

LETTER

Coexistence through spatio-temporal heterogeneity and species sorting in grassland plant communities

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Abstract

The effect of spatial heterogeneity on species coexistence relies on the degree of niche heterogeneity in the habitat and the ability of species to exploit the available niche opportunities. We studied species coexistence in a perennial grassland, and tested whether small-scale disturbances create environmental heterogeneity that affects coexistence and whether the functional diversity of species in the species pool affects the ability of community composition to reflect heterogeneity through species sorting. We manipulated the spatio-temporal heterogeneity of disturbance and the functional diversity of species added as seed and measured their impact on the spatial turnover of species composition. Disturbance increased environmental heterogeneity and spatial turnover, and the effect of heterogeneity on turnover was greatest in the presence of a functionally diverse species pool, showing the importance of trait variation among species for exploiting environmental heterogeneity, and suggesting that coexistence occurred due to species sorting among heterogeneous niches.

Keywords

Complementarity, dispersal, disturbance, heterogeneity, species coexistence, species pool, species sorting, successional niche.

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INTRODUCTION

Coexistence theory predicts that spatial heterogeneity of environmental factors that affect fitness, such as resources and abiotic conditions, will promote coexistence through species–environment sorting (Tilman & Pacala 1993; Reynolds *et al.* 2007). When species exhibit tradeoffs for environmental factors that are distributed heterogeneously among patches in a habitat, different species will be favoured in different patches, leading to spatial turnover of community composition and coexistence at the community scale (Tilman & Pacala 1993; Huston 1994; Chase & Leibold 2003). The importance of environmental heterogeneity for regulating plant species coexistence and diversity has been evaluated experimentally by varying nutrients, soil physical characteristics and light levels in spatially heterogeneous, vs. homogeneous, patterns (Vivian-Smith 1997; Collins & Wein 1998; Stevens & Carson 2002; Baer *et al.* 2004; Wijesinghe *et al.* 2005; Reynolds *et al.* 2007); however, these studies had mixed results and most showed no effect of heterogeneity on diversity (but see Vivian-Smith 1997). One reason why experimental heterogeneity may not have increased diversity in these studies could be that the

manipulated heterogeneity was not extensive enough to increase sorting opportunities. Another explanation for this result is that dominant grasses or other clonal species may be able to integrate their resource use across patch types, thus using homogeneous and heterogeneous habitats similarly and excluding other species from the community (Baer *et al.* 2004; Reynolds *et al.* 2007). A third explanation is that the community response to heterogeneity may have been limited by dispersal from the available species pool (Vivian-Smith 1997; Reynolds *et al.* 2007).

In fact, a number of studies show that plant species richness can often be more limited by species pools and dispersal constraints than by niche availability (e.g. Tilman 1997; Zobel *et al.* 2000; Foster & Dickson 2004), leaving many communities undersaturated with species and with potentially underexploited niche heterogeneity. Thus, plant community diversity may be influenced not only by spatial environmental heterogeneity (spatial niche dimensionality), but also by the availability of species that are able to exploit the existing heterogeneity (species pool dimensionality). For community composition to reflect heterogeneity by species sorting among patches, the species pool must not only contain a sufficient number of species and propagules, it

must also contain species with the functional traits necessary to exploit the various niche opportunities available throughout the habitat. We hypothesize that species diversity will be greatest in communities with the most environmental heterogeneity, minimal dispersal limitation, and a functionally diverse species pool. We predict that experimental enhancement of spatial niche dimensionality and species pool dimensionality will increase species sorting, spatial turnover of species composition, and coexistence at the community scale.

In this study, we experimentally evaluate the interplay of spatial niche dimensionality and species pool dimensionality in regulating grassland plant diversity. Unlike previous studies that used fertilizer application to manipulate the heterogeneity of soil nutrients, we investigate the importance of small-scale disturbances for creating spatio-temporal heterogeneity in grasslands. In contrast to nutrient enhancement, disturbance can create successional niche opportunities that favour the growth of competitively inferior species through the increased availability of establishment microsites, areas with reduced competition where seeds can germinate and grow (Grubb 1977; Zobel *et al.* 2000), and altered ratios of resources important for plant growth (e.g. soil nutrients and light levels; Grubb 1977; Tilman & Pacala 1993; Tilman 1994; Chesson & Huntly 1997; Pacala & Rees 1998; Amarasekare 2003; Chase & Leibold 2003). Disturbance is critical for maintaining species coexistence in non-equilibrium ecosystems like grasslands (Grubb 1977; Hobbs & Huenneke 1992; Howe 1994; Tilman 1994; Collins *et al.* 1998; Pacala & Rees 1998) where spatio-temporal variation in disturbance patterns can create successional niche heterogeneity that is important for plant species coexistence at the community scale (Tilman & Pacala 1993; Chesson & Huntly 1997).

Small mammals often create heterogeneous, small-scale disturbance patterns in grasslands that have persistent effects on plant community composition (Hobbs & Mooney 1985, 1995; Seabloom & Richards 2003). In cool-season grasslands of northeastern Kansas where we conduct research, prairie voles, *Microtus ochrogaster* (Wagner, 1842), can be extremely abundant, and their burrows increase plant diversity throughout the community (Questad & Foster 2007), providing an ideal system for testing the effect of disturbance heterogeneity on plant diversity. Prairie vole burrowing activity enhances spatial environmental heterogeneity by creating disturbed patches with environmental conditions that contrast strongly with the undisturbed grass-dominated matrix (Kalisz & Davis 1992; Questad & Foster 2007). In addition, resources and abiotic conditions important for plant growth vary more among burrows than among undisturbed matrix areas, creating an additional source of heterogeneity, which may be due to differences in the size, intensity, and timing of the disturbances. Here, we

experimentally disturbed 1-m² patches within 4 × 4-m communities. We created disturbed patches seasonally and inter-annually to increase spatio-temporal heterogeneity by mimicking the formation of burrows through time.

In addition to these disturbance manipulations, we used seed addition treatments to test the effect of species pool dimensionality on diversity and its interaction with disturbance heterogeneity. Most previous seed addition experiments, designed to examine the role of dispersal limitation on plant diversity, compared plots without seeds added to plots enriched with a mixture of many species from many functional groups (e.g. Tilman 1997; Zobel *et al.* 2000; Foster & Dickson 2004; Gross *et al.* 2005). By using only one seed mixture, these studies cannot distinguish the relative importance of enhancing the number of species available to the community vs. enhancing the diversity of functional traits. It has been demonstrated that functional complementarity, or adaptations to different resources, among species is important for coexistence in niche-structured communities (Tilman 1997; Fargione *et al.* 2003). We hypothesize that as the degree of functional complementarity in the available species pool increases, there will be an increased capacity for niche partitioning and coexistence, especially in the presence of environmental heterogeneity. We tested the importance of species pool complementarity by comparing plots with no seeds added to plots enriched with either 13 species with redundant functional traits or 13 species with diverse functional traits. These two seed addition treatments allowed us to determine the importance of species pool complementarity while keeping the number of species and propagule pressure constant.

If both spatial niche dimensionality and species pool dimensionality influence species coexistence, we make the following predictions: (i) communities with the greatest heterogeneity will have the greatest diversity; (ii) increasing species pool complementarity will increase diversity, as species with different traits exploit patches with different environmental conditions; and (iii) communities with the greatest amount of environmental heterogeneity and a species pool with the greatest functional complementarity will have the greatest capacity for coexistence through species sorting, which will lead to high spatial turnover in community composition among patches.

METHODS

The study site was in the Nelson Environmental Studies Area (NESA), part of the University of Kansas Field Station and Ecological Reserves. NESA is located at the prairie-forest ecotone of northeastern Kansas in Jefferson County (39°03' N, 95°12' W), 10 km north of the city of Lawrence. The site was mid-successional grassland, dominated by the cool-season perennial grasses smooth brome (*Bromus inermis*

Leyss.), tall fescue [*Schedonorus phoenix* (Scop.) Holub] and Kentucky bluegrass (*Poa pratensis* L.).

In April 2005, we established 72 4 × 4-m plots in six randomized blocks. Each plot was separated by a 1-m buffer, and blocks were separated by a 2-m buffer. We employed a factorial combination of four disturbance treatments with three seed addition treatments, replicated six times. Within each 4 × 4-m plot, we randomly located eight 1-m² patches in a grid (Fig. 1). We defined a community as a plot containing multiple 1-m² patches, and a patch as a contiguous area in which the impact of disturbance (or no disturbance) on the locally residing individuals was uniform (Petraitis *et al.* 1989).

The disturbance treatments were four manipulated levels of spatio-temporal patch heterogeneity applied at the scale of the 1-m² patches: (i) no disturbance (ND), (ii) spring disturbance (SD), (iii) fall disturbance (FD), and (iv) spring/fall disturbance (SFD). All patches were left undisturbed in ND treatments (Fig. 1). In the SD, FD, and SFD treatments, four of the 1-m² patches were disturbed and four were left undisturbed (Fig. 1). We disturbed two of these patches in 2005, and two in 2006 to create inter-annual variability. To create seasonal variability, SD and FD treatments had two patches per year disturbed during the same season, and SFD treatments had one patch per year disturbed in spring and one in fall.

Disturbed patches approximated the soil disturbance associated with prairie vole burrows and were created with a combination of herbicide application and roto-tilling. First, we sprayed a 2% solution of Roundup Pro (41% glyphosate as an isopropylamine salt) with a backpack sprayer at a rate of approximately 0.4 L m⁻² and used a plywood frame to prevent overspray into undisturbed areas. After waiting at least 14 days, we then used a rear-tine roto-tiller to disturb the top 150 mm of soil, which is the depth of most vole burrowing disturbance (Davis & Kalisz 1992). We selected the time of disturbance application to coincide with times of vole burrowing activity (Jameson 1947). Spring patches were roto-tilled on 17 May 2005 and 22 May 2006. Fall patches

were roto-tilled on 18, 19 and 24 October 2005 and 20 October 2006. All areas outside the eight patches were left undisturbed in all plots.

The seed addition treatments were considered either functionally complementary or redundant based on several classes of traits that affect a species' resource use (Naeem & Wright 2003): regeneration strategy (annual, biennial, perennial), life form (grass, forb, legume) and family (Grime 2001). The functionally redundant species pool was made up of 13 perennial grass species. The functionally diverse pool contained 13 species with a variety of life-history traits (Table 1). The mean seed size (*t*-test, $t_{21} = 1.13$, $P = 0.273$) and the variance in seed size (*F*-test, $F_{12,12} = 0.48$, $P = 0.222$) among species were equivalent between pools to minimize colonization or competition differences due to seed size (Rees *et al.* 2001). Seeds were added four times to seed addition plots, once in late May and once in late October in 2005 and 2006. Each time they were added at a rate of 75 seeds species⁻¹ m⁻². The resident species pool treatment had no species added. Two of the added species, *Andropogon virginicus* L. and *Tridens flavus* (L.) Hitchc., were present in at least one resident pool treatment plot in the first year of the study, suggesting that these two species were also resident species.

From 18 June 2007 to 2 July 2007, we visually estimated the percent cover of all plant species, bare ground, and litter in each plot and in a 0.5 × 0.5-m quadrat placed in the center of each of the eight patches. We calculated community richness as the number of species present in each 4 × 4-m plot; patch richness as the mean number of species in the eight 0.5 × 0.5-m quadrats; and spatial turnover as community richness minus patch richness (Lande 1996). We used this additive measure of spatial turnover instead of a community dissimilarity metric to directly compare the contributions of patch richness and spatial turnover to community richness. We calculated these three diversity measures for the complete community of resident and added species. We also tested the effect of the treatments on the establishment of the species we directly

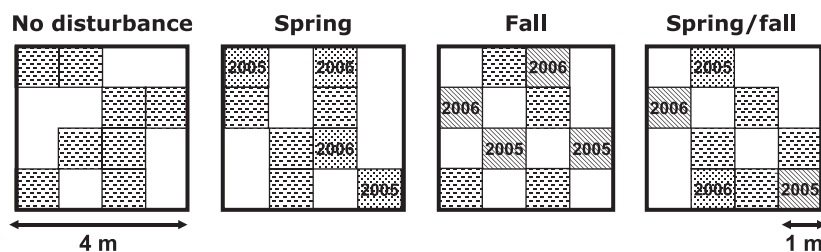


Figure 1 Experimental plot design. Each plot was a 4 × 4-m square. Eight 1-m² patches were randomly located in a grid. We administered disturbance to four patches in Spring (dotted squares), Fall (hatched squares), and Spring/Fall disturbance treatments. Two patches received disturbance in 2005 and two in 2006. We left four patches undisturbed in these three treatments and all eight patches undisturbed in the No Disturbance treatment (dashed squares). Areas outside the eight patches were left undisturbed.

Table 1 Species in added species pools

Redundant pool		Complementary pool	
<i>Scientific name</i>	<i>Functional group</i>	<i>Scientific name</i>	<i>Functional group</i>
<i>Andropogon gerardii</i>	Perennial C4 grass	<i>Andropogon gerardii</i>	Perennial C4 grass
<i>Andropogon virginicus</i>	Perennial C4 grass	<i>Sorghastrum nutans</i>	Perennial C4 grass
<i>Agropyron smithii</i>	Perennial C3 grass	<i>Koeleria pyramidata</i>	Perennial C3 grass
<i>Agrostis hyemalis</i>	Perennial C3 grass	<i>Cassia chamaecrista</i>	Annual forb, Fabaceae
<i>Bouteloua curtipendula</i>	Perennial C4 grass	<i>Helianthus annuus</i>	Annual forb, Asteraceae
<i>Elymus canadensis</i>	Perennial C3 grass	<i>Rudbeckia hirta</i>	Biennial forb, Asteraceae
<i>Elymus virginicus</i>	Perennial C3 grass	<i>Echinacea pallida</i>	Perennial forb, Asteraceae
<i>Koeleria pyramidata</i>	Perennial C3 grass	<i>Ratibida columnifera</i>	Perennial forb, Asteraceae
<i>Panicum virgatum</i>	Perennial C4 grass	<i>Dalea purpurea</i>	Perennial forb, Fabaceae
<i>Schizachyrium scoparium</i>	Perennial C4 grass	<i>Amorpha canescens</i>	Perennial forb, Fabaceae
<i>Sorghastrum nutans</i>	Perennial C4 grass	<i>Monarda fistulosa</i>	Perennial forb, Lamiaceae
<i>Sporobolus cryptandrus</i>	Perennial C4 grass	<i>Salvia azurea</i>	Perennial forb, Lamiaceae
<i>Tridens flavus</i>	Perennial C4 grass	<i>Asclepias tuberosa</i>	Perennial forb, Asclepiadaceae

The functionally redundant species pool is equal numbers of seeds of 13 perennial grass species. The functionally complementary species pool is equal numbers of seeds of 13 species in many functional groups. C3 denotes cool-season grass species that use a 3-carbon compound during photosynthesis. C4 denotes warm-season grass species that use a 4-carbon compound. Nomenclature follows GPFA (1986).

manipulated, and we calculated patch richness, spatial turnover, and community richness in the same way for added species only.

To measure whether our treatments affected the heterogeneity of environmental variables important for plant growth, we calculated the coefficient of variation (CV) of bare ground and litter cover among the eight patches in each plot. We also measured light penetrating through the canopy as below canopy photosynthetically active radiation (PAR)/above canopy PAR. We took 16 measurements in a 4 × 4-m grid in each plot using an Accupar LP 80 (Decagon Devices; Pullman, WA, USA). Measurements were taken on clear days (31 May and 4–6 June 2007) within 2 h of solar noon. We calculated the CV of light penetration among the 16 measurements.

We used factorial analysis of variance (ANOVA) to test the effect of disturbance (four levels), seed addition (three levels), the disturbance × seed addition interaction and a random blocking factor on the measures of patch richness, spatial turnover, community richness and the three environmental heterogeneity variables. To test whether seasonal disturbance treatments affected diversity measures, we removed the ND plots and reran the ANOVA's. If we found a significant main effect or interaction, we used Tukey simultaneous tests to determine significant differences in group means ($P < 0.05$). When necessary, data were square root-transformed to meet the assumption of homogeneity of variance (HOV). We calculated Pearson product moment correlation coefficients to determine whether spatial turnover was associated with environmental heterogeneity variables. We used a general linear model to test whether seed addition treatments affected the relationship between

environmental heterogeneity variables and spatial turnover. If species sorting occurred we expected the complementary species pool to increase the slope of the relationship between spatial turnover and environmental heterogeneity by providing species with trait variation to sort among heterogeneous resources. We performed a separate test for each environmental heterogeneity variable (bare ground, litter and light penetration) using seed addition as a fixed factor, the CV of the environmental variable as a covariate and including the seed addition × CV interaction. We used Minitab version 14.1 for all analyses (Minitab, Inc., State College, PA, USA).

RESULTS

Effect of treatments on environmental heterogeneity

Disturbance increased the CV of litter and light ($P < 0.001$), but not the CV of bare ground ($P > 0.15$). There was no effect of seed addition or the disturbance × seed addition interaction on any environmental heterogeneity variable ($P > 0.1$).

Effect of treatments on the complete community – resident and added species

We found significant increases of patch richness, spatial turnover and community richness in response to disturbance and seed addition (Table 2a). There was a significant disturbance × seed addition interaction for spatial turnover and community richness, but not patch richness, in the model including ND plots. This interaction occurred

Table 2 Patch richness, spatial turnover and community richness for analysis of all species and added species

	Disturbance × Seed addition	Disturbance	Seed addition	Block
(a) ND treatment included				
All species				
Community richness	2.39*	99.14***	25.35***	4.89**
Spatial turnover	3.05*	92.07***	23.76***	3.81**
Patch richness	0.45	43.50***	11.16***	6.01***
Added species				
Community richness	6.92***	58.96***	272.77***	1.51
Spatial turnover	8.32***	48.85***	258.82***	1.12
Patch richness	4.37**	35.59***	161.83***	7.19***
(b) ND treatment excluded				
All species				
Community richness	2.05	2.50	29.89***	2.76*
Spatial turnover	2.76*	4.09*	26.69***	2.06
Patch richness	0.33	0.18	11.63***	4.86**
Added species				
Community richness	5.40**	11.74***	517.85***	1.02
Spatial turnover	8.45***	7.46**	505.29***	2.57*
Patch richness	0.34	1.51	148.66***	3.73**

F-statistics reported for (a) ANOVA including ND treatment. The model included block as a random variable (d.f. = 5), disturbance (d.f. = 3) and seed addition (d.f. = 2) as fixed variables, disturbance × seed addition (d.f. = 6) and error (d.f. = 55). Added community richness and added spatial turnover were square root-transformed to improve HOV. (b) ANOVA excluding ND treatment to test for differences in richness among disturbance treatments. Model terms were block (d.f. = 5), disturbance (d.f. = 2), seed addition (d.f. = 2), disturbance × seed addition (d.f. = 4) and error (d.f. = 40). Added spatial turnover was square root-transformed to improve HOV.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

because seed addition increased spatial turnover and community richness in the presence of disturbance, but had no effect in the absence of disturbance (Fig. 2a–c). When the ND plots were removed from analysis, the interaction term remained significant only for spatial turnover (Table 2b). Post-hoc tests from the model with ND plots removed revealed that the complementary species pool increased spatial turnover over the resident pool at all disturbance levels (SD, FD and SFD), but the redundant pool only increased spatial turnover over the resident pool for two of three (FD and SFD) disturbance levels (Fig. 2b), showing that the effect of disturbance on spatial turnover was consistently greatest when seeds of complementary species were added. There was also a trend toward greatest spatial turnover in the treatment combination of SFD with the complementary species pool, which represented a combination of the greatest level of disturbance heterogeneity and greatest functional diversity of the species pool (Fig. 2b).

In contrast to spatial turnover, community and patch richness were influenced only by seed addition, and not disturbance treatment, when ND plots were removed (Table 2b). Post-hoc tests of the model excluding ND plots showed that the complementary seed addition treatment, but not the redundant treatment, increased patch richness

over the resident pool (Fig. 2a; $P < 0.05$). Both seed addition treatments increased community richness over the resident pool, and the complementary treatment caused the greatest increase (Fig. 2c; $P < 0.05$).

Effect of treatments on added species

In the model including ND plots, patch richness, spatial turnover and community richness of added species increased with disturbance and seed addition, with a significant disturbance × seed addition interaction for all three diversity measures (Table 2a). This interaction occurred because both seed addition treatments increased diversity over the resident pool in the presence of disturbance, but only the complementary treatment increased diversity in the absence of disturbance (Fig. 2d–f). When the ND plots were removed, the interaction remained significant for spatial turnover and community richness (Table 2b). Although both seed addition treatments increased spatial turnover and community richness over the resident pool, the combination of the complementary species pool treatment with the SD and SFD treatments maintained the highest spatial turnover and community richness, which represented the effect of the greatest functional diversity of the species

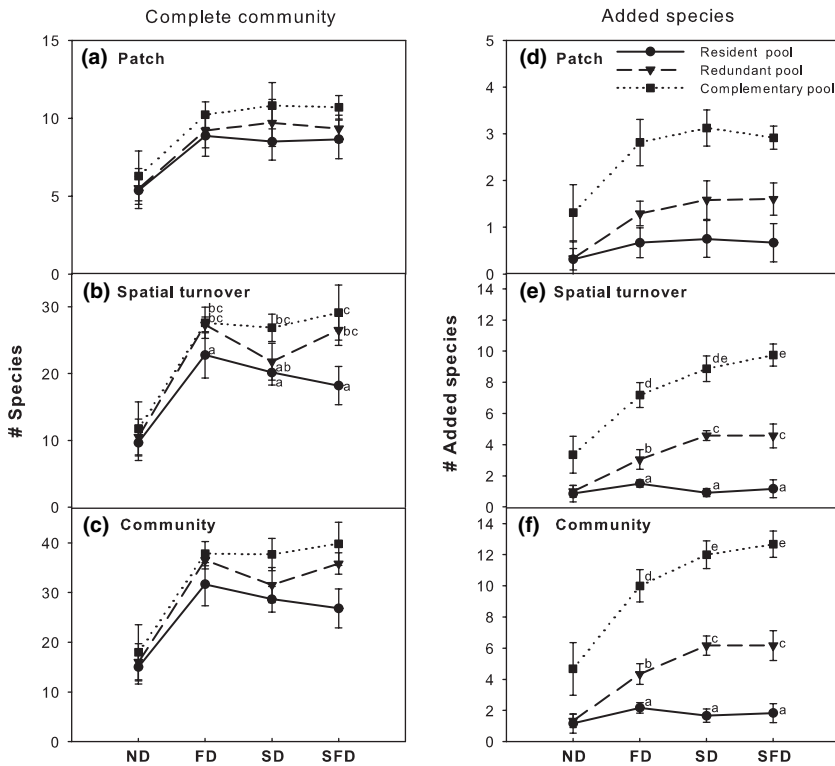


Figure 2 Interaction plots for patch richness, spatial turnover, and community richness of the complete community (a–c) and added species (d–f). Disturbance treatments are on the x-axis. Lines represent seed addition treatments: resident pool (solid lines and circles), redundant pool (dashed lines and triangles), and complementary pool (dotted lines and squares). Symbols represent mean values, error bars are two standard errors. Letters indicate significant differences among means based on Tukey post-hoc tests for significant interaction terms from models with ND treatments removed.

pool combined with two levels of disturbance heterogeneity (Fig. 2e and f).

In contrast to spatial turnover and community richness, patch richness was only influenced by seed addition, and not disturbance, when ND plots were removed (Table 2b). Post-hoc tests of the model excluding ND plots showed that both seed addition treatments increased patch richness over the resident pool, and the complementary treatment caused the greatest increase (Fig. 2d; $P < 0.05$).

Relationship between environmental heterogeneity and spatial turnover

Spatial turnover was significantly ($\alpha = 0.05$) correlated with CV of litter ($r^2 = 0.30$, $P < 0.001$) and CV of light penetration ($r^2 = 0.42$, $P < 0.001$). There was a trend toward a relationship between spatial turnover and the CV of bare ground, although it was not significant ($r^2 = 0.05$, $P = 0.06$). There was a significant seed addition \times CV interaction term for litter (Table 3, Fig. 3), showing that seed addition affected the response of spatial turnover to litter heterogeneity. There was evidence of a similar effect of seed addition on the response of spatial turnover to light heterogeneity, but the interaction term was not statistically significant (Fig. 3; $P = 0.059$). This interaction between seed addition and environmental heterogeneity variables occurred because the seed addition treatments increased the

Table 3 Effect of seed addition on the response of spatial turnover to environmental heterogeneity

Resource variable	Seed addition \times CV	Seed addition	CV
Litter	2.96†	0.69	35.13***
Bare ground	0.60	1.39	1.98
Light penetration	3.41*	1.26	59.08***

F-statistics reported for general linear model. The model included seed addition (d.f. = 2) as a fixed variable, the CV of each environmental variable as a covariate (d.f. = 1), and the seed addition \times CV interaction (d.f. = 2). The error term had 66 d.f. † $P = 0.059$, * $P < 0.05$, *** $P < 0.001$.

effect of environmental heterogeneity on spatial turnover. There was a trend toward the greatest effect of environmental heterogeneity on spatial turnover, indicated by the greatest slope, when seeds of complementary species were added (Fig. 3).

DISCUSSION

We found evidence supporting our predictions about the effect of spatial niche dimensionality, species pool dimensionality, and species sorting on coexistence. Our disturbance treatments created successional niche heterogeneity that increased diversity. Functional complementarity among

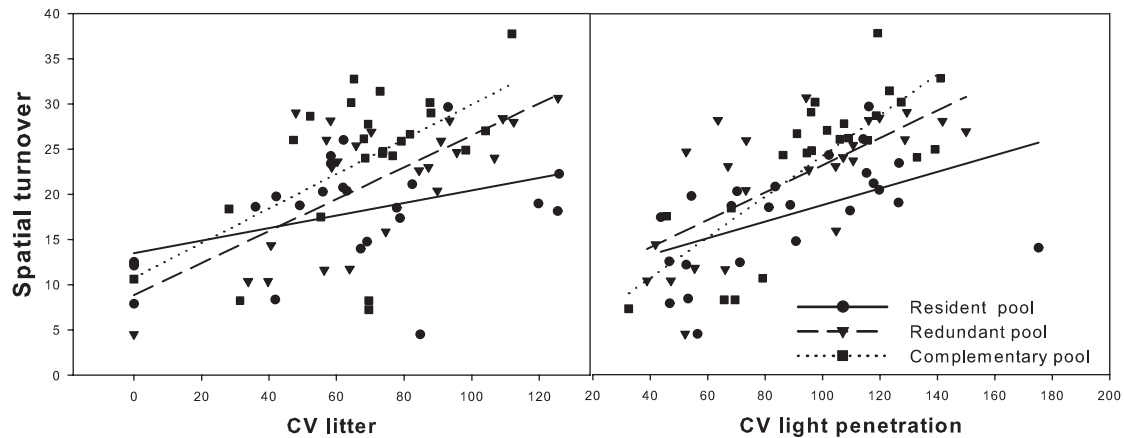


Figure 3 Interaction plots for the effect of seed addition and resource heterogeneity on spatial turnover. Seed addition treatments are resident pool (solid lines and circles), redundant pool (dashed lines and triangles) and complementary pool (dotted lines and squares).

added species also increased diversity compared with communities that had functionally redundant species or no species added. The effect of environmental heterogeneity on the spatial turnover of community composition was the greatest in the presence of a complementary species pool, showing the importance of trait variation among species for exploiting variation among patches, and suggesting niche-based coexistence through species sorting.

Niche and dispersal limitation

We found evidence for both niche and dispersal limitation of diversity and that these two constraints on coexistence interact in this system. Disturbance increased all measures of diversity both in the absence and presence of seed addition, showing that the availability of establishment microsites limits colonization and species richness in this grassland. There was an interaction between disturbance and seed addition for several measures of diversity, including richness of the complete community, indicating that the ability of disturbance to influence coexistence is constrained by the available species pool. In general, the magnitude of the interaction was greater for added species compared with the complete community. This result is not surprising since the added species were experimentally manipulated and the complete community contained naturally occurring variation in species composition among plots; however, it does show that disturbance and an enhanced species pool had a relatively greater effect on colonization and recruitment than on overall community richness. The effect of the interaction was consistently significant for spatial turnover of both the added species and the complete community, suggesting that disturbance created environmental heterogeneity and the community response to this heterogeneity was limited by the available species pool.

In fact, disturbance increased spatial turnover as well as the heterogeneity of litter and light, two factors that can strongly influence plant performance at the establishment stage (Grubb 1977; Foster & Gross 1998; Rees *et al.* 2001). These results suggest that spatial turnover among patches increased when disturbance created successional niche opportunities, which were likely due to the increased availability of establishment microsites that were exploited by competitively inferior species (Grubb 1977; Connell 1978; Huston 1979; Sousa 1979) and an increase in the spatial heterogeneity of environmental conditions important for plant growth. This finding is consistent with our previous study of prairie vole burrows, which found that community composition, litter biomass and light levels were more variable on burrows than in undisturbed grassland (Questad & Foster 2007), suggesting that although vole burrows can create dynamic, non-equilibrium environments at small scales, they may create stable coexistence at the community scale by maintaining successional niche opportunities throughout the habitat (Pacala & Rees 1998; Amarasekare 2003; Chase & Leibold 2003; Kneitel & Chase 2004; Urban 2004; Chase *et al.* 2005; Vandvik & Goldberg 2006; Cadotte 2007; Questad & Foster 2007).

Complementarity and species sorting

Complementarity of the species pool also influenced spatial turnover, providing support for deterministic species sorting among patches in the community. This result contrasts with a neutral expectation that any observed spatial turnover in species composition should occur independent of differences in competitive traits or demographic rates (Hubbell 2001). In this study, we observed that spatial turnover was consistently greater in plots that received seeds from the complementary pool compared to the redundant pool,

illustrating the importance of functional trait diversity and trade-offs among species for partitioning environmental differences among patches.

Thus, species sorting appeared to influence coexistence in these communities when disturbance increased niche opportunities *and* when the species pool contained species that could exploit these niches. We found the effect of disturbance on spatial turnover to be consistently greater when the species pool contained complementary species. There was also a trend toward greatest spatial turnover with the most heterogeneous disturbance treatment, but only when the species pool contained complementary species. Furthermore, the addition of complementary species caused litter and light heterogeneity to have the greatest impact on spatial turnover. These results all emphasize that coexistence depended on sufficient trait variation among species in the species pool, which allowed them to exploit environmental differences among patches. We found that both spatial niche dimensionality and species pool dimensionality strongly influenced species sorting and community-scale coexistence in our experiment, and we suggest that these factors may also affect species sorting at larger spatial scales, such as among local communities in a metacommunity (Leibold *et al.* 2004).

In addition to spatial turnover, the complementary seed addition also increased patch richness of the complete community over the resident pool, but the redundant seed addition did not, showing that patch diversity was limited by the functional complementarity of species in the species pool and not just the number of new species. Competition with the dominant perennial grass species may have reduced the establishment of the redundant grass species pool, and the establishment of complementary species may have been facilitated by reduced competition with the dominant species and with each other. Our results provide an important extension of previous seed addition studies (e.g. Tilman 1997; Zobel *et al.* 2000; Foster & Dickson 2004) by showing that the effect of an enhanced species pool on local diversity was largely a result of complementarity among species that promoted their coexistence. It is possible that the outcome may have differed if we had tested redundant pools of species other than perennial grasses; however, we chose perennial grasses because they dominate the regional landscape and are maintained through management for cattle production. Thus, in addition to highlighting the importance of complementarity for coexistence, we also show how a landscape-scale change to dominance by a single functional group may reduce the ability of the species pool to affect coexistence.

Comparison with other studies

Two other studies have examined the interplay between environmental heterogeneity and species pools. In contrast

to our results, Reynolds *et al.* (2007) found that in a nutrient-poor grassland there was no effect of fertilizer heterogeneity on species richness even in the presence of species added to reduce dispersal limitation. In their study, nitrophilic clonal species appeared to exploit patches of fertilizer, leaving few resources available for other species colonizing from seed (Reynolds *et al.* 2007). It is possible that by manipulating spatio-temporal disturbance patterns, we created niche opportunities that did not exist in their study, which enhanced the spatial niche dimensionality of our communities. Our results are similar to a study of microtopographic heterogeneity in wetlands in which three species pools with different numbers of species were added to homogeneous and heterogeneous environments (Vivian-Smith 1997). The wetland study showed that heterogeneity increased diversity, but this increase was greatest when the greatest number of species were added to the heterogeneous habitat. Our results suggest that this increase in diversity may have been due to the increased trait diversity in the species pool that allowed species to partition resources among patches, affecting coexistence through species sorting.

Previous studies have also shown that disturbance can decrease turnover in community composition by consistently favouring the same disturbance-adapted species (Chase 2003, 2007; Collins & Smith 2006; Houseman *et al.* in press). Our study provides contrasting evidence, which suggests that the effect of disturbance on turnover in community composition is context-dependent. By creating disturbances at different times, we may have created colonization opportunities for disturbance-adapted species that disperse at different times or that exploit resources seasonally through phenological differences. In addition, it is possible that disturbance can increase spatial turnover when species that take advantage of colonization opportunities are spatially distributed, such as in the seedbank, or when species pool complementarity is high, and species that can exploit colonization opportunities are not dispersal-limited; whereas disturbance may decrease spatial turnover if the species pool does not contain sufficient functional diversity.

CONCLUSION

By manipulating environmental heterogeneity and species pool complementarity in a spatially explicit experimental framework, we have demonstrated the importance of both spatial niche dimensionality and species pool dimensionality for influencing coexistence through species sorting. Our experiment showed that spatio-temporal disturbance patterns increase diversity by creating colonization opportunities and increasing successional niche heterogeneity. Complementarity among species increased the effect of the species pool on diversity, most likely due to decreased competition and the ability of species with different traits to

exploit environmental differences among patches. We manipulated resource pulses instead of constant supply rates, which is a departure from the traditional equilibrium framework used by other studies of environmental heterogeneity in grasslands (Collins & Wein 1998; Stevens & Carson 2002; Baer *et al.* 2004; Wijesinghe *et al.* 2005; Reynolds *et al.* 2007). Our study emphasizes that community-scale coexistence in perennial grasslands can be enhanced by small-scale non-equilibrium dynamics and species sorting among heterogeneous niches.

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REFERENCES

- Amarasekare, P. (2003). Competitive coexistence in spatially structured environments: a synthesis. *Ecol. Lett.*, 6, 1109–1122.
- Baer, S.G., Blair, J.M., Collins, S.L. & Knapp, A.K. (2004). Plant community responses to resource availability and heterogeneity during restoration. *Oecologia*, 139, 617–629.
- Cadotte, M.W. (2007). Competition-colonization tradeoffs and disturbance effects at multiple scales. *Ecology*, 88, 823–829.
- Chase, J.M. (2003). Community assembly: when should history matter? *Oecologia*, 136, 489–498.
- Chase, J.M. (2007). Drought mediates the importance of stochastic community assembly. *Proc. Natl Acad. Sci. USA*, 104, 17430–17434.
- Chase, J.M. & Leibold, M.A. (2003). *Ecological Niches: Linking Classical and Contemporary Approaches*. University of Chicago Press, Chicago.
- Chase, J.M., Amarasekare, P., Cottenie, K., Gonzalez, A., Holt, R.D., Holyoak, M. *et al.* (2005). Competing theories for competitive metacommunities. In: *Metacommunities: Spatial Dynamics and Ecological Communities* (eds Holyoak, M., Leibold, M.A. & Holt, R.D.). University of Chicago Press, Chicago, pp. 335–354.
- Chesson, P. & Huntly, N. (1997). The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *Am. Nat.*, 150, 519–553.
- Collins, S.L. & Smith, M.D. (2006). Scale-dependent interaction of fire and grazing on community heterogeneity in tallgrass prairie. *Ecology*, 87, 2058–2067.
- Collins, B. & Wein, G. (1998). Soil resource heterogeneity effects on early succession. *Oikos*, 82, 238–245.
- Collins, S.L., Knapp, A.K., Briggs, J.M., Blair, J.M. & Steinauer, E.M. (1998). Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science*, 280, 745–747.
- Connell, J.H. (1978). Diversity in tropical rain forests and coral reefs: high diversity of trees and corals is maintained only in a nonequilibrium state. *Science*, 199, 1302–1310.
- Davis, W.H. & Kalisz, P.J. (1992). Burrow systems of the prairie vole, *Microtus ochrogaster*, in central Kentucky. *J. Mammal*, 73, 582–585.
- Fargione, J., Brown, C.S. & Tilman, D. (2003). Community assembly and invasion: an experimental test of neutral versus niches processes. *Proc. Natl Acad. Sci. USA*, 100, 8916–8920.
- Foster, B.L. & Dickson, T.L. (2004). Grassland diversity and productivity: the interplay of resource availability and propagule pools. *Ecology*, 85, 1541–1547.
- Foster, B.L. & Gross, K.L. (1998). Species richness in a successional grassland: effects of nitrogen enrichment and plant litter. *Ecology*, 79, 2593–2602.
- GPFA (1986). *Flora of the Great Plains*. University of Kansas Press, Lawrence, KS.
- Grime, J.P. (2001). *Plant Strategies, Vegetation Processes, and Ecosystem Properties*, 2nd edn. John Wiley & Sons Ltd, West Sussex, UK.
- Gross, K.L., Mittelbach, G.G. & Reynolds, H.L. (2005). Grassland invasibility and diversity: responses to nutrients, seed input, and disturbance. *Ecology*, 86, 476–486.
- Grubb, P.J. (1977). The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol. Rev.*, 52, 107–145.
- Hobbs, R.J. & Huenneke, L.F. (1992). Disturbance, diversity, and invasion: implications for conservation. *Conserv. Biol.*, 6, 324–337.
- Hobbs, R.J. & Mooney, H.A. (1985). Community and population dynamics of serpentine grassland annuals in relation to gopher disturbance. *Oecologia*, 67, 342–351.
- Hobbs, R.J. & Mooney, H.A. (1995). Spatial and temporal variability in California annual grassland: results from a long-term study. *J. Veg. Sci.*, 6, 43–56.
- Houseman, G.R., Mittelbach, G.G., Reynolds, H.L. & Gross, K.L. (in press). Perturbations alter community convergence, divergence, and formation of multiple community states. *Ecology*.
- Howe, H.F. (1994). Managing species diversity in tallgrass prairie: assumptions and implications. *Conserv. Biol.*, 8, 691–704.
- Hubbell, S.P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ.
- Huston, M.A. (1979). A general hypothesis of species diversity. *Am. Nat.*, 113, 81–101.
- Huston, M.A. (1994). *Biological Diversity: The Coexistence of Species on Changing Landscapes*. Cambridge University Press, Cambridge.
- Jameson, E.W. (1947). Natural history of the prairie vole (mammalian genus *Microtus*). *Univ. Kansas Mus. Nat. Hist.*, 1, 125–151.
- Kalisz, P.J. & Davis, W.H. (1992). Effect of prairie voles on vegetation and soils in central Kentucky. *Am. Midl. Nat.*, 127, 392–399.
- Kneitel, J.M. & Chase, J.M. (2004). Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecol. Lett.*, 7, 69–80.
- Lande, R. (1996). Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos*, 76, 5–13.
- Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F. *et al.* (2004). The metacommunity concept:

- a framework for multi-scale community ecology. *Ecol. Lett.*, 7, 601–613.
- Naem, S. & Wright, J.P. (2003). Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecol. Lett.*, 6, 567–579.
- Pacala, S.W. & Rees, M. (1998). Models suggesting field experiments to test two hypotheses explaining successional diversity. *Am. Nat.*, 152, 729–737.
- Petraitis, P.S., Latham, R.E. & Niesenbaum, R.A. (1989). The maintenance of species-diversity by disturbance. *Q. Rev. Biol.*, 64, 393–418.
- Questad, E.J. & Foster, B.L. (2007). Vole disturbances and plant diversity in a grassland metacommunity. *Oecologia*, 153, 341–351.
- Rees, M., Condit, R., Crawley, M., Pacala, S. & Tilman, D. (2001). Long-term studies of vegetation dynamics. *Science*, 293, 650–655.
- Reynolds, H.L., Mittelbach, G.G., Darcy-Hall, T.L., Houseman, G.R. & Gross, K.L. (2007). No effect of varying soil resource heterogeneity on plant species richness in a low fertility grassland. *J. Ecol.*, 95, 723–733.
- Seabloom, E.W. & Richards, S.A. (2003). Multiple stable equilibria in grasslands mediated by herbivore population dynamics and foraging behavior. *Ecology*, 84, 2891–2904.
- Sousa, W.P. (1979). Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology*, 60, 1225–1239.
- Stevens, M.H.H. & Carson, W.P. (2002). Resource quantity, not resource heterogeneity, maintains plant diversity. *Ecol. Lett.*, 5, 420–426.
- Tilman, D. (1994). Competition and biodiversity in spatially structured habitats. *Ecology*, 75, 2–16.
- Tilman, D. (1997). Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology*, 78, 81–92.
- Tilman, D. & Pacala, S. (1993). The maintenance of species richness in plant communities. In: *Species Diversity in Ecological Communities: Historical and Geographical Perspectives* (eds Ricklefs, R.E. & Schluter, D.). University of Chicago Press, Chicago, pp. 13–25.
- Urban, M.C. (2004). Disturbance heterogeneity determines freshwater metacommunity structure. *Ecology*, 85, 2971–2978.
- Vandvik, V. & Goldberg, D.E. (2006). Sources of diversity in a grassland metacommunity: quantifying the contribution of dispersal to species richness. *Am. Nat.*, 168, 157–167.
- Vivian-Smith, G. (1997). Microtopographic heterogeneity and floristic diversity in experimental wetland communities. *J. Ecol.*, 85, 71–82.
- Wijesinghe, D.K., John, E.A. & Hutchings, M.J. (2005). Does pattern of soil resource heterogeneity determine plant community structure? An experimental investigation. *J. Ecol.*, 93, 99–112.
- Zobel, M., Otsus, M., Liira, J., Moora, M. & Mols, T. (2000). Is small-scale species richness limited by seed availability or microsite availability? *Ecology*, 81, 3274–3282.

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