass species, mainly *Andropogon gerardii*, *A. scoparius*, and *Sorghastrum nutans* and to a lesser extent *Bouteloua curtipendula* and *Panicum virgatum*. A wide array of subordinate  $C_3$  grass, forb and woody species comprise the bulk of the diversity. For this experiment, we selected a homogeneous upland site with relatively shallow soils in a watershed burned at an intermediate fire frequency [every 4 years in the spring (April 15 ± 15 days) since 1986]. Fire is an inherent natural feature of this grassland with most key community and ecosystem characteristics dependent on frequent fire (Knapp *et al.* 1998).

### Experimental design

In May 2000, we established 72 0.5 m × 1.0 m plots each separated by a 0.5–1.0 m buffer. The entire site was burned several weeks earlier. The number of individual stems (tillers) of each species in each plot was censused over a two-week period. Total stem densities ranged from 510 to 913 stems per plot (average: 682.3 ± 98.6 SD). Only a few species were highly frequent and abundant at the study site, whereas most species were infrequent and uncommon (Fig. 1a). We designated the  $C_4$  grasses, *A. gerardii*, *S. nutans*, and *B. curtipendula*, as the most dominant species for the study site, because they collectively were more frequent and productive (Fig. 1a, inset) and comprised a greater proportion of total abundance (density) than all other species. The range in stem densities for these species was 173–519 stems (average: 368.9 ± 87.5 SD). Average richness for the plots



**Figure 1** (a) Rank–abundance curve for the local pool of plant species in the 72 grassland plots in which density and richness were manipulated. Species were classified as dominant (ranks 1–8; open circles) and subordinate (ranks 9–48; closed circles) based on their relative frequencies, abundance and biomass for the study site. Inset: Note that the dominant species, particularly *Andropogon gerardii* (rank 1), have substantially greater average biomass than the subordinate species. (b) Average ( $\pm 1$  SD) minimum rank of species removed with each of the richness treatments. Note that the three most frequent species (ranks 1–3) were never removed. Range in minimum-ranked species removed is also given in parentheses. Different letters denote significant differences among richness treatments.

was 14.1 ( $\pm 2.0$  SD) with a minimum of 10 species and a maximum of 18 species per plot. Based on average density of the dominant species and richness for the site, we selected target density levels of high (ambient), medium (25% reduction in abundance) and low (50% reduction). The richness treatments we selected were 13–16 species (ambient), 10–12, 7–9, and 4–6 species for the most depauperate community.

Assignment of density and richness treatments to the plots (12 treatment combinations each with six replicates) was stratified and semi-random due to constraints of natural richness and stem densities. We first divided the plots into the three levels of dominant grass abundance, so that high (ambient) density plots had at minimum 307 stems of the dominant C<sub>4</sub> grasses (average:  $429.2 \pm 53.8$  SD), medium density plots had at minimum of 243 stems (average:  $378.5 \pm 69.2$  SD), and low density plots had at minimum of 173 stems (average:  $298.9 \pm 83.3$  SD). Each had similar initial average richness: high – 14.8 (range: 10–18 species), medium – 13.8 (10–18), and low – 13.9 (11–17). Then for each density level, six plots that had 13 or greater species were first assigned to the high (13–16 species) richness treatment. Since only four (low), nine (medium), and five (high) of the 24 plots per density level had less than 13 species, these assignments were essentially random. The remaining plots were then assigned randomly to the other richness treatments. For each richness treatment, plots were randomly assigned to particular target richness value. The assignments resulted in an average initial richness of 15.4 (1.4 SD; range: 13–18) for the 13–16 richness treatment, 13.6 (1.7 SD; range: 10–17) for the 10–12 richness treatment, 14.3 (2.4 SD; range: 10–18) for the 7–9 richness treatment, and 13.1 (1.7 SD; range: 11–18) for the 4–6 richness treatment. Thus, for all but the ambient (high) richness treatment, average initial richness did not differ significantly among the richness reduction treatments.

In early June 2000, we reduced total richness and abundance of the dominant grasses in the plots by clipping individuals and applying herbicide (glyphosate) to the cut stem. Application of herbicide to the stems was precise with minimal non-target effects to neighbours. Richness was reduced by permanently removing plant species based inversely on their probability of occurrence (relative frequency) in the whole community (Fig. 1a), which was strongly correlated with their biomass production (Fig. 1a, inset) and abundance (average stem density) in the community ( $r = 0.68$ ,  $P < 0.001$ ; excluding *A. gerardii*,  $r = 0.84$ ,  $P < 0.001$ ). For each plot, species that occurred least frequently across the study site were removed first and then species that were more frequent were removed until a target richness level was achieved. This resulted in a greater chance for more frequent (smaller ranked) species to be removed with the lower richness treatments ( $F_{2,71} = 16.0$ ,  $P < 0.001$ ), however the three most frequent species (*A. gerardii*, *Dichanthelium oligosanthes*, and *Aster ericoides*) were never removed (Fig. 1b). Richness was reduced to some extent in most of the plots. On average, 7.9 species ( $\pm 2.1$  SD, range: 5–13) were removed with the 4–6 richness treatment, 6.1 ( $\pm 2.1$  SD, range: 2–11) with the 7–9 treatment, 2.7 ( $\pm 2.1$  SD, range: 0–6) with the 10–12 treatment, and 1.3 ( $\pm 1.0$  SD, range: 0–3) with the 13–16

treatment. For the density treatments, densities of the dominant, highly productive species, mainly *A. gerardii*, *S. nutans* and *B. curtipendula* (Fig. 1, inset), were reduced in all but the high-density plots. In general, *A. gerardii* comprised 80% of the stems removed and *S. nutans*, *B. curtipendula* and other species comprised 10–20% of stems removed. These proportions reflected natural abundance patterns observed in the plots (data not shown). All biomass removed with the treatments was collected, dried at 60 °C and weighed. Both treatments resulted in a significantly greater amount of biomass removed from the moderate and low-density plots ( $F_{2,71} = 60.0$ ,  $P < 0.001$ ), equivalent to 10 and 20% of maximum end-of-season (2000) biomass in the high density plots. In contrast, there was no difference in the amount of biomass removed from the richness treatments ( $F_{3,71} = 0.5$ ,  $P = 0.69$ ).

After all treatments were applied, stem densities were recensused to confirm treatment levels. In 2000, high-density plots had on average 450.3 (13.2 SE) stems of the dominant grasses per plot (total stem density:  $781.2 \pm 23.8$  SE). We were able to reduce abundance dominant grasses in low density plots by 47% to an average stem density of 161.3 ( $\pm 17.9$  SE) stems per plot (total stem density:  $364.8 \pm 14.2$  SE) and medium density plots by 23% to an average density of 296.8 ( $\pm 16.9$  SE) stems per plot (total stem density:  $554.5 \pm 14.7$  SE). In 2001, dominant grass stem densities averaged 561.9  $\pm$  22.0 (total: 993.8  $\pm$  24.2 SE), 426.1  $\pm$  13.6 SE (total: 772.9  $\pm$  15.7 SE), and 281.0  $\pm$  27.9 SE (total: 522.7  $\pm$  19.9 SE) stems for high-, medium- and low-density plots, respectively. Because the density treatments remained in place in 2001, the plots required only minor adjustments of the richness levels.

Throughout the growing season in both years, we measured photon flux density (PFD) on a weekly basis above the canopy and at the soil surface within each plot using a sunfleck ceptometer (0.5 m, Decagon, Pullman, WA). Based on measurements at two locations within each plot, PFD availability was calculated as the proportion of soil surface-level light to above-canopy light. For both years, at the end of the growing season (late August to mid September), we counted all stems and harvested, dried and weighed all above-ground biomass of each species separately, summing these to estimate ANPP, an integrative measure of ecosystem function in this system (Briggs & Knapp 1995). Productivity was further divided into dominant (three most abundant and productive  $C_4$  grasses, Fig. 1) and that of all other species (hereafter referred to as subordinate) components for subsequent analyses.

### Statistical analyses

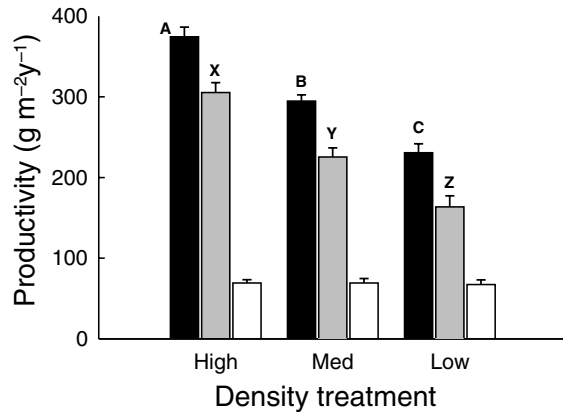
Data were analysed using SAS (version 8.1) statistical software (SAS Institute, Cary, NC), and significance levels

for all analyses were set at  $P \leq 0.05$ . ANPP and the productivity of dominant and subordinate components were analyzed using analysis of covariance, with density and richness treatments as main effects and the amount of biomass removed to establish the richness and density treatments as a covariate. Although we expected that the amount of biomass removed might differentially affect the density and richness treatments, we found that the covariate had no significant effect (data not shown). The effects of the density and richness treatments on total, dominant and subordinate productivity were also examined with two-way repeated measures analysis of variance (ANOVA, Proc MIXED procedure). There were no significant interactions between year and richness or density and richness treatments, but there was a significant year effect (total:  $F_{1,10} = 15.6$ ,  $P < 0.001$ ; dominant:  $F_{1,10} = 15.3$ ,  $P = 0.003$ ) and year and density interaction for total ( $F_{2,20} = 24.9$ ,  $P < 0.001$ ) and dominant productivity ( $F_{2,20} = 12.8$ ,  $P < 0.001$ ). Thus, we present results from simple linear regression analyses of end-of-season (realized) richness and ANPP or productivity of dominant and subordinate species averaged across the density treatments for each year separately. Initial community richness may influence productivity responses to species loss, perhaps due to spatial heterogeneity in resources or because the abundance of dominant species may drive initial variation in richness among the plots. Thus, we also examined these relationships using pre-treatment richness.

### RESULTS

Reductions in abundance (density) of the dominant species in this grassland had immediate, negative effects on total ANPP in both years of the study (Fig. 2). Total ANPP was reduced by 30% with 20% of dominant stems removed and by >50% with 50% removal, compared to the high (ambient) density communities (repeated measures ANOVA:  $F_{2,10} = 69.2$ ,  $P < 0.001$ ). The reduction in total ANPP was driven by reduced production of the dominant  $C_4$  grasses (repeated measures ANOVA:  $F_{2,10} = 44.6$ ,  $P < 0.001$ ), which comprised 70–80% of total production in this grassland community (Fig. 2). Because reduced densities of the dominant species altered canopy structure and increased light availability to the remaining plants (ANOVA year 1:  $F_{2,71} = 60.0$ ,  $P < 0.001$ ; year 2:  $F_{2,71} = 7.52$ ,  $P = 0.001$ ), we expected that production of the subordinate species would be enhanced through competitive release. This was not observed during the 2 years of the study (Fig. 2); instead, production of the subordinate species was unaffected by even a 50% reduction in density (repeated measures ANOVA:  $F_{2,20} = 0.06$ ,  $P = 0.94$ ).

In regression analysis of average ANPP and end-of-season (realized) richness, total ANPP was not affected



**Figure 2** Total aboveground net primary production (ANPP, black bars) and production of dominant (grey bars) and subordinate species (open bars) with 0 (high), ~25 (medium), and ~50% (low) reductions in the density of dominant species. Mean ( $\pm 1$  SE) are shown for low-, medium-, and high-density plots averaged across all richness levels and both years. Different letters denote significant differences among density treatments.

by a reduction in the number of subordinate species during the 2-year study period (2000:  $r^2 = 0.36$ ,  $P = 0.07$ ; 2001:  $r^2 = 0.11$ ,  $P = 0.29$ ; Fig. 3a), although there was a trend for increasing productivity with declining richness. Total ANPP was maintained with species loss in both years due to increased productivity of the dominant component of the community (2000:  $r^2 = 0.72$ ,  $P = 0.002$ ; 2001:  $r^2 = 0.66$ ,  $P = 0.001$ ; Fig. 3b). This resulted from greater biomass per individual (repeated measures ANOVA:  $F_{3,30} = 22.8$ ,  $P < 0.001$ ), rather than an increase in stem densities (repeated measures ANOVA:  $F_{3,30} = 1.38$ ,  $P = 0.25$ ). The negative effects of species loss were observed only when the subordinate component of the community was analysed separately. Average productivity of these species declined significantly with decreasing richness (2000:  $r^2 = 0.79$ ,  $P < 0.001$ ; 2001:  $r^2 = 0.81$ ,  $P < 0.001$ ; Fig. 3b). The patterns we observed were not influenced by initial richness of the communities. In 2000, pre-treatment richness and total, dominant and subordinate productivity were not significantly related ( $r^2 = 0.11$ ,  $P = 0.39$ ;  $r^2 = 0.22$ ,  $P = 0.20$ ;  $r^2 = 0.28$ ,  $P = 0.14$ , respectively). Therefore, the patterns we observed were most likely due to the richness reduction treatments rather than initial differences in richness or resource heterogeneity among plots.

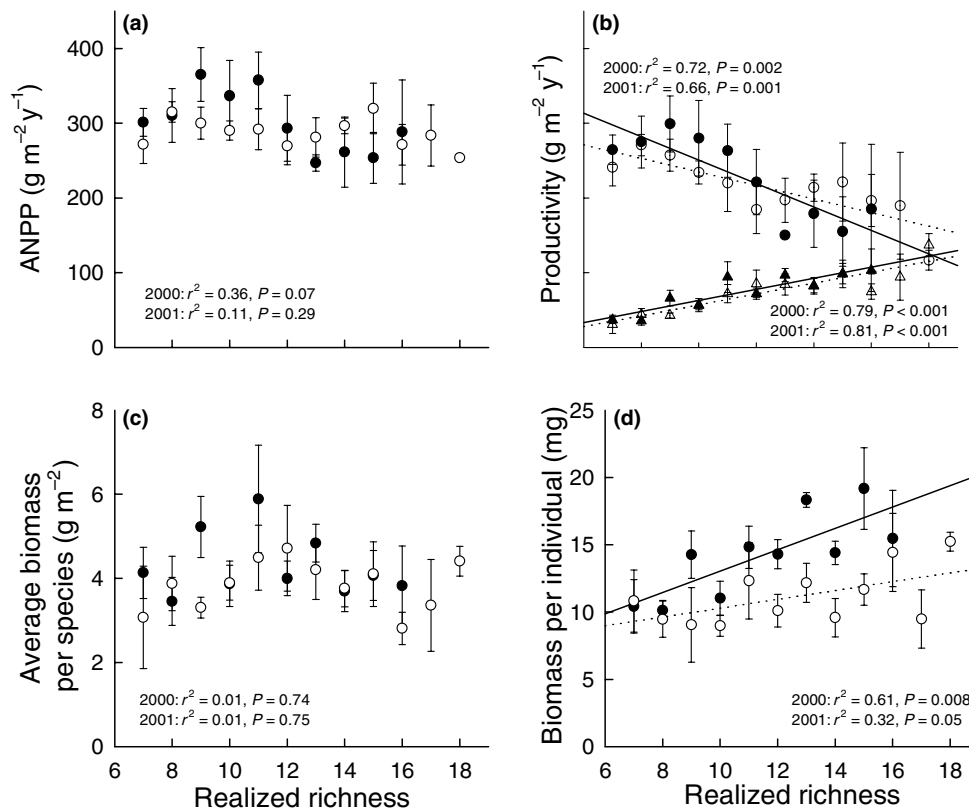
## DISCUSSION

The ecosystem consequences of loss of rare and uncommon species and reduced abundance of common species, a likely scenario of species loss in the field resulting from environmental changes (e.g. Tilman & El Haddi 1992;

Leach & Givnish 1996), were immediate and substantial. Total ANPP was reduced in this grassland by as much 50% with an equivalent reduction in the abundance of the most common and productive species. Similar impacts have been observed in other systems with complete removal of dominant species (e.g. MacGillivray *et al.* 1995; Hooper & Vitousek 1997; Symstad *et al.* 1998). As predicted by the 'mass ratio hypothesis' (Grime 1998; Geider *et al.* 2001), the major contributors to biomass, in this case a few common grasses (Fig. 1a, inset), primarily determined a key ecosystem process in this grassland.

We expected the subordinate component of the community would mitigate the loss in ANPP by responding positively to reduced abundance of the dominants, but this was not the case. Despite increased light and space availability, subordinate productivity did not increase as might be expected if their growth was suppressed by competition with the dominants. Grazing of the dominant grasses by ungulates in tallgrass prairie does lead to increased richness and abundance of rare and uncommon species by decreasing competition for limiting resources (Collins *et al.* 1998). However, it is likely that the complete removal of individuals in our study impacted microclimatic conditions and resources differently than in studies where foliage is only partially removed with grazing or mowing. Any positive effects of the increased resource availability on growth of the remaining rare and uncommon species may have been offset in our study by more stressful conditions, perhaps due to increased light availability and higher canopy temperatures causing enhanced evapotranspiration and decreased soil moisture (Knapp & Seastedt 1986). Alternatively, responses of the remaining subordinate species to increased resources may have been limited over the 2-year period by propagule supply (Foster 2001; Symstad & Tilman 2001) or by morphological and physiological constraints. The lack of response in the subordinate component to partial removal of the common grasses suggests that recovery of this grassland from complete loss of dominants could be protracted.

Loss of rare and uncommon species had no short-term (2 years) effect on our measure of ecosystem function (total ANPP) in this grassland. This contrasts with findings from studies using synthetic communities comprised of random assemblages of species (Tilman *et al.* 1996, 1997b, 2001; Symstad *et al.* 1998; Van der Heijden *et al.* 1998; Hector *et al.* 1999; Lepš *et al.* 2001; Loreau *et al.* 2001). In these studies, productivity and other ecosystem processes declined significantly with decreasing species richness. It has been argued that such declines may be a consequence of the sampling effect (Wardle 1999; Huston *et al.* 2000; Lepš *et al.* 2001), in which the chance of including dominant or unique species declines as richness declines (Aarssen 1997; Huston 1997; Tilman *et al.* 1997a). Although the sampling effect may result from stochastic community assembly processes (Tilman



**Figure 3** Effects of nonrandom patterns of species loss on: (a) total ANPP; and (b) productivity of dominant (circles) and subordinate (triangles) species in 2000 (closed symbols, solid line) and 2001 (open symbols, dashed line). Two potential mechanisms responsible for the decline in subordinate productivity with nonrandom species loss were examined using linear regression analysis. (c) The sampling effect, that is, greater chance of retaining a highly productive subordinate species with increasing richness, did not appear to be driving the decline in subordinate productivity with species loss. (d) The increase in average biomass per individual does provide evidence for loss of complementary interactions (i.e. increased resource use or positive interactions) among subordinate species reducing productivity of these species with species loss. Data points are mean  $\pm$  1 SE plot values averaged across density treatments.

*et al.* 1997a), there is evidence that it is primarily a statistical artifact of experiments that randomly assemble communities (Wardle 1999; Huston *et al.* 2000). In order to detect other mechanisms that may cause a decline in productivity with species loss, such as niche complementarity (Tilman *et al.* 1997a; Loreau 2000; Loreau & Hector 2001; Mulder *et al.* 2001; Cardinale *et al.* 2002), these studies have indirectly controlled for the sampling effect using comparisons between mixtures and monocultures (Hector *et al.* 1999; Loreau & Hector 2000). However, rigorous testing of the sampling effect requires that all species combinations at all diversity levels be replicated and examined (Loreau *et al.* 2001), something that is difficult with even a relatively small pool of species. No studies have tried to directly control for the sampling effect. Thus, the relative importance of different underlying mechanisms causing the observed declines in productivity with species loss remain unclear, given that studies to date can only conclude that both mechanisms may be important (Loreau *et al.* 2001).

In our study, total ANPP was maintained in the face of a threefold loss of species for several reasons. First, we were able to examine the impacts of species loss in the absence of the sampling effect because the dominant and most productive species were present at all richness levels. By retaining these species in all communities regardless of richness, we were able to show that ANPP was maintained by a few dominant species. We found that productivity of this component of the community increased as richness decreased, and thus compensated for reduced productivity resulting from loss of rare and uncommon species. This increase may reflect the ability of the dominant species to rapidly respond to increased resources in this system (Turner & Knapp 1996). Second, there is ample evidence that numerically uncommon species can have disproportionately large ecological effects (i.e. keystone species, Power *et al.* 1996) and therefore their loss could strongly affect ecosystem processes. None of the rare and uncommon species lost from our communities appeared to possess this

trait, at least for the ecosystem process measured and over the limited duration of the study. This may not be the case if we were to examine other ecosystem processes, such as nutrient retention or resistance to invasion, or if species from other trophic levels were lost.

A negative effect of species loss on productivity, as observed in other studies (Tilman *et al.* 1996, 1997b, 2001; Symstad *et al.* 1998; Van der Heijden *et al.* 1998; Hector *et al.* 1999; Loreau *et al.* 2001), was apparent only when the subordinate component of the community was examined separate from the dominant component. Clearly, the decline in subordinate productivity in the species-poor communities resulted, in part, from reduced densities of the subordinates (2000:  $r^2 = 0.71$ ,  $P = 0.002$ ; 2001:  $r^2 = 0.53$ ,  $P = 0.007$ ), but other mechanisms may be important as well. The significant decline in productivity of rare and uncommon species with reduced richness may have resulted from increased competition from the dominant grasses, which increased in production with declining richness. However, this does not appear to be the case given that the subordinate species did not respond positively to reduced abundance of the dominant species.

This decline also may have been a product of: (i) a greater chance of removing a highly productive subordinate species as richness decreased or retaining a highly productive species in more diverse communities (i.e. the sampling effect; Huston 1997); or (ii) loss of complementary interactions among the remaining subordinate species (Hector *et al.* 1999; Loreau *et al.* 2001). We examined the relative roles of each of these mechanisms by relating community richness to average biomass of the subordinate species retained and lost at each richness level (test for i) and to average individual (stem) biomass (calculated as total subordinate biomass divided by total subordinate stems per plot) of the subordinate species (test for ii) at each richness level. If the sampling effect influenced the relationship between richness and subordinate productivity, the average biomass of the subordinate species retained would decline as richness decreased, but this was not the case (Fig. 3c; 2000:  $r^2 = 0.01$ ,  $P = 0.74$ ; 2001:  $r^2 = 0.01$ ,  $P = 0.75$ ). Moreover, the chance of removing a more productive subordinate species as richness declined did not increase ( $r^2 = 0.001$ ,  $P = 0.81$ , data not shown). Thus, more productive subordinate species were as likely to be found at low richness levels as at higher richness levels. This suggests that the sampling effect was not driving the decline in subordinate productivity. In contrast, average biomass per individual decreased as community richness decreased (Fig. 3d; 2000:  $r^2 = 0.61$ ,  $P = 0.008$ ; 2001:  $r^2 = 0.32$ ,  $P = 0.05$ ). Thus, it appears that the reduction in subordinate production with declining richness not only resulted from reduced numbers individuals but also from reduced individual biomass. This suggests that loss of complementary interactions among the

subordinate species that may enhance individual biomass contributed to the reduction in their productivity with species loss.

We contend that the impacts of species loss on ecosystems need to be evaluated based on natural patterns of species abundances that reflect their contributions to ecosystem processes (Korner 1993; Schwartz *et al.* 2000; Geider *et al.* 2001; Grime 2002; Loreau *et al.* 2002). In doing so, we were able to independently assess the importance of dominant species versus numbers of species in maintaining productivity – something that has eluded researchers to date (Fridley 2001; Loreau *et al.* 2001). From our results, we conclude that species identity and ecosystem function are strongly linked (Grime 1998; Vanni *et al.* 2002). Dominant species in natural communities play a key role in conferring short-term resistance to reductions in ecosystem function, as rare and uncommon species are lost. Thus, dominant species impart short-term stability to ecosystems experiencing non-random patterns of species loss. However, productivity of the subordinate species, the most diverse component of the community, decreased as their richness declined. Therefore, loss of rare and uncommon plant species – thought to have little impact on most ecosystem processes (Schwartz *et al.* 2000; Geider *et al.* 2001; Loreau *et al.* 2001) – could have important long-term consequences for ecosystem resilience in the face of environmental change (Grime 1998; Chapin *et al.* 2000). This should be particularly true if the loss of rare and uncommon species accelerates the risk for local extinction of the remaining species, thereby altering the susceptibility of ecosystems to invasion by exotic species (Lyons & Schwartz 2001) and impacting important biotic interactions, community dynamics and other ecological services.

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