Invasibility and compositional stability in a grassland community: relationships to diversity and extrinsic factors

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We present results from an ongoing field study conducted in Kansas grassland to examine correlates of invasibility and community stability along a natural gradient of plant diversity. Invasibility was evaluated by sowing seeds of 34 plant species into 40 experimental plots and then measuring colonization success after two growing seasons. Compositional stability, defined as resistance to change in species relative abundances over two growing seasons and in response to experimental disturbance, was measured in a separate set of 40 plots.
We found that community susceptibility to invasion was greatest in high diversity microsites within this grassland. Multiple regression analyses suggested that the positive correlation between invasibility and plant diversity was due to the direct influences of the extrinsic factors that contribute to spatial variation in diversity (soil disturbances; light availability), not to any direct impact of diversity. In addition, we found that compositional stability in response to disturbance was greatest within low diversity microsites and was strongly related to the dominance (evenness) component of diversity.

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Understanding the factors that regulate the stability of ecological systems is a major goal in ecology and resource management. Concern regarding the impact of species loss on ecosystem services has stimulated great interest in the potential impacts of biodiversity on the stability of aggregate ecosystem parameters such as primary production and nutrient retention (Ehrlich and Ehrlich 1992, McNaughton 1993, Schulze and Mooney 1993, Tilman and Downing 1994, McGrady-Steed et al. 1997, Naeem and Li 1997, Kinzig et al. 2001). Also of concern are processes that govern community-level phenomena such as invasibility (Elton 1958, Burke and Grime 1996, Knops et al. 1999, Levine and D'Antonio 1999, Davis et al. 2000) and compositional stability (Elton 1958, May 1972, Mellinger and McNaughton 1975, MacGillivray et al. 1995, Tilman 1996, Sankaran and McNaughton 1999). Elton (1958) argued forcefully

that diverse communities should be more resistant to invasion than species-poor ones. Although subject to alternative interpretation, recent experiments involving in situ manipulations of diversity have been offered in support of Elton's classic hypothesis (Knops et al. 1999, Levine 2000, Naeem et al. 2000, Prieur-Richard et al. 2000, Symstad 2000, Wardle 2001). In contrast, correlational studies evaluating community invasibility along natural diversity gradients generally suggest that diverse communities are more susceptible to invasion than species-poor ones (Wiser et al. 1998, Levine and D'Antonio 1999, Stohlgren et al. 1999, Levine 2000, Wardle 2001). The positive correlation between invasibility and diversity found in observational studies appears to reflect the direct impact of uncontrolled and covarying extrinsic factors (resource availability, disturbance regime etc.) on colonization and diversity, overwhelm-

ing any potential direct impact of diversity on invasibility (Levine and D'Antonio 1999, Stohlgren et al. 1999, Naeem et al. 2000).

Compositional stability refers to the constancy of community membership and the resistance to change in species relative abundances in response to perturbation (population stability sensu May 1973, Tilman 1996, Sankaran and McNaughton 1999). Although Elton (1958) hypothesized that species abundances should be less oscillatory in diverse communities, early support for this view was largely anecdotal (Goodman 1975, Tilman et al. 2001). As pointed out by Tilman (1996, 1999), theoretical investigations of multi-species interaction have not generally supported Elton's hypothesis and have predicted primarily that population dynamics within communities will be either destabilized or unaffected by diversity (May 1972, 1973, DeAngelis 1975, Pimm 1979, Tilman 1999, Lehman and Tilman 2000). Empirical studies in old-fields of New York, USA (Mellinger and McNaughton 1975, McNaughton 1977), and grasslands of Africa (McNaughton 1977), Minnesota, USA (Tilman 1996) and India (Sankaran and McNaughton 1999), report negative associations between compositional stability and diversity. In contrast, Frank and McNaughton (1991) report a positive association between compositional stability and community diversity in the grasslands of Yellowstone National Park, USA. These contrasting empirical patterns suggest that the nature of the relationship between compositional stability and diversity likely varies with ecological circumstance.

Here we present results from an ongoing field experiment in Kansas grassland that is being conducted along a natural gradient of plant diversity. The objectives of the study were to examine the dependence of community invasibility and compositional stability on plant diversity and on extrinsic factors correlated with diversity. Our results show that community susceptibility to invasion is greatest in high diversity sites in this grassland and that this effect is due most probably to the direct influence of extrinsic factors that generate spatial variation in diversity, not to any direct effect of diversity per se. We also show that compositional stability in response to an experimentally-imposed disturbance was greatest in low diversity sites, and appears to be directly related to the dominance component of diversity.

Methods

We examined community invasibility and compositional stability over a two-year period in a 20-ha successional grassland located in the prairie-forest ecotone of northeastern Kansas (Nelson Environmental Studies Area; University of Kansas). The grassland was abandoned from hay production in 1984 and is dominated

by introduced, C3 perennial grasses: *Bromus inermis* Leyss.; *Festuca arundinaceae* Schreb.; and *Poa pratensis* L. The experiment consists of forty 2.5×2.5 m blocks of four 1×1 m plots, established in September 1999 throughout the 20-ha field site (Foster 2001). Within each block, plots were separated by 0.5 m walkways. In January 2000, a 2×2 factor array of treatments was randomly applied to the plots in each block: two levels of seed addition of 34 grassland species (seeds added, no seeds added); and two levels of experimentally imposed disturbance (plots disturbed, plots not disturbed). Of primary concern here are plots from two of the four original treatments: (1) undisturbed plots that received experimental additions of seed (referred to below as treatment 2 plots), used in this study to investigate community invisibility and; (2) disturbed plots in which no seeds were added (referred to below as treatment 3), used in this study to examine compositional stability in response to a moderate perturbation.

Invasibility

The 34 species sown into treatment 2 plots included native and introduced grassland species that span a wide-range of life history types and habitat affinities (Table 1). In the fall of 1999, prior to the addition of the seeds, 16 of the 34 sown species occurred naturally within the 20-ha study site, and the remaining 18 species were found in nearby old-field and prairie habitats (within 2 km of the study site). Of the 16 sown species present within the 20-ha site, 9 of these were recorded as being initially present in some of the treatment 2 plots during a September 1999 pre-treatment survey. In January 2000, 400 seeds of each species were added to the treatment 2 plots by hand. We calculated the invasibility of a plot as follows:

$$I = (S_{2001} - S_{1999})/(34 - S_{1999})$$

where S_{1999} = the number of sown species that were initially present in treatment 2 plots in the 1999 survey (pre-treatment); S_{2001} = the number of sown species recorded in treatment 2 plots in the September 2001 survey (end of the second growing season); and 34 = the total number of species sown. This measure expresses invasibility as a proportion of species sown, and adjusts for any sown species that were initially present in a plot in 1999. This index does not adjust for the potential contribution of sown species that may have colonized treatment 2 plots after 1999 through natural means (not as a result of being experimentally sown). However, no such adjustment to the index was necessary because no sown species, other than the few that were already present in 1999, were recorded in the undisturbed control plots in 2000 and 2001 (data not shown). Therefore we assume that all values of *I* re-

ported here reflect the contribution of species that had colonized the seed addition plots as a result of being experimentally sown.

Compositional stability in response to perturbation

Beginning in 2000, moderate experimental disturbances were applied to treatment 3 plots to disrupt the soil and vegetation canopy. Disturbances were applied by: (1) removing litter and scarifying the soil with a rake in January 2000 and February 2001; and (2) clipping the vegetation canopy to 15 cm height in April and June of each year. Although the experimental disturbances were not initially designed to mimic a specific type of natural disturbance (Foster 2001), these disturbances were of a magnitude common to intact grasslands (mowing, small-mammal disturbance etc.). Compositional stability in response to experimental disturbance was evaluated as the resistance to compositional change (RCC; Sankaran and McNaughton 1999). RCC measured the

Table 1. Species added as seed to the treatment 2 plots. Taxonomy follows McGregor et al. (1986).

Species	Life form*	Origin†
Achillea millefolium	PF	N
Amorpha canescens	PL	N
Andropogon gerardi	PG	N
Asclepias tuberosa	PF	N
Aster novae-angliae	PF	N
Bouteloua curtipendula	PG	N
Chrysanthemum leucanthemum	PF	I
Dactylis glomerata	PG	I
Desmanthus illinoensis	PL	N
Echinacea pallida	PF	N
Elymus canadensis	PG	N
Eragrostis trichodes	PG	N
Festuca arundinacea	PG	I
Festuca ovina	PG	N
Lespedeza capitata	PL	N
Liatris pycnostachya	PF	N
Medicago sativa	PL	I
Melilotus officinalis	BL	I
Monarda fistulosa	PF	N
Panicum virgatum	PG	N
Petalostemum candidum	PL	N
Petalostemum purpurea	PL	N
Phleum pratense	PG	I
Poa pratensis	PG	I
Ratibida columnifera	PF	N
Ratibida pinnata	PF	N
Rudbeckia hirta	PF	N
Salvia azurea	PF	N
Schizachyrium scoparium	PG	N
Sorghastrum nutans	PG	N
Sporobolus cryptandrus	PG	N
Trifolium pratense	PL	I
Trifolium repens	PL	I
Tripsacum dactyloides	PG	N

* P = perennial, B = biennial, L = legume forb, F = non-legume forb, G = grass.
† N = native, I = introduced.

proportional shift in species relative abundances between September 1999 (pre-disturbance) and September 2001 (post-disturbance) in treatment 3 plots. Compositional stability was calculated as follows:

$$RCC = \sum_{i=1}^{m} \min(x_{i\,1999},\ x_{i\,2001})$$

where $x_{i\,1999}$ and $x_{i\,2001}$ represent relative cover of the ith species in the 1999 and 2001 surveys respectively and m represents the total number of species in a plot common to both surveys. RCC is equivalent to the percent similarity index (Gauch 1982, Pielou 1984) and can have values ranging from 0 to 1. A value close to zero indicates a high degree of change in relative abundance among species (low degree of resistance). A value close to one indicates a low degree of change in relative abundance among species (high degree of resistance).

Extrinsic factors

The extrinsic factors measured in each block included: above-ground standing crop; percent light penetration; soil moisture and an index of soil disturbance. Standing crop was harvested for each block in July 2000 and 2001 in the undisturbed spaces between plots. The arithmetic average of the 2000 and 2001 standing crops was used as an index of potential productivity for all plots in each block over the two-year period. Light penetration to the soil was measured in all treatment plots four times during the 2000 and 2001 growing season using a PAR ceptometer (Decagon Devices). Light penetration (%) for each plot of each treatment was expressed as the average across all sampling dates. Soil moisture (% volumetric) was measured in mid-June 2000 in each plot using time domain reflectometry four days following rainfall. A disturbance index provided a measure of ambient, non-experimental soil disturbance within each plot, and was estimated visually in January 2000 (prior to application of treatments) as the percentage of ground surface within a plot characterized as disturbed soil. Soil disturbances due to small-mammal activity (rodent runways and burrows) and to soil expansion-contraction (freeze-thaw and soil wetting-drying cycles) are common in this grassland and are readily apparent in the winter months.

Analyses

To assess the underlying environmental gradients that produce variation in diversity within the site we used univariate regression to examine relationships between initial (pre-treatment) diversity (Shannon-Weiner index in 1999) and extrinsic factors in the undisturbed treatment 2 plots. Regression was also used to examine the

dependence of invasibility and compositional stability on initial plot diversity in treatment 2 and treatment 3 plots respectively.

Backward-elimination multiple regression was used to evaluate the dependence of invasibility in the treatment 2 plots and compositional stability in the treatment 3 plots on initial diversity and the extrinsic variables. The disturbance index was not included as a predictor of compositional stability in the regression analyses because the experimental raking disturbances applied to treatment 3 plots obliterated any underlying natural soil disturbances within them. Several predictor variables (standing crop, light penetration and the disturbance index) were log transformed before the multiple regression analyses to improve the linearity of relationships. Because there were inter-correlations among some predictor variables, the extent of collinearity was determined for each multiple regression (Norusis 1993). Acceptable levels of collinearity were judged using the following criteria: condition index < 30; variance inflation $< 1/(1 - R^2)$; variance proportions not close to one (Freund and Littell 1991). All data analyses were performed using SPSS 9.0 for Windows.

Results

Species diversity in relation to extrinsic factors

Initial diversity (H') in the treatment 2 plots varied strongly among blocks. This gradient in diversity was negatively correlated with the gradient in standing crop ($r^2 = 0.16$, $P < 0.05$; Fig. 1A) and positively correlated with gradients of light penetration ($r^2 = 0.32$, $P < 0.001$; Fig. 1B) and disturbance ($r^2 = 0.15$, $P < 0.05$; Fig. 1C).

Invasibility

Our measure of community invasibility was positively correlated with initial diversity (H'; $r^2 = 0.32$, $P < 0.001$; Fig. 2A) indicating that low diversity microsites were less invasable than high diversity microsites. However, invasibility was also correlated with three of the four extrinsic factors that we measured. Invasibility was negatively correlated with standing crop ($r^2 = 0.35$, $P < 0.001$; $y = -0.1337Ln(x) + 0.9726$), positively correlated with light penetration ($r^2 = 0.61$, $P < 0.0001$; $y = 0.0822Ln(x) + 0.0277$) and positively correlated with disturbance ($r^2 = 0.34$, $P < 0.001$; $y = 0.1148Ln(x) + 0.171$).

In the backward-elimination multiple regression we included initial species diversity (H'), light penetration, disturbance and soil moisture as predictors of
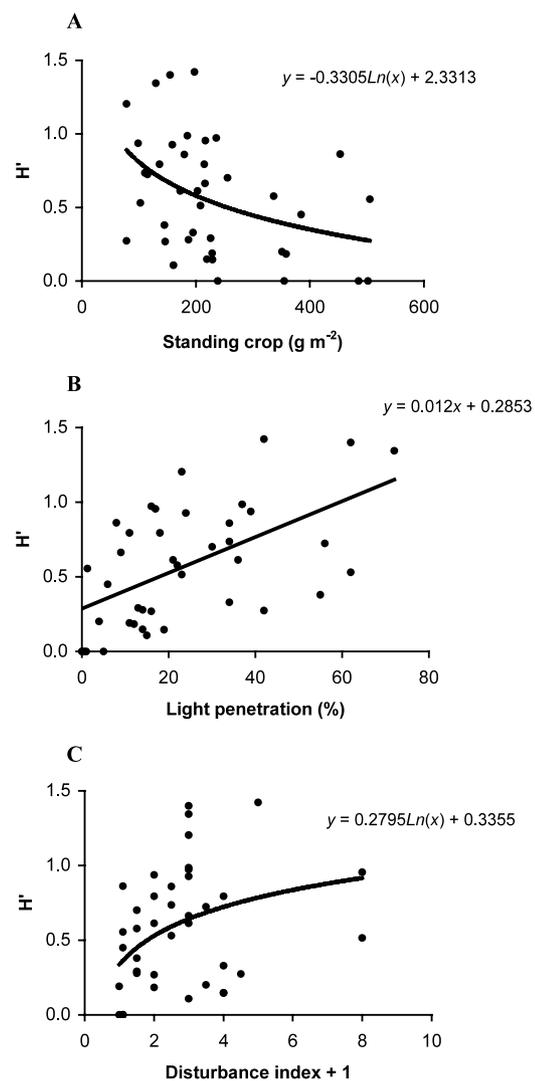

Fig. 1. Dependence of community diversity (H'; Shannon-Weiner Index), measured in treatment 2 plots in 1999, on extrinsic variables: (A) standing crop ($r^2 = 0.16$, $P < 0.05$); (B) light penetration ($r^2 = 0.32$, $P < 0.001$); and (C) disturbance index $+ 1$ ($r^2 = 0.15$, $P < 0.05$). The value 1 was added to the disturbance index in order to fit a logarithmic function to the data.

invasibility. Unfortunately standing crop could not be included in the analysis of treatment 2 data because its inclusion in the regression models led to marginal problems with collinearity (high condition index values). In the final regression model, light penetration and disturbance were retained as significant predictors of invasibility, whereas H' and soil moisture were eliminated (Table 2). The coefficients for both retained variables were positive in sign, suggesting that light availability and small-scale disturbance each had independent and direct positive influences on community invasibility.
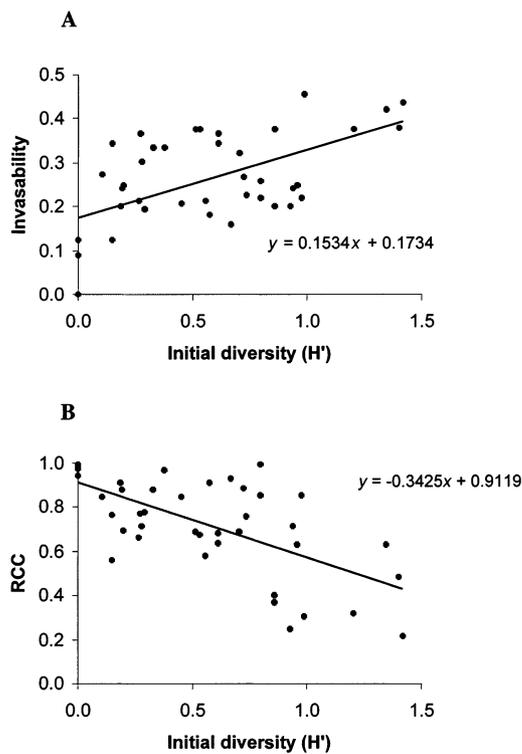
Fig. 2. Dependence of invasibility (A; $r^2 = 0.32$, $P < 0.001$) and compositional stability (B; RCC; $r^2 = 0.40$, $P < 0.001$) on initial diversity.

Compositional stability

Resistance to compositional change (RCC) was negatively correlated with initial diversity (H'; $r^2 = 0.40$, $P < 0.001$; Fig. 2B) indicating that low diversity microsites were more compositionally stable in response to the experimentally applied disturbance than high diversity microsites. RCC was negatively correlated with light penetration ($r^2 = 0.20$, $P < 0.01$; $y = -0.1042 Ln(x) + 0.9887$), but was not significantly correlated with any other extrinsic variable ($P > 0.05$ for all other extrinsic variables).

In a backward-elimination multiple regression, including initial species diversity (H'), standing crop, light penetration and soil moisture as predictor variables, only diversity (H') was retained as a significant predic-

tor of RCC in the final model (Table 3A). Because diversity (H') is determined by both species richness and species dominance (evenness), we performed an additional backward-elimination regression to assess the independent contributions of richness and species dominance in explaining variation in RCC. Because evenness includes species richness in its calculation ($H'/\ln S$) we could not use it in the analysis. Instead, the initial (1999) relative cover of the most abundant species in each treatment 3 plot was used as a simple measure of species dominance. In the multiple regression analysis, only species dominance was retained as a significant predictor of RCC (Table 3B). The regression coefficient in the final model was positive, indicating that RCC tended to be greatest in communities strongly dominated by a single species.

Discussion

The results of this study conflict with the general hypothesis of Elton (1958) that invasion resistance and compositional stability increase with diversity.

Invasibility

Consistent with the sowing experiment of Robinson et al. (1995), but in contrast to the sowing experiment of Tilman (1997), we found that community invasibility was maximal in microsites that were naturally more diverse. Our results appear to reflect the positive establishment response of invading plant species to two important extrinsic environmental factors that promote colonization and diversity in this grassland: light availability and small-scale disturbance. The role of light in regulating seedling establishment and diversity in herbaceous plant communities is well known (Newman 1973, Carson and Barrett 1988, Goldberg and Miller 1990, Grace and Pugesek 1997, Foster and Gross 1998, Foster 2001). Small-scale soil disturbances, particularly those generated by animal activity, can play an important role in promoting invasion by providing establishment microsites and by increasing the availability of key resources (Platt 1975, Pickett and

Table 2. Backward-elimination multiple regression for the dependence of invasibility on initial diversity, light penetration, disturbance and soil moisture.

Predictor variables	Invasibility (I)		
	Parameter estimate	Partial correlation	P
Initial H' (1999)	eliminated	–	–
Ln(light penetration)	0.069	0.705	<0.001
Ln(disturbance index + 1)	0.054	0.392	0.015
Relative soil moisture	eliminated	–	–

Final model: $df = 2, 39$; $F = 37.3$, $r^2 = 0.66$; $P < 0.0001$

Table 3. Backward-elimination multiple regressions for the dependence of compositional stability on: (A) initial diversity, standing crop, light penetration and soil moisture; and (B) initial richness, species dominance, standing crop, light penetration and soil moisture.

	Predictor variables	Compositional stability (RCC)		
		Parameter estimate	Partial correlation	P
A.	Initial H' (1999)	−0.340	−0.621	<0.001
	Ln(Standing crop)	eliminated	–	–
	Ln(light penetration)	eliminated	–	–
	Relative soil moisture	eliminated	–	–
B.	Initial richness (1999)	eliminated	–	–
	Species dominance (1999)	0.527	0.518	0.001
	Ln(Standing crop)	eliminated	–	–
	Ln(light penetration)	eliminated	–	–
	Relative soil moisture	eliminated	–	–

A. Final model: $df = 1, 38$; $F = 23.2$, $r^2 = 0.38$; $P < 0.001$
B. Final model: $df = 1, 38$; $F = 13.5$, $r^2 = 0.27$; $P < 0.01$

White 1985, Carson and Pickett 1990, Huston 1994, Robinson et al. 1995, Davis et al. 2000). In this study, both diversity and invasibility were at their maximum in disturbed locations often characterized by low standing crop and high light availability. These results are consistent with several theories which predict that communities will be most invasible and most diverse under non-equilibrium conditions and when resource supply exceeds uptake (Grime 1979, Huston 1994, Burke and Grime 1996, Davis et al. 2000, Wardle 2001).

Our conclusion that extrinsic factors, and not species diversity per se, were primarily responsible for the regulation of invasibility in this grassland is based on several lines of evidence. First, three extrinsic variables measured in the plots (standing crop, light penetration and disturbance) each explained a greater proportion of the variance in invasibility than did initial plot diversity. Light penetration was the single best predictor of invasibility, explaining 29% more of the variance than diversity (61% versus 32%). Second, when statistically controlling for multiple predictors using backward-elimination multiple regression, diversity was eliminated from the final regression model, while light penetration and disturbance were retained. Third, the observed correlation between invasibility and diversity was opposite in sign of that predicted by Elton (1958), but was consistent with a number of studies that have shown a positive link between invasibility and extrinsic factors along natural diversity gradients (Pickard 1984, Robinson et al. 1995, Planty-Tabacchi et al. 1996, Wiser et al. 1998, Stohlgren et al. 1999, Levine 2000). Finally, it seems improbable that diversity would be the primary determinant of invasibility in the case where the two variables are positively correlated as found in this study and others. Greater diversity could potentially increase invasibility by enhancing opportunities for facilitation. However, we have no evidence for facilitation in this study, but there is strong evidence from prior work in this grassland, and from other studies in herbaceous vegetation, that implicate the importance of habitat productivity, light availability and disturbance in regulating colonization dynamics and thus invasibility (Foster and Gross 1998, Grace 1999, Stohlgren et al. 1999, Foster 2001).

Our results do not preclude the possibility that high levels of local diversity can directly inhibit invasibility in this grassland as predicted by Elton's hypothesis. However, the results do indicate that if any such effects occur, they are likely obscured by the more significant impact of extrinsic factors on invasibility and diversity. Several experimental studies that directly manipulated diversity in plant communities suggest that inhibitory effects of diversity on invasibility can be detected when extrinsic factors are controlled for experimentally (Knops et al. 1999, Levine 2000, Naeem et al. 2000, Prieur-Richard et al. 2000). Although these studies have been criticized (Wardle 2001), the results provide some evidence that in situ losses of biodiversity within a community can increase a community's susceptibility to invasion. However, as noted by Naeem et al. (2000), it is important not to extend the results of biodiversity manipulation experiments to argue that diverse communities in nature are inherently less invasible than species-poor ones.

Compositional stability

Consistent with prior theoretical work (May 1972, 1973, Tilman 1999, Lehman and Tilman 2000) and the field studies of Hurd et al. (1971), Mellinger and McNaughton (1975), McNaughton (1977), Tilman (1996) and Sankaran and McNaughton (1999), we found that compositional stability, defined as resistance to relative species abundance change, decreased with increased diversity. Mellinger and McNaughton (1975), McNaughton (1977), and Tilman (1996), report empirical negative associations between compositional stability and diversity in support of the hypothesis that species diversity stabilizes ecosystem-level properties (biomass

stability) via the mechanism of resource use complimentarity. If resource use complimentarity is a dominant factor regulating ecosystem stability in response to disturbance, one should expect to find an inverse relationship between compositional stability and diversity due to compensatory responses of species (McNaughton 1977, Tilman 1996, Lehman and Tilman 2000). However, from the results of Hurd et al. (1971), Mellinger and McNaughton (1975), McNaughton (1977), and Tilman (1996) it is unclear whether negative associations observed in the field between plant compositional stability and plant diversity reflect compensatory fluctuations of species (and thus direct influences of diversity on compositional and ecosystem stability) or indirect relationships arising secondarily through the impact of covarying factors such as successional age or resource availability (Givnish 1994, Huston 1997).

Unlike Mellinger and McNaughton (1975), McNaughton (1977) and Tilman (1996), Sankaran and McNaughton (1999) attributed the negative correlation that they found between compositional stability and diversity to the direct impact of other factors that varied among their grassland sites, rather than to the direct influence of diversity. In our study, multiple regression analyses suggested a possible direct causal link between compositional stability and diversity, specifically the dominance component of diversity. Low diversity plots that were initially dominated by a single plant species tended to be dominated by the same plant species two years following the implementation of experimental disturbance.

Does the link between compositional stability and diversity in our study reflect compensatory fluctuations of species abundances in response to disturbance? Because compositional stability was more directly associated with dominance than richness in our study, we suggest that the observed negative correlation between stability and diversity was less a function of there being high levels of compensatory fluctuations among species at high diversity than it was a function of the capacity of highly dominant species in low diversity microsites to recover rapidly from a moderate disturbance. Although our analyses do suggest a direct link between dominance and compositional stability, we indeed cannot rule out the possibility that this link is more a reflection of the influence of particular dominant species or a dominant functional group. Within our grassland site, as in most natural communities, gradients in diversity are not independent of gradients in species composition. Low diversity plots at our site are typically dominated by one of three fast-growing, perennial grasses (*Bromis inermis*, *Festuca arundenacea* or *Poa pratensis*), all of which possess a capacity for rapid clonal spread and which might be expected to recover quickly from the particular type of disturbance applied in this study. Disturbances of a different frequency, intensity or type (fire, flooding, herbicides etc.) might have resulted in a different outcome with respect to the relationship between stability and diversity in this grassland. Stability measured over a longer time frame (more than two growing seasons) may have also yielded a different result or interpretation. Although these constraints limit the extent to which we can generalize our results to other disturbance conditions, our findings do suggest that under conditions of moderate disturbance some community-level parameters may be most stable in low diversity microsites rather than in high diversity ones.

In conclusion, we found that community invasibility was positively correlated with diversity and that compositional stability was negatively correlated with diversity along a natural grassland diversity gradient. The observed correlation between invasibility and diversity can largely be explained by the direct impact of those extrinsic factors that generate spatial variation in diversity at the site rather than through any direct impact of diversity. In contrast, compositional stability in this grassland appears to be directly linked to the dominance component of diversity or to the influence of particular species that are capable of attaining high levels of local dominance in this grassland.

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