

Environmental heterogeneity has a weak effect on diversity during community assembly in tallgrass prairie

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Abstract. Understanding what constrains the persistence of species in communities is at the heart of community assembly theory and its application to conserving and enhancing biodiversity. The “environmental heterogeneity hypothesis” predicts greater species coexistence in habitats with greater resource variability. In the context of community assembly, environmental heterogeneity may influence the variety and strength of abiotic conditions and competitive interactions (environmental filters) to affect the relative abundance of species and biodiversity. We manipulated key resources that influence plant diversity in tallgrass prairie (i.e., soil depth and nitrogen availability) to increase environmental heterogeneity prior to sowing native prairie species into a former agricultural field. We compared variability in nutrient availability, aboveground annual net primary productivity (ANPP), and the composition of species between replicate plots containing soil heterogeneity manipulations and plots with no resource manipulations ($n = 4$ per treatment) during the first 15 yr of community assembly as a test of the “environmental heterogeneity hypothesis.” The manipulations increased environmental heterogeneity, measured as the coefficient of variation in $\text{NO}_3\text{-N}$ availability and ANPP. Plant diversity, however, was similar and decayed exponentially and indiscriminately over time between the heterogeneity treatments. Species richness declined linearly over time in both heterogeneity treatments, but richness was higher in the more heterogeneous soil 2 yr following a second propagule addition 8 yr after the initial sowing. As a result, there was a lower rate of species loss over time in the more heterogeneous soil (0.60 species yr^{-1}) relative to the control soil (0.96 species yr^{-1}). Communities in each treatment exhibited strong convergence over time resulting from a shift in dominant species across all treatments and a gradual increase in the clonal C_4 grass, *Andropogon gerardii*. We attribute the weak effect of heterogeneity on diversity to increasing dominance of a clonal species, which decreased the scale of soil treatments relative to plant size, dispersal limitation, and absence of a key driver (grazing) known to increase plant diversity under a frequent fire regime. Thus, steering community assembly to attain high biodiversity may depend more on manipulating processes that reduce dominance and facilitate the arrival of new species than promoting environmental heterogeneity.

Key words: biodiversity; carbon addition; dispersal; grassland; nutrient enrichment; restoration; soil heterogeneity.

INTRODUCTION

Local species diversity is a function of the regional species pool, colonization, and local extinction (Ricklefs 1987, Tilman 2004). Regional processes influencing dispersal generally govern the arrival of species, but their persistence in communities is influenced by environmental “filters,” i.e., local processes that affect the ability of species to tolerate abiotic and biotic conditions (Keddy 1992, Loreau et al. 2001). Human intervention can override dispersal limitation and alter conditions to steer

community assembly toward a desired state in degraded environments (Hobbs et al. 2004, 2011). Ecological theory and knowledge of factors influencing community composition in non-degraded systems may be used to guide restoration, and outcomes may be used to refine theory and reveal how community assembly processes can be manipulated to achieve restoration goals (Palmer et al. 1997). For example, understanding the relative importance of neutral [e.g., regional species pool (Hubbell 2001)] and local [e.g., niche availability (Tilman 1982)] processes, and the interaction between them (Foster and Dickson 2004, Long et al. 2014) can indicate whether augmenting the species pool, manipulating the environment, or both interventions are required to restore diverse communities (Hulvey and Aigner 2014). However, long-term studies

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are needed to evaluate the strength and duration of dispersal limitation and environmental filters on community assembly beyond their effects on pioneering species (Wilson et al. 1996, Pywell et al. 2002, Fukami et al. 2005, Longworth et al. 2014, Ray and Collinge 2014).

Environmental heterogeneity is a deterministic niche-based mechanism invoked to explain species coexistence (Grime 1979, Huston 1979, Tilman 1993, Caldwell and Pearcy 1994, Stein et al. 2014). The hypothesis that heterogeneous environments support more species through greater niche availability, refugia, and resource partitioning is well supported in theory (Levin 1974, Chesson 2000) and substantiated by numerous observations in animal communities (reviewed by Huston 1979). Ricklefs (1977) hypothesized that environmental heterogeneity, principally spatial variability in soil and microsite conditions maintained through a variety of successional states within a tropical forest, underlies large-scale geographic variation in plant diversity. At much smaller scales, soil heterogeneity has been shown to promote variation in the establishment of plants with different germination requirements (Harper et al. 1965, Silvertown and Wilkin 1983). Positive relationships between soil heterogeneity and plant diversity have been documented in many observational studies (Lundholm 2009), but few field experiments have shown that soil heterogeneity, *per se*, increases plant diversity (e.g., Richardson et al. 2012, Williams and Houseman 2014). One explanation for no effect of manipulated heterogeneity on plant diversity is the role of plant size relative to the scale of heterogeneity treatments (Lundholm 2009), particularly in communities dominated by clonal species (Eilts et al. 2011). Further, a functionally diverse species pool may be needed to exploit environmental heterogeneity (Questad and Foster 2008).

Clonal grasses dominate productivity and biomass in tallgrass prairie (Epstein et al. 1998). These “core” species, which reach greatest cover in annually burned and ungrazed prairie, are a primary determinant of diversity because they tend to suppress the richness and abundance of subordinate species (Collins and Calabrese 2012, Gough et al. 2012). Floristic diversity of tallgrass prairie, however, is driven by the presence of numerous subordinate (or “satellite”) species that are maintained by heterogeneity in topography, fire and grazing, and animal disturbance to vegetation and soil (Collins 1992, Glenn et al. 1992, Hartnett et al. 1996, Knapp et al. 1999, Rogers and Hartnett 2001, Bakker et al. 2003, Collins and Smith 2006, McMillan et al. 2011). More locally, soil nutrient availability and depth influence diversity through their effects on grass dominance. For example, nitrogen enrichment promotes high grass dominance and low diversity (Collins et al. 1998), and higher plant diversity occurs where there is less grass dominance in shallow soil uplands relative to deep soil lowlands (Gibson and Hulbert 1987). Thus, these factors represent local processes (environmental filters) that potentially could be manipulated to steer restoration of biodiversity in degraded prairie.

By far, the most widespread disturbance to the prairie ecosystem has been conversion to row-crop agriculture (Samson and Knopf 1994), wherein soil properties are homogenized to achieve uniform production (Robertson et al. 1993, Rover and Kaiser 1999). The effect of agricultural conversion on soil and knowledge of processes that influence diversity in native tallgrass prairie motivated our hypothesis that experimentally increasing spatial heterogeneity in soil resources would increase diversity in restored prairie on former agricultural lands. To test this hypothesis, we manipulated soil nutrient availability and depth prior to sowing native species into a former agricultural field that had been conventionally tilled for >50 yr prior to our experiment. During the first 3 yr of plant community establishment (1998–2000), the nutrient treatments strongly affected cover of native and exotic species, diversity, and similarity in composition to never-cultivated prairie (Baer et al. 2003, 2004). However, there were limited short-term effects of soil heterogeneity *per se* on community structure (Baer et al. 2005). Short-term community dynamics in response to altered resource availability, however, may not be indicative of long-term outcomes if communities converge over time through shared resources (Pywell et al. 2002) or historical contingencies result from initial divergence in species composition (Fukami et al. 2005, Houseman et al. 2008). In 2005 (8 yr after the initial sowing), we added propagules of new species to override potential dispersal limitation. We predicted that communities developed in plots with high soil resource heterogeneity would diverge in diversity, richness, and composition relative to communities developed under uniform resource conditions. We further predicted that a propagule addition would increase community divergence if regional processes interacted with local deterministic processes to affect community assembly (Questad and Foster 2008, Long et al. 2014).

METHODS

Study site

Research plots were located in a former lowland agricultural field that had been cultivated for >50 yr at Konza Prairie Biological Station (KPBS), a long-term ecological research site located 9 km south of Manhattan, KS, USA (39°05' N, 96°35' W; 340 m asl). The 30 yr average annual precipitation at KPBS is 835 mm/yr, of which 75% is received during the growing season (April–September). Average annual precipitation in the 15 yr of study was 857 mm, of which 73% was received during the growing season (Appendix S1). The soil at the site was a gently sloping (0–1%) Reading silt loam (mesic Typic Arguidoll) formed by colluvial and alluvial deposits. Prior to cultivation, the plant community would have been representative of lowland native tallgrass prairie at KPBS, dominated by warm-season (C_4) grasses (*Andropogon gerardii* Vitman, *Schizachyrium scoparium* Michx., *Sorghastrum nutans* [L.], and *Panicum virgatum* L.) and, to a lesser extent, C_3 grasses and eudicots (Abrams and Hulbert 1987).

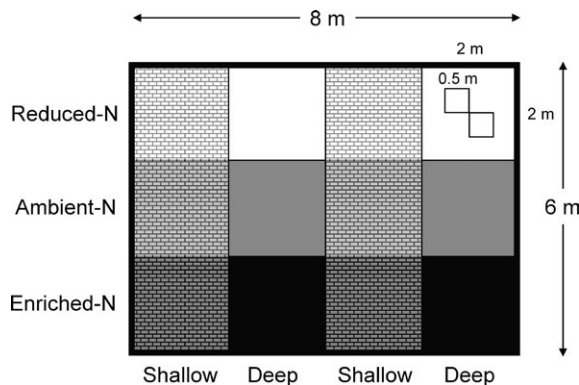


FIG. 1. Maximum heterogeneity treatment whole-plot design including subplot and species composition sampling (two 0.5×0.5 m quadrats in each subplot). Control plots had the same layout and sampling design, but did not include nutrient or depth manipulations.

Experimental design

In June 1997, sixteen 6×8 m whole-plots (with 6 m buffer strips between all plots) were delineated in the recently fallowed field and assigned to four whole-plot treatments according to a randomized complete block design. Two whole-plot treatments ($n = 8$) were sampled multiple times over the course of 15 yr: maximum heterogeneity (MAXHET) with altered soil conditions and control (CON) containing no manipulations (Fig. 1). All plots were divided into 12 subplots (2×2 m) for sampling. Each MAXHET whole-plot treatment included two levels of soil depth assigned to alternating 2×6 m vertical strips crossed with three levels of soil nitrogen (N) availability randomly assigned to 2×8 m horizontal strips, a split block design. All of the plots had surface soil temporarily removed to a depth of approximately 25 cm, and natural limestone slabs were laid in strips assigned to the shallow soil treatment. The soil from all plots was then replaced, leveled, and disked (2–3 cm deep). In February 1998, we incorporated sawdust (49% C; C : N ratio = 122) into the strips assigned to the reduced-N treatment. The average C concentration and bulk density in the surface 15 cm following long-term cultivation was 1.5% and 1.2 g/cm^3 , respectively. Sawdust was tilled into the soil at a rate of $5.5 \text{ kg dry mass/m}^2$ to achieve a C concentration representative of native prairie soil (approximately 3% C). This application effectively immobilized N for 3 years (Baer et al. 2003). Because net N mineralization rates increased over time as the sawdust decomposed, we began surface applications of granular sugar in 2004 at a rate of $200 \text{ g sucrose/m}^2$ (84.22 g C/m^2) 3–4 times each growing season. Strips assigned to the enriched-N treatment were fertilized with $5 \text{ g N/m}^2/\text{yr}$ (applied as ammonium-nitrate) in July of the first growing season and early June of each subsequent year.

Restoration approach

The research area was tilled prior to planting. In April 1998, all plots were sown with 42 native prairie species at rates selected to achieve a log-normal distribution of

species representative of native prairie (Howe 1994b). All plots received the same seed mix comprised of species assigned to four sowing density categories: dominant grasses (160 seeds/m^2), common (16 seeds/m^2); frequent (10 seeds/m^2); and uncommon (5 seeds/m^2) species (Appendix S2). Sowing rates were based on live seed, which accounted for germination, dormancy, and purity. Prior to sowing, all plots were lightly raked. The four dominant grasses were sown with a grass drill (Truax Company, Minneapolis, Minnesota) over the entire experimental area, including the buffer strips to reduce potential edge effects. Seeds of 38 non-dominant grasses and forbs were mixed with damp builder's sand and hand broadcast evenly over plots. Baer et al. (1999, 2003) provide details on plot establishment, species sowing rates, seed sources, storage, and seed treatment procedures. A second seed addition was conducted prior to the eighth growing season of this experiment. In March 2005, we performed a propagule addition using species that had not been previously sown or observed in the experiment (Appendix S2). We added propagules of 15 species, each sown at a rate of 25 live seeds/ m^2 (total over seeding rate of $375 \text{ live seeds/m}^2$).

Management of the site consisted of excluding large browsers, implementing prescribed fire, and removing invasive species. A fence was erected around the site at the start of the experiment to exclude deer. The experiment was burned in early spring prior to each growing season, with the exception of 2000. An invasive exotic legume, *Securigera varia* (L.) Lassen (crown vetch), was controlled through hand weeding and leaf-applied herbicide at the start of each growing season. Two subplots heavily invaded by 2006 were not included in any subsequent analyses. A 4-m swath of the central area of the buffers between plots was mowed twice each growing season, which prevented flowering and seed production; a 1-m buffer around each plot was not mowed.

Long-term response variables

Relative inorganic N availability was assessed using buried ion exchange resins in 1998, 1999, 2000, 2005, 2006, and 2012. Resin bags were constructed of nylon and contained 10 g of strongly basic anion exchange resins preloaded with Cl^- (manufactured by Dowex; 1X8-50 resins). Two resin bags were buried in the surface 10 cm of each subplot in June or July and retrieved in September or October, depending on the year. Nitrate was extracted from resin bags by shaking each bag in 75 mL of 2 mol/L KCl at 200 rpm (rotation frequency 3.33 Hz) for 1 h, then filtering each solution through $0.4 \text{ }\mu\text{m}$ polycarbonate membrane. Resin-collected NO_3^- -N was determined colorimetrically on an OI Flow Solution IV autoanalyzer (OI Analytical, College Station, Texas, USA).

Aboveground net primary productivity (ANPP) was measured in years 1, 2, 3, 7, 8, and 15. At the end of the growing season corresponding with peak biomass, vegetation was clipped at the ground surface from a 0.10 m^2

area outside of permanently located species composition sampling quadrats in each subplot. The current year's biomass was separated from any residual previous year's biomass. All plant material was dried at 60°C and weighed to estimate ANPP (Briggs and Knapp 1991).

Species composition was measured in nine growing seasons during the 15 yr of community establishment. The percent cover of each plant species was visually estimated in spring (June) and summer (late August through early September) for all plants rooted within two permanently located 50 × 50 cm quadrats in every subplot ($n = 24$ per plot). The maximum cover value of each species from the two seasonal surveys was used in all analyses of species composition. Cover values were averaged from the replicate 0.25-m² quadrats in each subplot prior to calculating all plot-level and subplot community metrics. Plot-level diversity (H') was calculated from the average cover of each species across all subplots within a plot. Plot-level richness was calculated by summing the total number of species from all subplots within a plot.

Statistical analyses

We performed univariate analyses to (1) evaluate whether the soil heterogeneity treatment increased variability in the physical and biological environment, and (2) identify how manipulated factors (soil N and depth) influenced the community over the long term. The whole-plot heterogeneity effect (HETTRT) on the variation in resin-collected NO₃-N, variation in ANPP, plot-level diversity, plot-level richness, and cover of an increasingly dominant species (*Andropogon gerardii*) was analyzed according to a randomized complete block design with repeated measures using the mixed model procedure in SAS (SAS Institute 2011). If there was a significant interaction between HETTRT and YEAR, we used contrast statements to test for differences between the whole-plot treatments within each year. We performed a separate (subplot-level) mixed model analysis in SAS using only the maximum heterogeneity plots to examine the main effects and interaction between levels of nitrogen (NUT) and soil depth (DEPTH) in resin-collected NO₃-N, ANPP, subplot-level diversity, subplot-level richness, and the cover of two dominant species. Subplots within each NUT and DEPTH level were assigned to vertical (VS) and horizontal (HS) strips, respectively. Block, VS(NUT), and HS(DEPTH) were assigned as random effects in the model. Resin-collected NO₃-N, richness and cover of *A. gerardii* and *P. virgatum* were log-transformed to improve normality. The least squares means procedure was used to compare main effect means. For both univariate analyses, we use Kenward-Roger method to estimate degrees of freedom if the model contained repeated measures. We ran each repeated measures analysis with compound symmetry (CS), autoregressive (AR), and unstructured (UN) options assigned to the covariance structure, and selected the analysis with the lowest AIC (Littell et al. 2006). The covariance structure accompanies

each F -value, followed by numerator and denominator degrees of freedom. There were no significant three-way interactions (DEPTH × NUT × YEAR) or interactions between DEPTH and YEAR. Contrast and estimate statements were used to compare nutrient means within a year if there was significant NUT × YEAR interaction. Significance was assigned at $\alpha = 0.025$ for the whole-plot analyses of the heterogeneity treatment due to the directional hypothesis; for all other analyses $\alpha = 0.05$.

Temporal dynamics of diversity, species richness, and cover of two dominant species (*A. gerardii* and *P. virgatum*) were modeled with TABLE CURVE 2D 5.01 (SYSTAT Software Inc., 2002) to evaluate simple equations (i.e., linear, exponential, power, log-normal) that best described temporal dynamics using model rankings by coefficients of determination and significance level of the model fit. If there was no main effect of HETTRT or interaction with YEAR in the univariate analyses, we pooled the data (referred to as “pooled models”). There was an interaction between YEAR and HETTRT for plot-level richness and a linear change in this variable over time in both whole-plot treatments. We compared the slopes of the two regressions using analysis of covariance (ANCOVA) in the general linear models procedure (SAS Institute 2011).

We used a nonmetric multidimensional scaling (NMDS) ordination based on a Bray-Curtis dissimilarity matrix to assess change in community composition over time at the subplot and whole-plot levels from 1998 to 2012. Bray-Curtis dissimilarity is an appropriate distance measure for relative abundance data that performs well in multivariate analyses (Clarke and Warwick 2001). Species that occurred in fewer than 5% of the samples were deleted from all analyses (McCune and Grace 2002). We also used permutational multivariate analysis of variance (PERMANOVA; Anderson and ter Braak 2003) to assess treatment effects on plant community composition, followed by a *post hoc* similarity percentage (SIMPER) analysis to determine which species contributed most to differences among treatments at the whole plot or subplot scales. Finally, we used a SIMPER analysis at the subplot level to quantify changes in compositional heterogeneity over time. All multivariate analyses were run using PRIMER 6.0.

RESULTS

Manipulating soil resources effectively increased and maintained higher heterogeneity in N availability. In all years measured, variation in inorganic N availability among the subplots, indexed by the coefficient of variation (CV) in resin-collected NO₃-N, was an average of 2.5 times higher in the MAXHET than CONTROL whole-plot treatments (HETTRT main effect: $F_{1,11.9\text{AR}(1)} = 92.33$; $P < 0.001$; Fig. 2A). Higher variability in NO₃-N in the MAXHET plots was primarily due to the fertilizer addition where the quantity of NO₃-N was 5.6–36.9 times higher in this treatment relative to the control. There was a significant interaction between NUT and YEAR

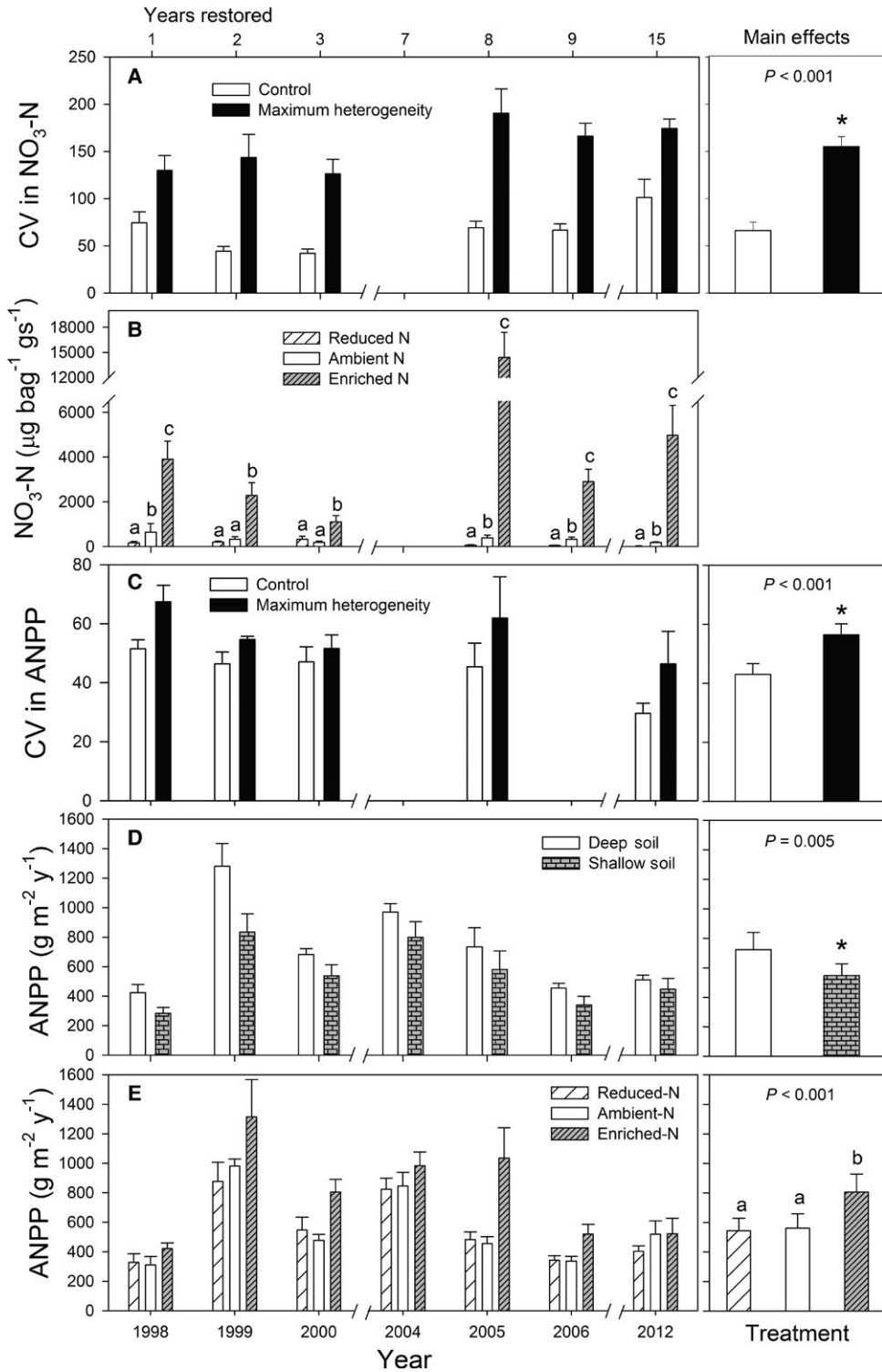


FIG. 2. Effects of soil heterogeneity manipulations on (A) variability in resin-collected $\text{NO}_3\text{-N}$ in the whole-plot treatments, (B) the amount of resin-collected $\text{NO}_3\text{-N}$ in the subplot nutrient treatments within the maximum heterogeneity plots, (C) variability in aboveground annual net primary productivity (ANPP) in the whole-plot treatments, and ANPP in response to the (D) soil depth and (E) nutrient subplot treatments within the maximum heterogeneity plots. Each bar represents the least-squares mean for the whole-plot ($n = 4$ per level) or subplot ($n = 4$ per level) treatment \pm SE. Variability was measured as the coefficient of variation (CV) among the 12 subplots within each whole-plot; * indicate differences between whole plot treatments within a year or averaged over all years if there was a significant main effect (terminal graph to the right of each panel). Nutrient treatment means accompanied by the same letter were not significantly different ($\alpha = 0.05$). Differences between the subplot soil depth treatments are indicated by an *.

on resin-collected $\text{NO}_3\text{-N}$ resulting from greater differences among the NUT treatments in some years relative to others ($F_{(\text{UN})10,51.9} = 8.53, P < 0.001$). In all years the $\text{NO}_3\text{-N}$ was significantly higher in the enriched-N than reduced-N treatment, with the ambient-N soil intermediate to both nutrient manipulations (Fig. 2B).

Both whole-plot treatments and manipulated subplot factors influenced ANPP. Across all years, CV of ANPP was 13% higher in the MAXHET than CONTROL whole-plot treatment ($F_{1,13.8} = 12.30, P = 0.005$; Fig. 2C). Both subplot factors contributed to higher variability in plant biomass. Across all years and nutrient treatments, the buried limestone reduced ANPP by 24% relative to that in the deep soil ($F_{1,11.2} = 12.30, P = 0.005$; Fig. 2D). There was also a main effect of NUT on ANPP ($F_{2,66} = 9.21, P = 0.003$; Fig. 2E) with 43–48% higher ANPP in the enriched-N soil relative to both ambient-N and reduced-N soil. There was also a strong main effect of YEAR on ANPP ($F_{6,216} = 26.82, P < 0.001$) in the maximum heterogeneity plots resulting from differences in ANPP among some years, but no discernible trend in ANPP over time. There were no significant interactions between YEAR, DEPTH, and NUT.

Temporal changes in plant diversity (H') were similar between the whole-plot heterogeneity treatments across all years (HETTRT main effect: $F_{(\text{CS})1.3} = 0.08; P = 0.797$) and within each year (interaction: $F_{(\text{CS})8,48} = 0.72; P = 0.673$) (Fig. 3A). There was a main effect of YEAR on plot-level diversity ($F_{(\text{CS})8,48} = 23.98; P < 0.001$), which declined exponentially over time (Fig. 3B). At the subplot level, H' was affected by an interaction between NUT and DEPTH ($F_{(\text{AR})2,63} = 3.92; P = 0.027$) and interaction between NUT and YEAR ($F_{(\text{AR})16,309} = 2.64; P < 0.001$). The significant NUT \times DEPTH interaction resulted from differences in H' among the nutrient treatments only in the shallow soil and differences in diversity between the soil depths that occurred only in the ambient-N treatment (Table 1). There were no differences in H' among the nutrient treatments in the deep soil, but H' was higher in ambient N relative to enriched N in shallow soil. Reducing soil depth only affected H' in ambient-N conditions, where H' was higher in the shallow soil treatment. The significant interaction between NUT and YEAR resulted from no differences in H' among the nutrient treatments in years 6, 12 and 15 (2003, 2009, and 2012, respectively); higher H' in the reduced-N relative to the enriched-N soil in years 3, 8, and 9 (2000, 2005, and 2006, respectively); and lower H' in reduced-N relative to ambient-N soil in years 1, 2, and 14 (1998, 1999, and 2011, respectively; Appendix S3). Since 2003, with the exception of 2011, H' in the ambient-N treatment was intermediate or equal to the reduced-N and enriched-N treatments.

Similar to plot-level diversity, plot-level richness declined over time but there were differences between the whole-plot heterogeneity treatments in some years. There was significant interaction between HETTRT and YEAR for plot-level richness ($F_{(\text{AR}[1])8,43} = 2.41; P = 0.030$) due to higher richness in the MAXHET treatment in

one year following the second propagule addition in 2005 (Fig. 3C). Plot-level richness declined linearly over time in both heterogeneity treatments (CON: $r^2 = 0.77, P < 0.001$; MAXHET: $r^2 = 0.52, P < 0.001$; Fig. 3D), but the rate of species loss per plot was lower in the MAXHET treatment (ANCOVA: $F = 6.76, P = 0.011$). At the subplot level, there was a significant NUT \times YEAR interaction on species richness ($F_{(\text{AR})16,308} = 2.82; P < 0.001$) resulting from inconsistent differences among the NUT treatments over time (Appendix S3). There were no differences in richness among the NUT treatments in years 6, 8, 12, and 15 (2003, 2006, 2009, and 2012, respectively) and no consistent effects of the enriched or reduced N treatment in other years, with the exception that richness was never highest in the enriched-N treatment.

Two C_4 grasses comprised the majority of cover at different times during the 15 yr of grassland community assembly. Cover of *P. virgatum* increased during the first 3 yr of restoration, then declined exponentially and indistinguishably between the whole-plot heterogeneity treatments, described by a 4 parameter log-normal peak equation ($r^2 = 0.73; P < 0.001$; Fig. 4A). By 2012, *P. virgatum* comprised <5% of total plant cover. *Andropogon gerardii* cover increased steadily, linearly, and indiscriminately between the whole-plot heterogeneity treatments over time ($r^2 = 0.66; P < 0.001$; Fig. 4B). As a result, plot-level richness was inversely correlated with the cover of *A. gerardii* (Fig. 5).

Over all years, there was a significant interaction between DEPTH and NUT on *A. gerardii* cover ($F_{(\text{UN})2,24} = 4.20; P = 0.027$) among subplots. This interaction resulted from a difference in cover between the soil depths that occurred in only one of the nutrient treatments (lower cover in shallow soil under ambient-N condition) and a difference in *A. gerardii* cover among nutrient treatments that only occurred in deep soil (similar in ambient-N and reduced-N conditions, but lower under enriched-N conditions). A significant interaction between NUT and YEAR on the cover of *P. virgatum* ($F_{(\text{CS})16,330} = 4.18; P < 0.001$) resulted from higher cover in N-enriched soil relative to the ambient-N or reduced-N soil in many years, but differences were not consistent among years, and there was no difference in the cover of this species among the nutrient treatments in 2012 (Appendix S3).

There was a clear temporal pattern of community change over time in both the MAXHET and CON treatments (Fig. 6). Whole-plots were primarily separated by year in the ordination up until the most recent samples, when community composition stabilized. We found no differences in community composition between MAXHET and CON plots at the whole-plot scale (PERMANOVA: $P > 0.05$ in all cases; Appendix S4). Significant differences in community composition at the subplot scale between enriched and ambient-N treatments occurred in all years except 2009 (PERMANOVA; Appendix S5). The NUT effect at the subplot scale was driven by different species over time (Appendix S6). Initially, differences between treatments primarily resulted from much higher cover of *P. virgatum* in response to N addition compared to ambi-

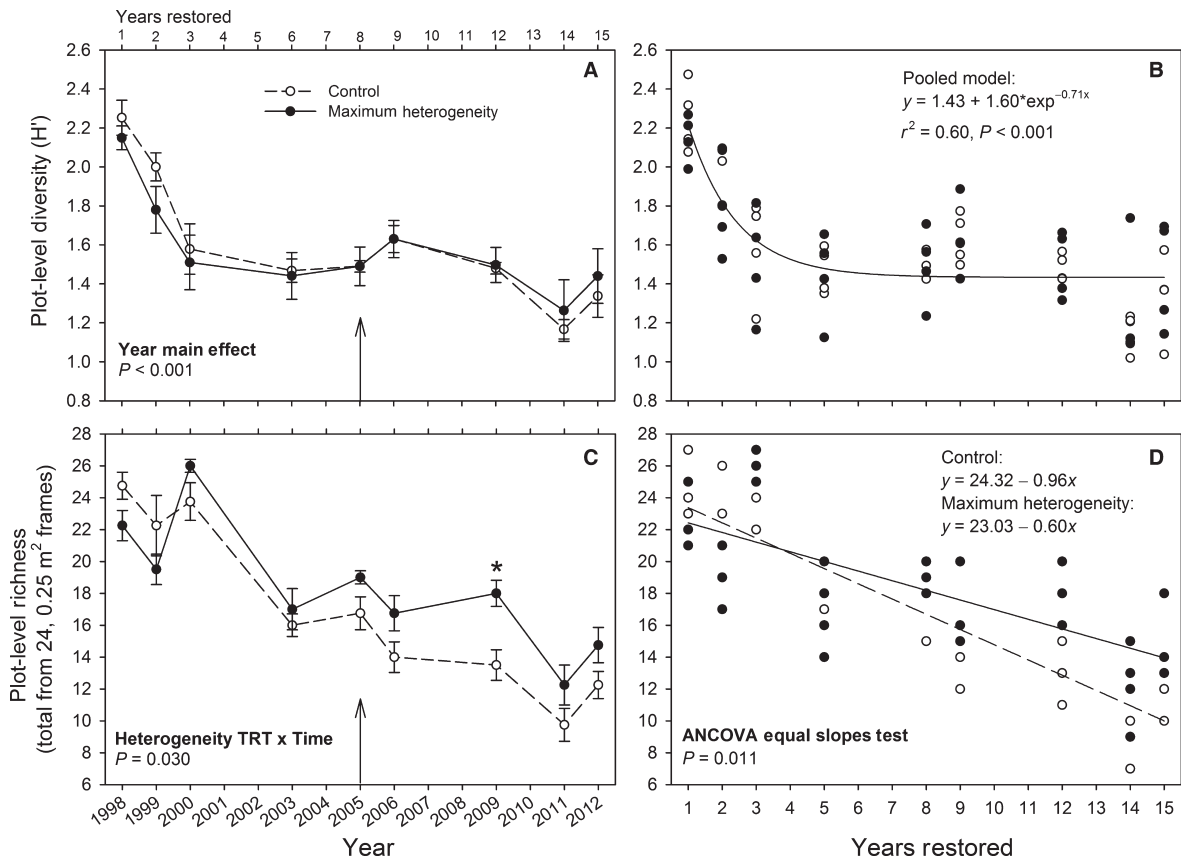


FIG. 3. Change in plant diversity and richness during 15 yr of restoration in the control and maximum heterogeneity whole-plot treatments. (A) Average (\pm SE) plot-level Shannon's diversity (H') was calculated from the average maximum cover of all species in 12 subplots; arrow indicates propagule addition. (B) Because there were no differences in H' between the heterogeneity treatments in any year, all plots were used to model change in diversity over time; data were best described by an exponential decay model. (C) Average (\pm SE) plot-level richness calculated from all species recorded in the two 0.25-m² frames per subplot; asterisk indicates significant difference between the whole-plot heterogeneity treatments within a year ($\alpha = 0.025$). (D) Due to differences in plot-level richness between the heterogeneity treatments, temporal change was modeled separately for each treatment. Linear models were fit to the data in each treatment, and the slopes were compared using analysis of covariance (ANCOVA).

ent N subplots. Over time, differences among treatments resulted from differences in the abundance of *A. gerardii* among treatments, and higher abundance of a tall statured forb, *Salvia azurea*, in the N-enriched subplots compared to ambient N subplots. Despite these species differences, subplot-level community composition exhibited strong convergence over time (Appendix S7).

DISCUSSION

Restoring native plant communities in degraded environments involves steering community assembly processes (Hobbs et al. 2004). Abiotic conditions and biotic interactions act as environmental sieves to reduce richness in the local species pool (species that can arrive

TABLE 1. Average (\pm SE) Shannon's diversity and percent cover of *Andropogon gerardii* in response to the soil nutrient and depth manipulations over all years.

	Soil depth	Soil nutrient treatment		
		Reduced-N	Ambient-N	Enriched-N
Diversity (H')	Deep	1.22 \pm 0.08 ^{ab}	1.12 \pm 0.11 ^a	1.16 \pm 0.08 ^a
	Shallow	1.32 \pm 0.05 ^{ab}	1.39 \pm 0.09 ^b	1.18 \pm 0.04 ^a
<i>A. gerardii</i> cover (%)	Deep	32.2 \pm 4.2 ^{ab}	37.7 \pm 5.7 ^a	20.2 \pm 1.9 ^d
	Shallow	25.9 \pm 2.5 ^{bc}	27.4 \pm 2.0 ^{bc}	24.7 \pm 2.3 ^{cd}

Notes: Means accompanied by the same letter were not significantly different ($\alpha = 0.05$). Superscripts indicate significant differences.

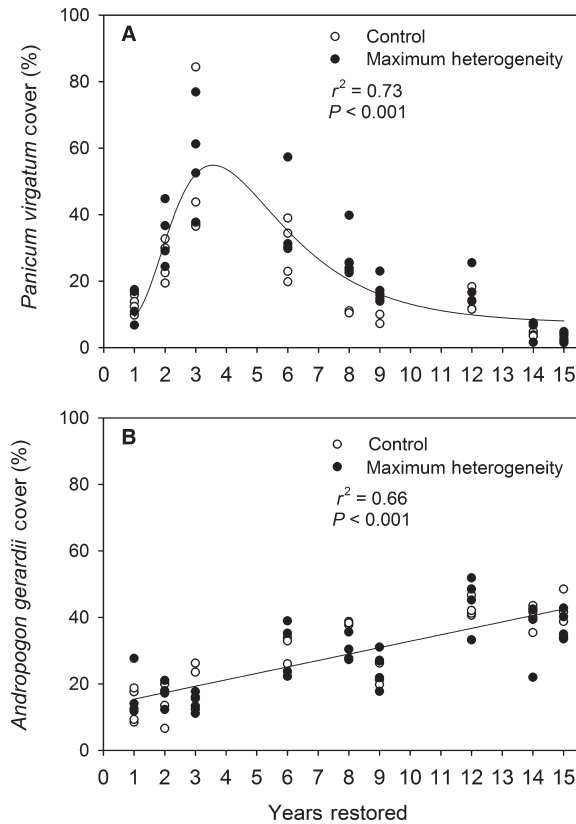


FIG. 4. Temporal changes in the percent cover of two dominant species during the initial 15 yr of restoration. Average percent cover of (A) *Panicum virgatum* and (B) *Andropogon gerardii* in each whole-plot did not differ among heterogeneity treatments. Temporal change in the cover of *P. virgatum* was best described by a log-normal peak equation; cover of *A. gerardii* was best described by a simple linear regression.

and coexist) and govern local community composition in an area (Zobel 1997). Strong filtering has the potential to alter species composition compared to undisturbed extant or pre-disturbance conditions (Howe 1999, Maina and Howe 2000). Diversity and composition may also be constrained by arrival of propagules of species that can exploit the availability and dimensionality of niches (Harpole and Tilman 2007). Thus, restoring biodiversity through ecological restoration may require manipulating the environment to enhance resource heterogeneity and promote niche space, as well as overcoming dispersal limitations through addition of propagules (Hulvey and Aigner 2014).

At the onset of this experiment, we supplied propagules to override dispersal limitation and manipulated resources known to influence plant diversity in tallgrass prairie (Gibson and Hulbert 1987, Clark and Tilman 2008, Dickson and Foster 2011) to test whether environmental heterogeneity can promote species coexistence during community assembly. Our results do not provide strong support for the “environmental heterogeneity hypothesis,” nor do they suggest it is an important deterministic influence on species diversity and community

assembly in this restored tallgrass prairie. Plant diversity was not higher and community composition was not different under more heterogeneous soil conditions. Despite the positive relationship between plant species diversity and environmental heterogeneity common in observational studies (correlation in the environment), lack of a treatment effect is often reported from experimental manipulations of heterogeneity across a variety of plant community types (Lundholm 2009, Eilts et al. 2011, Stromberg et al. 2011, Holl et al. 2013) with only two recent exceptions (Richardson et al. 2012, Williams and Houseman 2014). The primary mechanism ascribed to the lack of effect of heterogeneity on plant diversity in manipulated environments is a developing mismatch between the scale of treatment relative to plant size (Lundholm 2009, Eilts et al. 2011), which can become exacerbated as perennial species increase in size over time. It is difficult to ascertain the scale of treatment relative to plant size in the studies that documented a significant effect of manipulated heterogeneity on richness (Richardson et al. 2012, Williams and Houseman 2014). Both studies, however, were conducted during the first 2 years of community assembly, when the treatment:plant size ratio would be largest in communities developing from seed, and at a time when community assembly is likely governed more by stochastic than deterministic processes. The lack of strong support for environmental heterogeneity in promoting plant diversity appears to be emerging as general phenomenon when heterogeneity is experimentally manipulated. This suggests that either our knowledge of all resources influencing plant diversity and dominance in many communities is incomplete, plants induce much of the heterogeneity in soil to result in positive correlations between diversity and soil heterogeneity, or dispersal limitation constrains the potential for heterogeneity to promote diversity.

The decline in diversity over time coupled with high similarity and low dispersion of species between the contrasting heterogeneity treatments in the 15 yr community

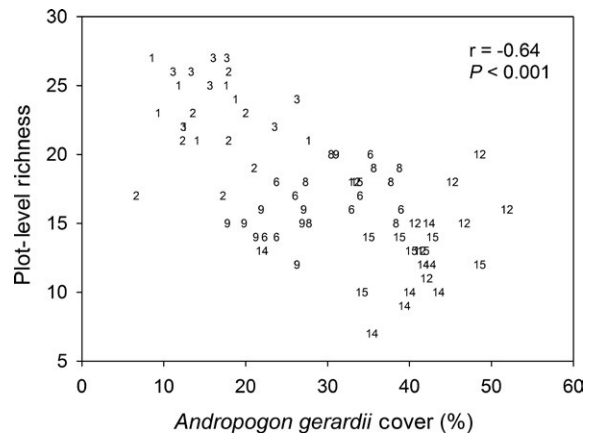


FIG. 5. Correlation between percent cover of *Andropogon gerardii* and plot-level richness from the 8 whole-plots measured during the initial 15 yr of restoration; year indicated by the symbol.

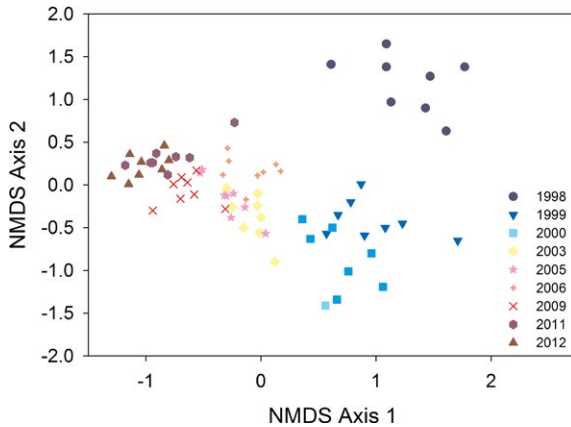


FIG. 6. Change in whole-plot community composition from 1998 (year 1) to 2012 (year 15). Control and maximum heterogeneity treatments are not identified in each year because no significant differences in community composition occurred (PERMANOVA, Appendix S4).

“end states” of this study suggest strong species sorting, which we attributed to strong deterministic processes including biotic interactions, disturbance, and dispersal filters. Two species dominated the restored communities in this experiment at different times: *Panicum virgatum* and *Andropogon gerardii*. Both species are high-statured, C_4 grasses that reproduce mostly asexually through tillering (Dalgleish and Hartnett 2009, Ott and Hartnett 2011). Tall clonal plants reduce the scale of treatment to plant size (Eilts et al. 2011), especially as the root system size and foraging footprint increase (Hutchings et al. 2003, Reynolds et al. 2007). We hypothesize that the ratio of the scale of treatment to plant size decreased over time due to the slow and steady increase in the cover of *A. gerardii*, with a strong capacity to exclude other species (Dickson et al. 2014) and reduce biotic heterogeneity that can facilitate species coexistence (Porensky et al. 2012). The decline in cover of *P. virgatum* after 3–5 yr since sowing most likely resulted from competition with *A. gerardii* for N. This result would be predicted from *A. gerardii*'s lower requirement (R^*) for soil nitrate relative to *P. virgatum* (Dybzinski and Tilman 2007) and progressive N limitation accruing in this experiment over time (Baer et al. 2003, Baer and Blair 2008). Interestingly, dominance of *P. virgatum* was not maintained over time even in subplots with supplemental N, which could have resulted from negative feedback (Hawkes et al. 2013), inability to compete effectively for other resources in more mature communities, or both.

Disturbance can act as a community assembly filter either indirectly or outright (White and Jentsch 2004). Annual spring burning is known to promote the vigor of C_4 grasses (Copeland et al. 2002), favor their dominance, and lower diversity and community heterogeneity in tall-grass prairie relative to infrequently burned prairie or to prairie where grazers modulate the effect of annual fire on diversity (Collins 1992, Collins et al. 1998, Collins and Calabrese 2012). Warm-season grass cover is also higher

and species richness lower under an annual spring (May) burn regime relative to summer (July) or no burn regimes and in restored prairie (Towne and Kemp 2008, Howe 2011). In addition to inhibiting C_4 grass growth, accumulation of litter acts as a seed trap in grassland and its removal through burning could further limit the role of dispersal in community assembly (Ruprecht and Szabo 2012, Ruprecht et al. 2013) and reduce local species pool for colonization. Alternatively, litter can create light limitation for emerging seedlings, but the effect of litter on plant populations is species dependent, which can affect community structure (Facelli and Pickett 1991).

Community divergence and development of alternative stable states are a function of dispersal, namely the frequency and density at which species are introduced (Gerla and Mooij 2014). Propagule supply can limit diversification of grasslands (Pywell et al. 2002, Long et al. 2014) and interact with local factors such as nutrients (Foster et al. 2011) and disturbance (Myers and Harms 2009) filters. Higher richness in the maximum heterogeneity treatments following the second propagule addition suggests that environmental heterogeneity interacts with the local species pool. However, colonization of a few more species that contributed little to total cover resulted in no effect on diversity. The richness response to propagule supply suggests that environmental heterogeneity created conditions for germination of new species, possibly with different niche requirements than those species in the surrounding community (Grubb 1977). Limited growth of new species signifies the importance of biotic interactions (i.e., competition) in the community assembly process. Community convergence over time resulted from the low frequency at which new species were introduced, coupled with the dominance of tall clonal species. Declining diversity coincident with increasing C_4 grass dominance is a very common phenomenon during prairie development in the absence of repeated propagule supply (Kindscher and Tieszen 1998, Sluis 2002, Camill et al. 2004, Martin et al. 2005, McLachlan and Knispel 2005, Heslinga and Grese 2010, Gibson et al. 2013). This pattern was also documented in restored prairies that received repeated over seeding, and was attributed to increasing budbank of C_4 grasses over time (Willand et al. 2013). Experimentally reducing cover of *A. gerardii* increased richness and diversity in prairie restored adjacent to this heterogeneity experiment and under ambient N conditions (McCain et al. 2010). This study demonstrates that the response of *A. gerardii* and diversity were not inversely related under altered soil depth and nutrient conditions.

The long-term effects of soil nutrient manipulations on plant diversity and composition in grassland are mixed, but diversification occurs when nutrients lessen dominance and promote evenness (Wilson et al. 1996). Changing soil nutrient availability at the onset of grassland development has been shown to alter species composition (Blumenthal et al. 2003, Baer et al. 2004), but greater community differentiation over time may require

priority effects imposed by initially different composition in the nutrient treatments (James et al. 2011) or an augmented propagule supply (Foster et al. 2011). Similar to Martin and Wilsey (2012), we did not document strong priority effects from initially different establishment in the soil nutrient treatments, particularly in the reduced-N treatment where non-native species cover was lower and similarity of the community to natural prairie was higher than in the ambient and enriched-N soil (Baer et al. 2004). Contrary to the initial years of community establishment (Baer et al. 2003), the effect of nutrients on diversity depended on soil depth (no effect in deep soil). Similar to natural prairie, diversity was higher in ambient-N soil relative to enriched-N soil, but only in the shallow soil treatment. Dornbush and Wilsey (2010) documented higher richness in deep relative to shallow soil in an area of tallgrass prairie with different climatic and edaphic conditions, which resulted from the shallow soil containing a subset of the species pool found in the deep soil. We found no effect of soil depth on species richness. Soil depth influenced diversity, but only under ambient N conditions. Consistent with never-cultivated prairie (Gibson and Hulbert 1987, Collins and Calabrese 2012), diversity was higher in shallow relative to deep soil and this response corresponded with the opposite response of *A. gerardii* cover. Nutrient addition, however, interrupts the inverse relationship between cover of *A. gerardii* and diversity and may impose some other limitation to diversity.

Conclusions and implications

Understanding factors that constrain persistence of species in communities is at the heart of community assembly theory (Diamond 1975, Keddy 1992, Lockwood et al. 1997, Belyea and Lancaster 1999, Weiher and Keddy 1999) and relevant to restoring biodiversity in degraded environments (Temperton et al. 2004). We hypothesized that local deterministic processes would influence community assembly (Longworth et al. 2014, Ray and Collinge 2014, van Leeuwen et al. 2014), specifically that greater environmental heterogeneity would promote species richness and diversity. Like many other studies, we found no strong effect of environmental heterogeneity on plant species diversity. However, we noted a small but significant positive effect of heterogeneity on species richness following a second propagule addition midway through the 15 yr study. This suggests that the influence of environmental heterogeneity on species coexistence interacts with limited dispersal of new species that can exploit niches that may become available during community assembly as a result of species sorting (McCook 1994), plant induced heterogeneity (Gross et al. 1995), or development of plant–soil feedback (Brandt et al. 2013).

The continuous increase in a tall, clonal species represents the strongest filter in the community assembly process that constrains species coexistence by excluding shorter statured and nonclonal species (Eilts et al. 2011, Dickson et al. 2014). Reducing dominance of *A. gerar-*

dii has the potential to increase diversity in a manner similar to never-cultivated prairie. Grazing by native and domestic ungulates has been shown to have a significant impact on plant community structure in mesic prairie (Collins 1987, Collins et al. 1998, Collins and Smith 2006) and seedling emergence in restored prairie (Wilsey and Martin 2015). Light to moderate grazing reduces the dominance of the highly competitive clonal grasses, which increases light availability and promotes coexistence of grasses and forbs (e.g., Hautier et al. 2009). Indeed, plant species richness is lower and coincides with a greater abundance of clonal grasses in ungrazed prairie relative to grazed prairie (Koerner et al. 2014). Grazing, in combination with repeated seed addition, may be needed to reduce dispersal limitation and promote diversity during grassland restoration (Martin and Wilsey 2006). Thus, steering community assembly to achieve high biodiversity likely depends more on manipulating processes that reduce dominance by clonal grasses and eliminating dispersal filters that constrain the arrival of new species than altering environmental heterogeneity.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1890/15-0888.1/supinfo>

DATA AVAILABILITY

Data associated with this paper have been deposited in Dryad: <http://dx.doi.org/10.5061/dryad.c2v92>