

# Spatial Variability in Plant Predation Determines the Strength of Stochastic Community Assembly

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**ABSTRACT:** High diversity is often poorly explained by trait-based deterministic models, in part because stochastic processes also influence community assembly. Testing how deterministic and stochastic processes combine to regulate diversity, however, has been limited by the spatial complexity of these interactions. Here, we demonstrate how spatial variability in small-mammal predation on plants, mostly by granivory, results in fine-scale switching between deterministically and stochastically regulated plant community assembly in an otherwise environmentally homogeneous tallgrass prairie. We initiated assembly with the uniform application of a 24-species mixture of prairie grasses and forbs, thereby setting the maximum level of diversity ( $\gamma$ -diversity). In field edges with higher densities of small mammals, traits reducing seed palatability deterministically produced homogeneous subsets of less palatable plant species within the first few months after planting (low  $\alpha$  and  $\beta$  diversity). As small-mammal densities decreased in more open areas, assembly unfolded stochastically on the basis of which planted species happened to land at a given location (high  $\alpha$  and  $\beta$  diversity). We used randomization models to validate that this higher  $\beta$  diversity was explained by true differences in community structure among plots rather than by the hidden effects of increasing  $\alpha$  diversity. The net effect at the site level was a spatially structured array of prairie species, including a positive relationship between diversity and environmental suitability relating to reduced predator intensity.

**Keywords:** community assembly, diversity, niche theory, stochasticity, priority effects, small mammals, granivory, herbivory, tallgrass prairie.

## Introduction

Many species-rich systems are characterized by the cooccurrence of large numbers of functionally similar species,

a pattern whose mechanistic underpinning has long been debated (Chase and Leibold 2003). Explanations range from deterministic (distributional variability corresponds to underlying environmental variability) to stochastic (distributional variability is explained by dispersal and ecological drift), with the most likely scenario being interactions between the two (Orrock and Fletcher 2005; Gravel et al. 2006; McGill et al. 2007; Chase 2010). Demonstrating how deterministic and stochastic processes interact, however, remains challenging, especially because these interactions are often scale dependent (Holyoak and Loreau 2006; McGill et al. 2007).

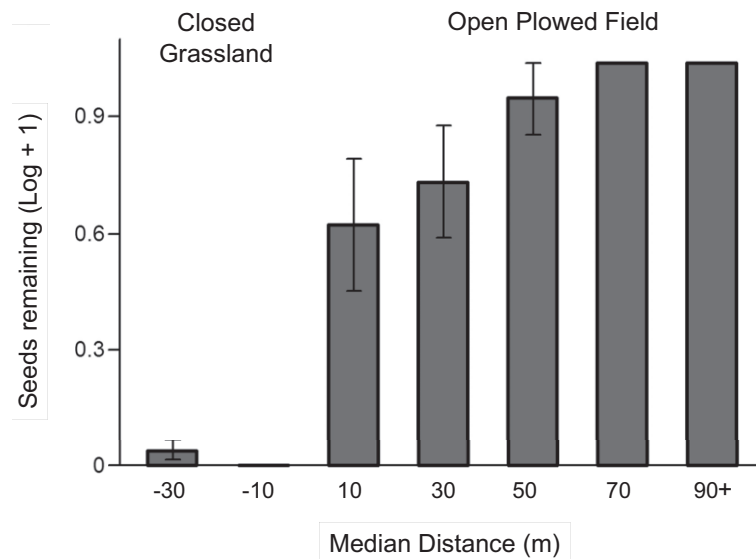
Most work has emphasized space-environment interactions, in which distance, dispersal limitation, and environmental turnover determine the relative influences of deterministic and stochastic processes on community structure (Snyder and Chesson 2003; Gilbert and Lechowicz 2004; Cottenie 2005; Holyoak and Loreau 2006; McPeck and Leibold 2006; Halpern et al. 2007; Pinto and MacDougall 2010). Recent research suggests an alternative possibility, in which variation in environmental factors alone can lead to shifts in the relative importance of deterministic and stochastic processes (Orrock and Fletcher 2005; Adler et al. 2007; Chase 2007, 2010; Chase et al. 2009). In stressful environments, trait-based differences among species are predicted to deterministically influence which species establish, resulting in tight relationships between environment and diversity, because the same subset of species tend to thrive. Under this scenario, the relationships between environmental conditions and trait-based species differences are highly correlated, with low plot-to-plot variability and uniform species composition (i.e., low  $\beta$  diversity). In areas of reduced stress, a greater proportion of the regional species pool can potentially establish and persist, such that local diversity can become stochastically regulated by factors such as priority effects (Samuels and Drake 1997; Chase et al. 2009). Under this

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**Figure 1:** Seed removal totals from 2-week cafeteria trials in early spring (April 2011), from within closed oldfield grassland and extending 150 m into adjacent open plowed field. The dashed line indicates the oldfield boundary. No seed removal occurred in seed stations beyond 30 m. Error bars represent  $\pm 1$  SE.

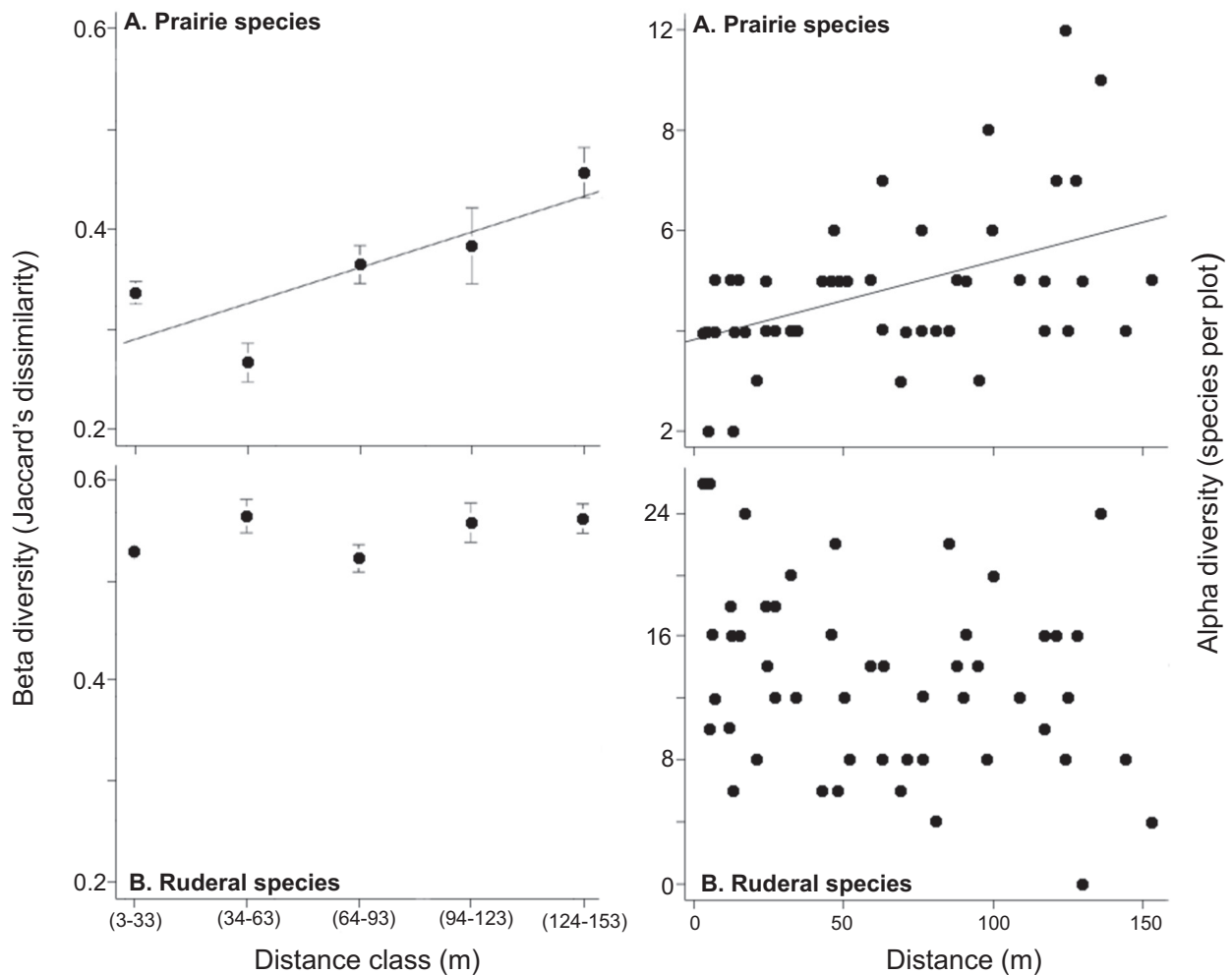
latter scenario, the relationships between environmental conditions and trait-based species differences are weakly correlated, with high plot-to-plot variability in species composition (i.e., high  $\beta$  diversity). This switching from deterministic- to stochastic-based regulation as conditions improve, with associated increases in plot-to-plot variability in community composition, is one possible explanation for the positive macroecological relationship sometimes observed between diversity and habitat suitability based on factors such as productivity (Davies 2005; Melbourne et al. 2006; Chase 2010; Harrison et al. 2011).

Environmentally regulated variation in deterministic and stochastic assembly should be especially prevalent in predator-prey systems, given that predator occurrences can deflect assembly in different directions in environments that are otherwise homogeneous (Chase et al. 2009). Describing how this unfolds, however, is often difficult because deterministic and stochastic predation can both produce prey communities that are very similar in structure. Deterministic predation, for example, can lead to either low-diversity prey communities by eliminating all but a subset of the regional species pool with traits for tolerating or avoiding attack (Fraser and Madson 2008) or high-diversity communities by targeting dominant prey species (Paine 1966; Howe and Brown 2001). Similarly, stochastic predation can limit diversity by reducing overall prey population densities and increasing the likelihood of extinction, especially for rarer species (Matthies et al. 2004), or increase diversity through frequency-dependent selection when more abundant species are targeted (Murdoch 1969;

Allen 1988; Abrams and Matsuda 2003; Bagchi et al. 2010). Untangling these contrasting predatory effects on the assembly of prey communities, however, requires connecting patterns of prey diversity with the underlying predatory-based mechanisms responsible for their formation (e.g., are areas with high prey diversity associated with high or low predation?).

Here, we examine these issues by testing the impacts of small-mammal predation on plant establishment in a large-scale (18-ha) tallgrass prairie assembly experiment. Small mammals, through the effects of granivory and seedling herbivory, can be major filters on community assembly in grasslands by preferentially favoring the establishment of less palatable plants (e.g., Brown and Heske 1990; Howe et al. 2002; MacDougall and Wilson 2007; Orrock et al. 2008; Bricker et al. 2010). More importantly, because small-mammal behavior is spatially nonrandom because of factors that include home range distance (Myllymäki 1977) or perceived predator risk (Abramsky et al. 2002; Vanhoenacker et al. 2009), the potential exists for fine-scale plant community assembly to unfold differently depending on whether small mammals are frequent, rare, or absent. The end product at the site level could be a community that shows no relationship between abiotic gradients and the distribution and diversity of its member species (i.e., its spatial structure appears to be random) but actually reflects the fine-scale variation in the strength of predation by small mammals.

We combined experimental, statistical, and survey-based approaches to test this hypothesis, examining



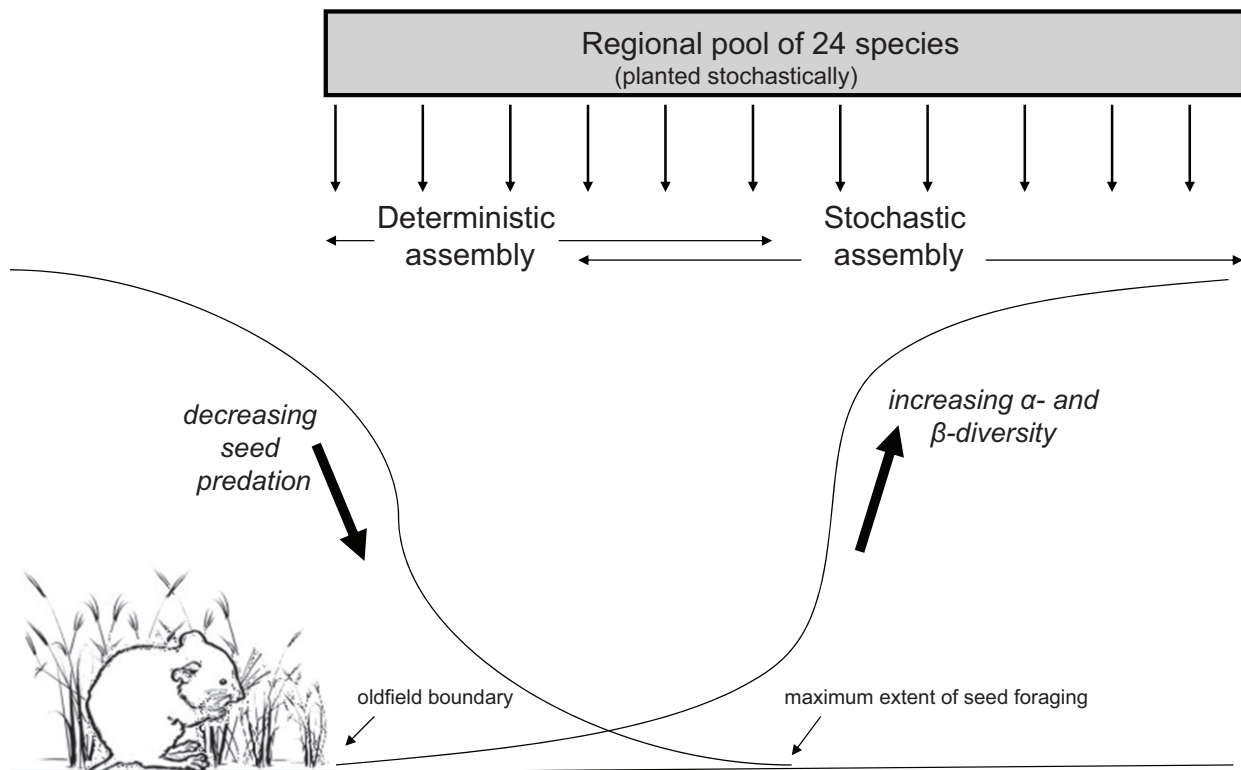
**Figure 2:** Changes in  $\beta$  and  $\alpha$  diversity of (A) planted prairie species and (B) naturally recruiting ruderal species. Planted species show significant increases with distance for both measures ( $\beta$ : bootstrap  $P = .012$ ;  $\alpha$ :  $F_{1,48} = 12.82$ ,  $P < .007$ ). Plot-level  $\beta$  and  $\alpha$  diversity for naturally recruiting species did not vary with distance ( $\beta$ : bootstrap  $P = .27$ ;  $\alpha$ :  $F_{1,48} = 3.82$ ,  $P = .06$ ). Error bars represent  $\pm 1$  SE.

whether assembly trajectories can vary depending on the intensity of small-mammal predation on recruiting plants. We first quantified deterministic-stochastic assembly dynamics at the site level, where 24 native late-successional tallgrass prairie species were seeded over an environmentally homogenous agricultural field that was devoid of existing vegetation because of decades of plowing and herbicide application. The random planting of seeds guaranteed that any resulting patchiness in plant communities would be the result of local mechanisms rather than dispersal limitation. We then conducted experiments to identify patterns and mechanisms of spatial variability in small-mammal impacts. We hypothesized that, if seed and seedling predation is the main stressor in this system, and with small mammals likely residing in areas adjacent to the study site (fig. A1; figs. A1–A4 available online),

this would lead to (i) high spatial use by small mammals in areas close to the prairie edge versus toward the prairie interior, with a corresponding stress gradient in predation, and (ii) an increase in the role of stochastic processes during plant assembly (higher  $\beta$  diversity) with distance from the prairie edge. Both hypotheses were confirmed.

### Methods

We worked in an 18-ha agricultural field in southwestern Ontario, Canada ( $43^{\circ}22.9'N$ ,  $80^{\circ}21.3'W$ ), which is relatively homogeneous in topography, drainage, and soil depth ( $>2$  m to bedrock; fig. A1). Levels of soil organic matter, nitrogen, and total carbon are typical of intensively farmed soils and show no significant spatial variability (table A1; tables A1 and A2 available online). The site is bounded



**Figure 3:** Schematic showing how community assembly shifts from deterministically to stochastically regulated as seed predation diminishes into the open seeded field.

by oldfield to the north and east and a residential hedgerow and road to the west and south, respectively. The oldfield was dominated by exotic perennial grasses (*Festuca rubra* and *Bromus intermis*) and perennial forbs, especially *Solidago canadensis* (fig. A1). We concentrated our work toward the southern and western sections of the study site, in a ~10-ha area bordering the oldfield. Before the commencement of our experiment, the study area had been cultivated with a corn-soybean rotation for more than 60 years, up to and including 2009, with herbicides eliminating perennial agronomic grasses that can constrain the establishment of restored tallgrass prairie. Soybeans had been planted in the 2 years before our work (2008–2009), because herbicides used in corn production can inhibit germination of native  $C_3$  and  $C_4$  prairie graminoids.

Seeding of 24 native tallgrass prairie species occurred in March 2010, with the late winter planting providing a cold-wet stratification period that is required for many tallgrass prairie species (e.g., Harnden et al. 2011). Seeds were broadcast from a modified tractor-drawn seeder at a density of ~1,000 seeds of all species per square meter (fig. A1). Because seeds fell from the seeder at random, each species had a similar probability of landing at any

given location, which is critical for testing for stochastic processes (Chase 2010). The pre-European plant cover of the site is undocumented, but the presence of centuries-old *Quercus macrocarpa* trees suggests an open and possibly grass-dominated system. Tallgrass prairie and oak savanna covered an estimated ~100,000 ha of southwestern Ontario at the time of European settlement; today, <1% remains (Bakowsky and Riley 1994).

We conducted tests of spatial variability in site-level community assembly in the first year of establishment (2010) and whether small mammals influenced this variability. We used a range of approaches to quantify (i) the spatial distribution of small-mammal populations and rates of seed removal; (ii) species-specific differences in seed removal, using cafeteria trials (e.g., are native species preferred over exotics and forbs preferred over grasses?) and evidence for the increased removal of less palatable species in the presence of highly palatable seeds; (iii) how predator risk affects small-mammal activity, using canopy removal and raptor decoys; (iv) background rates of seed predation at various distances from the field edge; and (v) whether spatial variability in small-mammal impacts corresponded to different trajectories of tallgrass prairie as-

sembly. In the second and third years of establishment (2011–2012), we ran several supplementary surveys and experiments to test whether the initial patterns persisted.

#### *Spatial Distribution of Small Mammals*

The spatial distribution of small-mammal occurrences in 2010 was measured using tracking tubes (Nams and Gillis 2003). The tracking tubes were laid out in late summer (August–September), with 60 tubes being randomly located along five transects extending from 5 m into the oldfield to 50 m into the planted prairie. Within the seasonal population cycling of small mammals, late summer corresponds to the time of highest population sizes in southern Ontario (Boonstra 1985), which we confirmed with monthly live trapping in 2012 (appendix, available online). The tubes were 25-cm lengths of 4-in-diameter ABS piping, which were lined with paper strips partially coated with mixed mineral oil and black pigment (Nams and Gillis 2003). The tracks left by small mammals after walking through this mixture were identified to species, with the frequency of tubes visited and the abundance of tracks per tube providing relative estimates of population size across the study site.

We did not estimate small-mammal distributions at the time of planting in 2010, when the 18-ha field was unvegetated (i.e., 100% bare soil; fig. A1). To retrospectively test the expectation that, under these conditions, small mammals would only rarely foray from the field edges into the open, we worked in an adjacent plowed field that matched the starting conditions of our experiment. Here, we measured small-mammal distribution and seed removals in early spring 2011, at the same time that planting occurred the previous year. Forty-five tubes were placed along a gradient extending from 30 m into oldfield bordering the field to 120 m into the open area. All tubes were placed a minimum of 10 m apart and were checked after 2 weeks. We also placed 100 seed stations at random locations along this gradient using palatable sunflower seeds (*Helianthus annuus*). Each station had 10 seeds, with 60 stations in the plowed field and 40 in the adjacent oldfield. We separated the samples by at least 10 m to eliminate the likelihood of seed stations drawing individuals out from the protective cover. We determined the rate of seed removal by location by recounting seeds at 24 h, 48 h, and 2 weeks.

#### *Cafeteria Trials and Exclosures*

We conducted cafeteria trials in late summer 2010 to test for seed selectivity and whether the presence of seeds of certain species increased the removal of others (“associational susceptibility”; Barbosa et al. 2009). We used 10

seeds of seven species from three functional groups to test whether small mammals preferentially removed specific species (forbs: *Helianthus divaricatus*, *Solidago juncea*, *Lespedeza capitata*; shrub: *Rosa blanda*; grasses: *Bromus inermis*, *B. kalmia*, *Sporobolus cryptandrus*). Most species are native to the northern range limits of North American tallgrass prairies. The one exception was *B. inermis*, whose invasion success across central North American grasslands has been attributed to low seed palatability (Everett et al. 1978).

Ten seeds of *H. annuus* (annual sunflower) were also added to half of the samples to test whether the presence of highly palatable seeds increased the removal of the less palatable native seeds. Background levels of seed removal by wind or ants (neither of which were observed) were controlled by covering half of the samples per treatment combination with 25-cm-diameter wire mesh exclosures. We replicated this design across four spatial blocks, each situated along a gradient from oldfield to prairie interior (5 m into the surrounding oldfield and 0, 25, and 50 m into the prairie). There were four replicate samples per combination of species  $\times$  *H. annuus* ( $\pm$ )  $\times$  exclosure ( $\pm$ )  $\times$  distance, for a total of 512 seed samples. We recorded the remaining number of seeds of the focal species after 48 h.

#### *Rodent Predation Risk Trials*

To test the effect of predator risk on small mammals in open areas, we factorially manipulated two factors hypothesized to restrict plant granivory and herbivory by small mammals: the absence of canopy cover (mowing), and the presence of a predator (a plastic great horned owl decoy that was attached to a 1.5-m pole). We randomly assigned treatment combinations to eight 6  $\times$  6-m plots in each of two spatial blocks, with mowing used to create the open areas. The blocks ran parallel to each other at two distances from the edge of the prairie (5 and 20 m). In each plot, we estimated small-mammal occurrences and impacts at two exclosed and two unexclosed seed stations containing 10 seeds each of *H. annuus* and *H. divaricatus* and with three unbaited tracking tubes. We used two species from our cafeteria trials to determine whether increased risk changed foraging behavior (e.g., taking fewer seeds and leaving the less palatable *H. divaricatus*). The trials were conducted August 29–31, 2010, during the moon’s wane (the proportion of moon illuminated decreased from 0.83 to 0.65 during this period; US Naval Observatory, available at <http://aa.usno.navy.mil/data/docs/MoonFraction.php>). There was no rainfall and limited cloud cover during this period, which can potentially inhibit small-mammal activity (O’Farrell 1974), whereas evening temperatures averaged 14.8°C (Environment Ca-

nada, National Climate Data and Information Archive, available at <http://www.climate.weatheroffice.gc.ca/climateData/>). After 24 and 48 h in the field, we recorded the number of seeds remaining at each seed station.

#### *Plant Community Assembly*

We tested whether species diversity in the assembling prairie community in 2010 differed by proximity to the surrounding oldfield, where granivory levels were determined to be the highest (see “Results”). Fifty 5 × 5-m plots were randomly located along a prairie edge-to-interior gradient in a 2.25-ha section of the field, with the maximum distance from the edge at 150 m. All planted and naturally recruiting unplanted species were identified in late August–October 2010, when most tallgrass prairie species are at their reproductive peak. We included the unplanted species in our surveys to test whether variability in the cover of unplanted species was associated with spatial patterns in the planted species (e.g., the presence of a potentially competitive unplanted dominant at the field edges, which may reduce prairie establishment independently of predation).

Using the plant survey data, we calculated the number of species per plot ( $\alpha$  diversity) and the turnover in species composition among plots ( $\beta$  diversity). We computed  $\beta$  diversity as the pairwise dissimilarities between plots using Jaccard’s dissimilarity index for analyses on presence-absence data (Legendre and Legendre 1998). Given that Jaccard’s indexes can be open to hidden biases (Cornwall et al. 2011; Chase et al. 2011), we used randomization trials and alternative measures of  $\beta$  diversity to test for evidence of these biases (see the appendix).

#### *Supplementary Work*

During the second and third year after planting, we conducted four supplementary experiments. We used monthly live trapping at the study site to test whether the tracking-tube estimates from 2010 accurately characterized seasonal fluctuations in small-mammal densities. We used large field exclosures combined with seed additions to directly test for differences in prairie establishment with and without the presence of small mammals. We used captive feeding trials to quantify the relative preferences on small mammals for seeds (granivory) versus newly established seedlings and adult plants (herbivory). Finally, we conducted plant diversity surveys 3 years after planting to test whether initial establishment patterns had persisted. Methodological descriptions of these additional experiments are provided in the appendix.

#### *Data Analysis*

Small-mammal abundances and the impacts of location and experimental treatments on seed removal were tested with ANOVA. We tested for the spatial patterns in spring 2011 seed removal after 24 h, 48 h, and 2 weeks using a one-way ANOVA with five 20-m interval distance categories. To test whether granivores were seed selective in the 2010 cafeteria trials, we included fixed effects of seed species, with and without *H. annuus*, their interaction, and a spatial block term on seed removal after 48 h. Data from 51 of our 256 exclosed seed stations were excluded before analysis, because the seed stations were breached by small mammals. We also tested whether seed removal and the number of small-mammal tracks per tube were sensitive to the predator risk environment using fixed effects of plant cover (with and without), decoy owls (with and without), their interaction, and a spatial block term. Seed removal was quantified for *H. annuus* and *H. divaricatus* seeds after 24 and 48 h. Because each plot contained four seed stations and three tracking tubes, analyses were conducted on the pooled plot-level data. Additionally, we only included tracks from species identified as granivores (i.e., red-backed vole *Clethrionomys gapperi*, meadow vole *Microtus pennsylvanicus*, deer mouse *Peromyscus maniculatus*, and meadow jumping mouse *Zapus hudsonicus*). We used Levene’s test to determine whether the data met the homogeneity of error variance required for analysis (Kuehl 2000). Any data that failed Levene’s test were  $\log_{10}(x + 1)$  transformed and reanalyzed. We  $\log_{10}(x + 1)$  transformed all seed removal data before analysis and calculated seed removal as the mean number of seeds remaining for each species in the exclosed seed stations from the number remaining in each unexclosed station. We performed Tukey’s tests on all significant ANOVA results. These analyses were conducted using S-Plus (Insightful, Seattle, WA).

To test whether  $\beta$  diversity increased with distance from the prairie edge, we assigned all 50 plots into five equal-distance classes to the edge. Each distance class spanned 30 m and centered at approximately 15, 45, 75, 105, and 135 m from the edge, respectively. We computed  $\beta$  diversity within each distance using the Jaccard’s dissimilarity index. A seven-step bootstrap procedure was used to determine the significance of the relationship between  $\beta$  diversity and distance from the edge as follows: (1) we computed the mean dissimilarity for each distance class, (2) regressed these mean dissimilarities versus the centers of the distance classes, (3) extracted the observed slope of that regression, (4) randomized the association between the plots and the distance classes, (5) repeated steps 1–3 to obtain a randomized bootstrap sample of slopes for that regression, (6) repeated steps 4 and 5 a total of 999 times, and (7) computed a *P* value for the relationship between

$\beta$  diversity and distance as the number of randomized bootstrap slopes that were greater than or equal to the observed slope, divided by the 1,000 samples. We performed this analysis with three types of species matrices as the basis for the pairwise dissimilarities: planted species only, unplanted species only, and both planted and unplanted species. This analysis was conducted in R with the “boot” package (Davison and Hinkley 1997; Canty and Ripley 2009).

Finally, we back-checked our analyses of  $\beta$  diversity by calculating Raup Crick  $\beta$  diversity ( $B_{rc}$ ), which tests whether changes in Jaccard’s dissimilarity are driven by increasing  $\alpha$  diversity rather than changes in  $\beta$  diversity (thus leading to an incorrect interpretation of among-plot community structure; Chase et al. 2011). This metric, however, is highly sensitive to cases in which  $\alpha$  levels are low relative to the size of the regional species pool (Chase et al. 2011), which we found to be the case. To confirm this diagnosis, we constructed a simulated data set with a known diversity structure that was parameterized with the values we observed in the field (see the appendix). We then tested the ability of the  $B_{rc}$  to detect this pattern and found it unable to do so. Additionally,  $\beta$  diversity was positively associated with areas of increased  $\alpha$  diversity, the opposite response predicted if changes in  $\beta$  diversity were purely a statistical artifact (Chase et al. 2011). We thus demonstrated that increasing plot dissimilarity from the field edges was indeed explained by real changes in community structure (i.e.,  $\beta$  diversity) and not by changes in  $\alpha$  diversity.

## Results

In early spring, we observed a significant linear decrease in small-mammal occurrences and granivore-based seed removal from the oldfield outwards. Within the oldfield, five visits were recorded in the seven tracking tubes over the 2-week sampling period. No activity was recorded in the 38 tracking tubes in the open prairie. In the cafeteria trials using palatable sunflower seeds, there was 100% removal of seeds in the oldfield, 45% within 30 m of the field edge, and no removals beyond this distance ( $F_{1,84} = 150.9$ ;  $P < .0001$ ; fig. 1).

In turn, this pattern was inversely correlated with the development of a significant positive linear increase in both  $\alpha$  and  $\beta$  diversity of planted prairie species away from the field edge (fig. 2A). Plots at the edge were composed of mostly the same three planted species: two  $C_4$  grasses, Indian grass *Sorghastrum nutans* and big bluestem *Andropogon gerardii*, and the small-seeded forb, black-eyed susan *Rudbeckia hirta*. In contrast, plots in the most distant open areas had diversity levels from 4 to 12 planted species per 25-m<sup>2</sup> plot, which often included the three species found

in the edge areas. This pattern was still evident by the third year after planting (fig. A2; see below). We were also able to create this pattern with the large enclosure experiment, with caged areas lacking small mammals having significantly higher diversity of planted species, especially large-seeded forbs and some grasses (appendix). These enclosure results were the same regardless of proximity to the edge, demonstrating that edge-to-interior gradient was not likely influenced by some underlying abiotic variable that we may have failed to measure.

Recruitment by unplanted weedy species in 2010 showed no relationship with distance from the edge (bootstrap:  $P = .269$ ; fig. 2B). The most abundant unplanted species were annual ruderals with seeds weighing  $<0.2$  mg/seed or species with traits known to reduce or prevent the predation of seed and seedlings (e.g., thorns: *Cirsium* species; toxicity: *Solanum pyramanthum* and *Solanum nigra*; Howe and Brown 1999; Radtke 2011; table A2). By 2012, most of the ruderal species were no longer evident, resulting in a significant net decrease in total diversity in all areas of the prairie. There was no net significant change in diversity of the planted species (appendix).

The cafeteria trials in 2010 revealed strong species-specific seed preferences by small mammals. There were significant preferences for mostly larger-seeded prairie forbs over other functional groups ( $F_{7,235} = 14.46$ ,  $P < .001$ ;  $P < .05$ , Tukey’s test). The only exception was when seeds of *Helianthus annuus* were present, which resulted in a 25% increase in seed removal of the other species ( $F_{1,189} = 13.7$ ,  $P < .001$ ). There was a very low amount of seed loss from the intact small-diameter cages (mean no. seeds remaining  $\pm$  SE,  $9.6 \pm 0.17$ ), indicating that removal by ants and wind was negligible.

In the early spring cafeteria trials with highly palatable sunflower seeds, it took 2 weeks for the complete removal of seeds from the oldfield, with no seed removed beyond 30 m in the open field ( $F_{1,84} = 150.9$ ;  $P < .0001$ ). As summer progressed, the gradient of seed removal from edge-to-open areas was only marginally significant ( $F_{3,235} = 1.13$ ,  $P = .080$ ), with seeds of palatable forbs fully predated within 48 h regardless of location. This indicates that small mammals were now occupying all areas of the planted prairie, suggesting that the spatial structure of the prairie was created within the first few months of prairie development, before the formation of a closed plant canopy by late July. Small-mammal occurrences, estimated by the number of tracks per tube, also revealed their presence throughout the planted prairie by late summer ( $F_{3,49} = 1.243$ ,  $P = .30$ ). This same spatial distribution of small mammals, with occurrences throughout the prairie, was also observed each month with live trapping from December 2011 to November 2012 (more details are provided in the appendix).

Despite small mammals occurring throughout the planted prairie by the first summer of establishment, the pattern of increasing floral diversity toward the prairie center was still evident by the end of the third growing season (fig. A2). Areas near the oldfield edge were dominated exclusively by one or more of the two  $C_4$  grasses and *R. hirta*. Areas beyond 50 m from the edge also had large numbers of  $C_4$  grasses and *R. hirta*, but with an additional 4–7 planted prairie species per 25-m<sup>2</sup> plot. The captive feeding trials indicated that small-mammal predation was largely restricted to seeds, with preferences for the same large-seeded forbs and grasses (fig. A3; appendix). There was some predation on seeds of *A. gerardii*, but only after the preferred species were fully consumed. After 2 weeks, there was herbivory on several seedlings of the forbs *Helianthus divaricatus* and *R. hirta*, after which we ended the experiment because no further seed or seedling predation or seed consumption was detected. No damage was observed on any adult plant during the trials.

The late-summer risk trials in 2010 revealed a significant inhibitory effect of canopy removal on granivory within 24 h after the openings were created. There was a 191% reduction in removal of *H. annuus* ( $F_{1,11} = 6.5$ ,  $P = .027$ ), and there were significantly fewer tracks of granivorous rodents per tube (mean tracks per tube  $\pm$  SE,  $1.0 \pm 0.27$  when open and  $4.0 \pm 1.19$  when closed;  $F_{1,11} = 6.1$ ,  $P = .03$ ). Seed removal of *H. annuus* decreased by 22% on average when a predator (artificial owl) was present, but this difference was not significant ( $F_{1,11} = 0.40$ ,  $P = .54$ ) and did not interact with the covered environment ( $F_{1,11} = 0.73$ ,  $P = .41$ ). The effect of cover removal disappeared after 48 h ( $F_{1,11} = 0.37$ ,  $P = .56$ ) as the granivores became acclimated to the openings, or possibly because of decreasing moonlight with the waning moon. Removal of *H. divaricatus*, however, did not respond to our experimental treatments at either time point (all  $P > .19$ ).

### Discussion

We tested whether fine-scale spatial variability in the intensity of small-mammal impacts resulted in different trajectories of community assembly in planted tallgrass prairie. We found strong supporting evidence, with reductions in the impacts of small mammals associated with higher plot-level diversity (a greater percentage of the total regional species pool) and higher among-plot diversity (greater among-plot differences in species composition) of the planted species that reflected our stochastic planting method. By contrast, prairie assembly unfolded deterministically in edge areas where small-mammal impacts appeared to be high, because plot-level diversity mostly derived from a small subset of species with traits for reducing

predation. Cafeteria trials and exclosures confirmed strong positive correlations between diversity in the prairie edges and the species not taken. The end product at the site level was a spatially structured mixture of species with increasing diversity toward areas where predation of seeds or seedlings in the first few months after planting was less prevalent (fig. 3). Our work demonstrates that trophic interactions can influence the relative strength of stochastic and deterministic factors during the assembly of producer communities in an environment where abiotic conditions were relatively homogeneous and dispersal from the regional species pool was not limiting (Brown and Heske 1990; Brown and Peet 2003; Chase 2007, 2010; Chase et al. 2009). It also supports earlier findings of small mammals strongly influencing diversity in grassland communities, with these influences unfolding “cryptically,” given the difficulties in observing their seasonal behaviors and the short time periods over which the impacts can occur (Keesing 2000; Howe et al. 2002; Orrock et al. 2008; MacDougall et al. 2010).

Our evidence suggests that the spatial structuring of plant diversity developed rapidly in the first year, within a few months between seed addition in early spring and canopy closure in midsummer, and that this pattern persisted for 3 years. Small-mammal populations in early spring 2010, when the planted prairie was completely devoid of vegetative cover, appear to have been concentrated in the adjacent oldfield in association with dense canopy of mostly nonnative grass species (e.g., *Festuca rubra* and *Bromus inermis*). Seed removal in cafeteria trials in early spring was 100% in oldfield areas, but the time-to-discovery was slow (up to 2 weeks), supporting the expectation that foraging pressure at this time of year can be intense but likely derives from relatively few individuals (Krebs et al. 1973). Seed foraging in the open field at this time only occurred within close proximity to the edge, and removal was rarely 100%, which suggests either infrequent visitation or concern over predation risk.

The foraging distances into the open field with the cafeteria trials were shorter than the distances observed in the suppression of  $\beta$  diversity in the planted prairie. This discrepancy may derive from differences in the spatial distribution of seeds. Our planting blanketed the entire prairie with seeds, potentially drawing small mammals farther into the open with the continuous availability of food. The cafeteria trials, in contrast, were widely spaced and non-continuous. These differences in foraging distance could reflect trade-offs between the availability of the palatable seeds versus perceived predator risk, given the high sensitivity of small mammals to extensive open areas (Orrock et al. 2004, 2008).

Our risk trials, testing rates of seed removal in 25-m<sup>2</sup> plots free from canopy cover, confirmed this sensitivity of



small mammals to open conditions, supporting the idea that foraging range could have been restricted initially to areas in proximity to the field edge. The short-term effectiveness of these relatively small openings, however, also illustrates how the impacts of seed predators can be scale dependent, with intense seed removal more likely at smaller spatial scales. The probability of seeds escaping granivory can be tied to spatial extent, with the dispersal of seeds over extensive areas, especially at low densities, increasing the likelihood of escaping detection (Crawley 2000). Experimental granivory trials, by contrast, are typically conducted with high densities of seeds added to relatively small plots, which can drive trait-based community assembly relating to seed palatability but also result in an overestimation of its effects (MacDougall and Wilson 2007). Howe and Brown (1999), for example, observed high bird granivory in 14 × 14-m plots with seed densities of 6,300 m<sup>-2</sup>. Our planting density over the 18-ha plowed field was six times lower, which may have limited the effects of seed removal by birds and explained the stochastic development of the community in areas where small mammals were rare. From a restoration perspective, our results suggest that the assembly of planted tallgrass prairie in sites bounded by oldfield and less than 300 m across could be entirely regulated by small mammals.

Despite small mammals being observed at similar densities throughout the planted prairie by late summer 2010 and throughout 2012, the spatial diversity gradient was still evident 3 years after planting. Our captive feeding trials suggest an explanation. In all replicates, small mammals preferentially targeted seeds of certain species (e.g., *Helianthus divaricatus* and *Lespedeza capitata*), were never observed to browse on adult plants or on the seeds of most grasses, and only occasionally targeted seedlings of a subset of forb species when seed supplies were exhausted (e.g., seedlings of *H. divaricatus* and *Rudbeckia hirta*). Scat analyses during live trapping in 2012 indicated greater consumption of insects by small mammals toward summer, suggesting that rodents have widened their diets beyond plant predation by this time (S. Schneider, unpublished data). In our system at least, substantial small-mammal effects on prairie plants appear to diminish once they have entered the seedling stage.

A remaining possibility is that small mammals will still regulate plant diversity in the long term, not by attacking established mature plants but by preventing their replacement from seeds. Testing this hypothesis would be difficult, because recruitment from seeds in established undisturbed tallgrass prairie is also restricted by the low availability of ground-level light and soil nutrients (Knapp et al. 1998). These resource-based constraints on seed recruitment explain why periodic fire or grazing can be critical for maintaining prairie diversity via seed recruitment (Howe 1994;

Leach and Givnish 1996; Collins 2000). However, prairie burning conducted in early spring, the typical time of prescribed burning, could also favor establishment from seeds by temporarily reducing granivory via the elimination of the protective canopy (Goheen et al. 2010).

Testing the role of predators on the assembly of prey communities in large-scale experiments is often difficult, because the absence of recruiting individuals could also be explained by dispersal limitation (i.e., is an individual absent because it was consumed or failed to arrive?). Here, we eliminated dispersal limitation by adding seeds everywhere and were able to demonstrate that variability in granivory translated into different fine-scale plant communities. This included evidence that the presence of highly palatable seeds increased the consumption of less palatable seeds that were in close proximity. This could further contribute to stochastic variability in fine-scale assembly, if the random arrival of big-seeded forbs leads to the predation of close-by seeds of less palatable species that might otherwise be ignored. Similarly, our planting density could stochastically influence fine-scale competitive interactions during prairie development by increasing the likelihood that potentially dominant native canopy species, such as *Sorghastrum nutans* and *Andropogon gerardii*, are absent from some plots (Orrock and Watling 2010). On the other hand, the deterministic removal of large-seeded species could influence competitive dynamics within prairie, compared with areas where these species are present, given the positive connection between seed mass and competitive ability in many plants, including tolerance of size-asymmetric competition (seedlings establishing among adult plants; Leishman et al. 2000).

The end result of the assembly process was a positive relationship between species diversity and site suitability, as determined mechanistically by the decrease in granivory toward more open habitat. Debate persists in the ecological literature regarding the impact of site suitability (often represented by resources or climate) on diversity, especially whether increasing suitability accelerates or dampens the accumulation of species (Waide et al. 1999; Brown and Peet 2003; Grace et al. 2007; Fridley et al. 2007; Adler et al. 2011). Here, our work agrees with recent perspectives that suggest that the outcome of this relationship is influenced by the relative influences of factors that facilitate and constrain community membership, including stochastic processes at the initial stages of assembly (Leibold et al. 2004; Chase 2010). The positive diversity-suitability relationship developed because seeds from the regional species pool were everywhere, whereas granivores were spatially restricted. In many systems, including tallgrass prairie, the former rarely happens due to the effects of acute dispersal limitation, which is exacerbated by the effects of habitat loss and patch isolation (Leach and Givnish

1996). This suggests that a positive relationship between diversity and suitability may have the potential to form more often than is typically observed, but this is prevented by immigration constraints that prevent the regional species pool from being fully expressed in local habitats (Levine 2000; Brown and Peet 2003).

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### Literature Cited

- Abrams, P. A., and H. Matsuda. 2003. Population dynamical consequences of reduced predator switching at low total prey densities. *Population Ecology* 45:175–185.
- Abramsky, Z., M. L. Rosenzweig, and A. Subach. 2002. The costs of apprehensive foraging. *Ecology* 83:1330–1340.
- Adler, P. B., J. Hille Ris Lambers, and J. M. Levine. 2007. A niche for neutrality. *Ecology Letters* 10:95–104.
- Adler, P. B., E. W. Seabloom, E. T. Borer, H. Hillebrand, Y. Hautier, A. Hector, W. Stanley Harpole, et al. 2011. Productivity is a poor predictor of plant species richness. *Science* 333:1750–1753.
- Allen, J. A. 1988. Frequency-dependent selection by predators. *Philosophical Transactions of the Royal Society B: Biological Sciences* 319:485–503.
- Bagchi, S., T. Swinfield, R. E. Gallery, O. T. Lewis, S. Gripenberg, L. Narayan, and R. P. Freckleton. 2010. Testing the Janzen-Connell mechanism: pathogens cause overcompensating density dependence in a tropical tree. *Ecology Letters* 13:1262–1269.
- Bakowsky, W., and J. Riley. 1994. A survey of the prairies and savanna of southern Ontario. Pages 7–16 in P. Wickett, P. Lewis, A. Woodcliffe, P. Pratt, eds. *Proceedings of the 13th North American Prairie Conference*. Department of Parks, Windsor, Ontario, Canada.
- Boonstra, R. 1985. Demography of *Microtus pennsylvanicus* in southern Ontario: enumeration versus Jolly-Seber estimation compared. *Canadian Journal of Zoology* 63:1174–1180.
- Bricker, M., D. E. Pearson, and J. L. Maron. 2010. Small mammal seed predation limits the recruitment and abundance of two perennial grassland forbs. *Ecology* 91:85–92.
- Brown, J. H., and E. J. Heske. 1990. Control of a desert-grassland transition by a keystone rodent guild. *Science* 250:1705–1707.
- Brown, R. L., and R. K. Peet. 2003. Diversity and invisibility of southern Appalachian plant communities. *Ecology* 84:32–39.
- Canty, A., and B. Ripley. 2009. boot: Bootstrap R (S-Plus) functions. R package version 1.2–37.
- Cappuccino, N., and J. T. Arnason. 2006. Novel chemistry of invasive exotic plants. *Biology Letters* 2:189–193.
- Chase, J. M. 2007. Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences of the USA* 104:17430–17434.
- . 2010. Stochastic community assembly causes higher biodiversity in more productive environments. *Science* 11:1388–1391.
- Chase, J. M., E. G. Biro, W. A. Ryberg, and K. G. Smith. 2009. Predators temper the relative importance of stochastic processes in the assembly of prey metacommunities. *Ecology* 12:1210–1218.
- Chase, J. M., N. J. B. Kraft, K. G. Smith, M. Vellend, and B. D. Inouye. 2011. Using null models to disentangle variation in community dissimilarity from variation in  $\alpha$ -diversity. *Ecosphere* 2: art24.
- Chase, J. M., and M. A. Leibold. 2003. *Ecological niches: linking classic and contemporary approaches*. University of Chicago Press, Chicago.
- Collins, S. L. 2000. Disturbance frequency and community stability in native tallgrass prairie. *American Naturalist* 155:311–325.
- Cottenie, K. 2005. Integrating environmental and spatial processes in ecological community dynamics. *Ecology Letters* 8:1175–1182.
- Crawley, M. J. 2000. Seed predators and plant population dynamics. Pages 167–182 in M. Fenner, ed. *Seeds: the ecology of regeneration in plant communities*. CABI, New York.
- Davison, A. C., and D. V. Hinkley. 1997. *Bootstrap methods and their applications*. Cambridge University Press, Cambridge.
- Everett, R. L., R. O. Meeuwig, and R. Stevens. 1978. Deer mouse preference for seed of commonly planted species, indigenous weed seed, and sacrifice foods. *Journal of Range Management* 31:70–73.
- Fraser, L. H., and E. B. Madson. 2008. The interacting effects of herbivore exclosures and seed addition in a wet meadow. *Oikos* 117:1057–1063.
- Fridley, J. D., J. J. Stachowicz, S. Naeem, D. F. Sax, E. W. Seabloom, M. D. Smith, T. J. Stohlgren, D. Tilman, and B. Von Holle. 2007. The invasion paradox: reconciling pattern and process in species invasion. *Ecology* 88:3–17.
- Germain, R. M., L. Johnson, S. Schneider, K. Cottenie, E. A. Gillis, A. S. MacDougall. 2013. Data from: Spatial variability in plant predation determines the strength of stochastic community assembly. *American Naturalist* 182:XXX–XXX, Dryad Digital Repository, doi:10.5061/dryad.n4v0c.
- Gilbert, B., and M. J. Lechowicz. 2004. Neutrality, niches, and dispersal in a temperate forest understory. *Proceedings of the National Academy of Sciences of the USA* 101:7651–7656.
- Goheen, J. R., T. M. Palmer, F. Keesing, C. Riginos, and T. P. Young. 2010. Large herbivores facilitate savanna tree establishment through diverse and indirect pathways. *Journal of Animal Ecology* 79:372–382.
- Grace, J. B., T. M. Anderson, M. D. Smith, E. Seabloom, S. Andelman, G. Meche, E. Weiher, et al. 2007. Does species diversity limit productivity in natural grassland communities? *Ecology Letters* 10: 680–689.
- Gravel, D., C. D. Canham, M. Beaudet, and C. Messier. 2006. Rec-

- onciling niche and neutrality: the continuum hypothesis. *Ecology Letters* 9: 399–409.
- Halpern, B. S., K. Cottenie, and B. Broitman. 2007. Strong top-down control in southern California kelp forest ecosystems. *Science* 312: 1230–1232.
- Harnden, J., A. S. MacDougall, and B. A. Sikes. 2011. Field based effects of allelopathy in invaded tallgrass prairie. *Botany* 89:227–234.
- Harrison, S., M. Vellend, and E. I. Damschen. 2011. “Structured” beta diversity increases with climatic productivity in a classic dataset. *Ecosphere* 2:1–13.
- Holyoak, M., and M. Loreau. 2006. Reconciling empirical ecology with neutral community models. *Ecology* 87:1370–1377.
- Howe, H. F. 1994. Managing species diversity in tallgrass prairie: assumptions and implications. *Conservation Biology* 8:691–704.
- Howe, H. F., and J. S. Brown. 1999. Effects of birds and rodents on synthetic tallgrass communities. *Ecology* 80:1776–1781.
- Howe, H. F., J. S. Brown, and B. Zorn-Arnold. 2002. A rodent plague on prairie diversity. *Ecology Letters* 5:30–36.
- Keesing, P. 2000. Cryptic consumers and the ecology of an African savanna. *BioScience* 50:205–215.
- Knapp, A. K., J. M. Briggs, D. C. Hartnett, and S. L. Collins. 1998. Grassland dynamics: long-term ecological research in tallgrass prairie. Oxford University Press, New York.
- Krebs, C. J., M. S. Gaines, B. L. Keller, J. H. Myers, and R. H. Tamarin. 1973. Population cycles in small rodents. *Science* 179:35–41.
- Kuehl, R. O. 2000. Design of experiments: statistical principles of research design and analysis. Duxbury, Pacific Grove, CA.
- Leach, M. K., and T. J. Givnish. 1996. Ecological determinants of species loss in remnant prairies. *Science* 273:1555–1558.
- Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7:601–613.
- Leishman, M. R., I. J. Wright, A. T. Moles, and M. Westoby. 2000. The evolutionary ecology of seed size. Pages 31–57 *in* M. Fenner, ed. *Seeds: the ecology of regeneration in plant communities*. 2nd ed. Wallingford, UK.
- Legendre, P., and L. Legendre. 1998. *Numerical ecology*. Elsevier, Amsterdam.
- Levine, J. L. 2000. Species diversity and biological invasions: relating local process to community pattern. *Science* 288:852–854.
- MacDougall, A. S., A. Duwyn, and N. Jones. 2010. Consumer-based limitations drive oak recruitment failure. *Ecology* 91:2092–2099.
- MacDougall, A. S., and S. D. Wilson. 2007. Herbivory limits recruitment in an old-field seed addition experiment. *Ecology* 88: 1105–1111.
- Martin, L. M., and B. J. Wilsey. 2006. Assessing grassland restoration success: relative roles of seed additions and native ungulate activities. *Journal of Applied Ecology* 43:1098–1110.
- Matthies, D., I. Brauer, W. Maibom, and T. Tschardt. 2004. Population size and the risk of local extinction: empirical evidence from rare plants. *Oikos* 105:481–488.
- McGill, B. J., R. S. Etienne, J. S. Gray, D. Alonso, M. J. Anderson, H. K. Benecha, M. Domelas, et al. 2007. Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecology Letters* 10:995–1015.
- Murdoch, W. W. 1969. Switching in generalist predators: experiments on prey specificity and stability of prey populations. *Ecological Monographs* 39:335–354.
- Myllymäki, A. 1977. Demographic mechanisms in the fluctuating populations of the field vole *Microtus agrestis*. *Oikos* 29:468–493.
- Nams, V. O., and E. A. Gillis. 2003. Changes in tracking tube use by small-mammals over time. *Journal of Mammalogy* 84:1374–1380.
- O’Farrell, M. J. 1974. Seasonal activity patterns of rodents in a sagebrush community. *Journal of Mammalogy* 55:809–823.
- Orrock, J. L., B. J. Danielson, and R. J. Brinkerhoff. 2004. Rodent foraging is affected by indirect, but not by direct, cues of predation risk. *Behavioral Ecology* 15:433–437.
- Orrock, J. L., and R. J. Fletcher. 2005. Changes in community size affect the outcome of competition. *American Naturalist* 166:107–111.
- Orrock, J. L., and J. I. Watling. 2010. Local community size mediates ecological drift and competition in meta-communities. *Proceedings of the Royal Society B: Biological Sciences* 277:2185–2191.
- Orrock, J. L., M. S. Witter, and O. J. Reichman. 2008. Apparent competition with an exotic plant reduces native plant establishment. *Ecology* 89:1168–1174.
- Ostfeld, R. S., R. H. Manson, and C. D. Canham. 1997. Effects of rodents on survival of tree seeds and seedlings invading old fields. *Ecology* 78:1531–1542.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* 100:65–75.
- Pinto, S. M., and A. S. MacDougall. 2010. Dispersal limitation and environmental structure interact to restrict the occupation of optimal habitat. *American Naturalist* 175:675–686.
- Radtke, T. M. 2011. Granivore seed-size preferences. *Seed Science Research* 21:81–83.
- Samuels, C. L., and J. A. Drake. 1997. Divergent perspectives on community convergence. *Trends in Ecology and Evolution* 12:427–432.
- Vanhoeacker, D., J. Ågren, and J. Ehrlén. 2009. Spatial variability in seed predation in *Primula farinosa*: local population legacy versus patch selection. *Oecologia (Berlin)* 160:77–86.
- Waide, R. B., M. R. Willig, C. F. Steiner, G. Mittelbach, L. Gough, S. I. Dodson, G. P. Juday, and R. Parmenter. 1999. The relationship between productivity and species richness. *Annual Review of Ecology and Systematics* 30:257–300.

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