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Seed availability constrains plant species sorting along a soil fertility gradient

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Summary

1. Spatial variation in species composition within and among communities may be caused by deterministic, niche-based species sorting in response to underlying environmental heterogeneity as well as by stochastic factors such as dispersal limitation and variable species pools. An important goal in ecology is to reconcile deterministic and stochastic perspectives of community assembly and to assess the contribution of each class of processes to community dynamics and structure.

2. We present an 8-year field experiment of grassland secondary succession that documents plant community differentiation in response to an experimental gradient of nitrogen (N) fertilization, factorially crossed with a manipulation of the available species pool achieved using a multi-species seed sowing treatment. We evaluate the hypothesis, adapted from meta-community theory, that seed availability limits the contribution of niche-based, species sorting to patterns of community variation along an environmental gradient.

3. The magnitude of species sorting and community differentiation observed in response to N fertilization (measured as N effect size on multivariate community composition) became progressively more distinct and more statistically significant over time in experimental plots as succession proceeded. However, this response was significantly more pronounced among plots that had been exposed to experimentally enriched propagule pools.

4. *Synthesis*. Our findings support the hypothesis that dispersal limitations and species pools can mediate the contribution of niche-based, species–environment sorting to plant community development and limit the extent to which underlying resource gradients become deterministically expressed in patterns of vegetation composition. We suggest that continued habitat destruction and fragmentation in the former prairie landscape where this study was conducted would further reduce native species pools and habitat connectivity, diminishing opportunities for species–environment sorting and compromising the capacity of these grassland systems to respond to environmental change.

Key-words: community assembly, community differentiation, determinants of plant community diversity and structure, dispersal limitation; grassland, meta-community, nitrogen gradient, secondary succession, species pool, species sorting

Introduction

Evaluating processes that generate spatial variation in species composition in ecological communities and along environmental gradients continues to be an important objective in ecology. A traditional view is that species turnover along gradients (β diversity) results from a deterministic sorting process whereby differentially adapted species reach optimal abundances at different locations along a gradient in accordance with environmental tolerances, competitive abilities and niche requirements (Whittaker 1956; Tilman 1987; Ellenberg 1988; Chase & Leibold 2003). From this perspective, abiotic filters, species interactions and trade-offs in ecological traits interact to generate close correspondence between community composition and environmental gradients.

However, it has long been recognized that stochastic factors influence community dynamics leading to patterns that emerge independent of deterministic species sorting (Zobel 1997;

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Hubbell 2001; Leibold *et al.* 2004; Cottenie 2005; Holyoak, Leibold & Holt 2005). An important task for ecologists is to reconcile stochastic and deterministic perspectives of community assembly and assess their relative significance to understanding species distributions, diversity and spatial structure (Tilman 2004; Cottenie 2005; Adler, Lambers & Levine 2007). Dispersal limitations, variable species pools and immigration history are important sources of stochasticity in communities (Zobel 1997; Hubbell 2001; Cottenie 2005) that may act to obscure the expression of species sorting and the development of community–environment relationships (del Moral, Titus & Cook 1995; Leibold *et al.* 2004; Ozinga *et al.* 2005). Indeed, a fundamental prediction of meta-community theory (Leibold & Norberg 2004; Leibold *et al.* 2004; Cottenie 2005; Holyoak, Leibold & Holt 2005) is that limitations on dispersal can influence the strength of species sorting and constrain the degree to which environmental gradients become expressed as community pattern. Here, species sorting and the correspondence of community structure and environment should be most strongly expressed in systems with high levels of environmental contrast among localities (high spatial niche dimensionality), that are exposed to functionally rich species pools (high species pool dimensionality; Questad & Foster 2008) and where habitat connectivity and dispersal are sufficient to assure that suitable species are available to colonize, compete and sort into preferred sites (Leibold & Norberg 2004). An implication of this perspective is that anthropogenic factors (e.g. fragmentation) that diminish connectivity, dispersal and species pools will change the balance of stochastic and deterministic forces governing community assembly.

The response of communities to gradients in soil fertility and productivity continues to be an important area for research in ecology (Al-Mufti *et al.* 1977; Grime 1979; Huston 1979; Tilman & Pacala 1993; Harpole & Tilman 2006). Community differentiation along fertility gradients and changes in community structure in response to nutrient enrichment has been widely reported, indicating the importance of resource-based sorting (Tilman 1987; DiTommaso & Aarssen 1989; Inouye & Tilman 1995; Harpole & Tilman 2006). Mechanistic competition models predict that the outcome of competition in a locality will be determined by resource supply (Tilman 1982; Grover 1997; Chase & Leibold 2003) and that sites along a fertility gradient will sort accordingly into local assemblages with distinct compositions (Inouye & Tilman 1988; Harpole & Tilman 2006). An implicit assumption of these models is that species with suitable traits are present to compete in their optimal sites. This assumption may not apply in many systems. In fragmented landscapes with low connectivity, diminished species pools and acute dispersal limitation, we may predict that competitive sorting will be weak, that spatial effects, historical influences and dispersal stochasticity will predominate, and that relationships between resources and community composition will be diffuse.

The importance of species sorting at a given point in time may also depend on disturbance history and successional status of the landscape in which communities are embedded. The notion that early successional communities are dispersal-limited and stochastic has a long history in ecology (Gleason 1939; Talling 1951; Margalef 1963; McCune & Allen 1985; del Moral, Titus & Cook 1995). From this perspective, communities are thought to increase in organization and predictability over time as dispersal constraints are gradually overcome and as species accumulate (Odum 1969; del Moral, Titus & Cook 1995). It follows that species sorting along resource gradients and community–environment affinities will be weak early in succession, but become increasingly attuned as succession proceeds.

Here we present results from a long-term field experiment of grassland secondary succession and community assembly conducted in an abandoned agricultural field in Kansas, USA. The overarching goal of the experiment is to evaluate community and ecosystem responses to fertilization and to a manipulation of plant propagule availability, achieved by imposing a multi-species seed sowing treatment to half of the experimental units. In this report we focus specifically on the role of seed availability and species pools in modulating species sorting and regulating the extent to which gradients of fertility become expressed as gradients of community composition.

We hypothesized that species sorting along the nitrogen (N) gradient would be contingent upon the availability of species and upon successional age of the community. We expected that communities undergoing succession in the presence of an experimentally enhanced species pool would exhibit significantly greater community differentiation along the N fertilization gradient than communities undergoing succession in the presence of a limited species pool. Secondarily, we expected that species sorting and community differentiation in response to N fertilization would become more pronounced and statistically significant over time.

Materials and methods

STUDY SITE AND EXPERIMENTAL PROCEDURE

This experiment was conducted in an abandoned agricultural field in eastern Kansas, USA, at the Nelson Environmental Studies Area which is part of the University of Kansas Field Station. The field site has a history of tillage, but prior to our study had been abandoned from hay production for a number of years and was dominated by introduced cool-season grasses (*Bromus inermis*, *Lolium arundinaceum*) just prior to the start of the study. In preparation for the experiment a rectangular area *c.* 70 × 120 m in size was sprayed with glyphosate herbicide in summer 2000, ploughed and then disked multiple times in March–April 2001.

In mid April 2001 we established six rectangular experimental blocks at the site (see Fig. S1 in Supporting Information). In each block we established two 10 × 26 m experimental main plots, each containing eight 4 × 5 m subplots (yielding a total of 96 subplots in the entire experiment). Blocks are separated by 12-m buffer strips, main plots within blocks are separated by 10-m buffer strips, and subplots within main plots are separated by 2-m buffer strips. To the entire array of 96 subplots we applied 16 unique experimental treatment combinations ($n = 6$) that conform to a 4 × 2 × 2 factorial design in split-plot configuration. Within each main plot, two split-plot factors were crossed in a 4 × 2 configuration: N fertilization added to subplots as ammonium-nitrate at four levels (0, 4, 8 and

16 g N m^{-2} $year^{-1}$); and phosphorus (P) fertilization added to subplots as super-phosphate at two levels (0 and 8 g P m^{-2} $year^{-1}$). In each block, one of the two main plots was randomly selected to receive multi-species seed additions (sowing treatment, main plot factor) to experimentally enhance the availability of species to subplots early in succession.

Nitrogen and P fertilizers were added to subplots annually starting in 2002, half applied in either April or May and half applied in June each year. Fertilizer was not added in 2001 because vegetative cover at the site was too sparse in that first year to absorb nutrients and to prevent losses via runoff and leaching. To accomplish sowing, seeds of 53 native and naturalized plant species were sown by hand into the appropriate subplots in April of 2002 and 2003 (see Table S1). All sown species are members of the regional and local landscape pool, chosen to represent a range of life histories, functional groups and habitat affinities. Seeds were sown at rates ranging from 100 to 320 seeds m^{-2} $year^{-1}$, depending on availability. Seeding rates were relatively high because, rather than attempting to mimic natural seed rain, our objective was to minimize chances that sown species would be absent from sown subplots due to seed limitation. In the first vegetation survey in 2001, conducted before sowing, none of the sown species were initially present in any of the subplots. However, all species had populations present in nearby old-fields or prairie remnants located within 1 km of the experimental site. During the course of this study, all plots in the experiment were subject to prescribed burns conducted in the month of April in 2005 and 2008.

DATA COLLECTION AND ANALYSES

We conducted percentage cover surveys of vegetation during mid-growing season (late June–early July). This was done by taking ocular estimates of percentage cover for each species rooted within two permanently marked 1 × 1 m sampling quadrats in each subplot. Composition for a subplot was determined by combining data from each quadrat, constructing a species list for the subplot and then calculating mean cover of each species across the two quadrats.

To visualize variation in species composition among treatments and across years we used Non-Metric Multidimensional Scaling (NMDS) and Detrended Correspondence Analysis (DCA; Hill & Gauch 1980) to produce ordinations using PC-ORD (McCune & Mefford 1999). Because ordinations produced by both methods were very similar, we report only DCA in the interest of brevity and because this method is more conceptually grounded as a method of gradient analysis than NMDS, with axes explicitly interpretable in terms of species turnover along environmental gradients (Hill & Gauch 1980). The percentage of variation in the plant data set explained by each DCA axis was estimated by calculating after-the-fact coefficients of determination relating relative Euclidean distance in unreduced species space and Euclidean distance in ordination space (McCune & Mefford 1999). In the DCA ordinations, treatments are represented in ordination space by treatment mean values of the ordination scores calculated for each year separately.

To formally test the hypothesis that species sorting and community differentiation in response to N fertilization is dependent on seed availability and successional age we used Permutational Multivariate Analysis of Variance (PERMANOVA) tailored for a blocked, split-plot design (Anderson 2001; McArdle & Anderson 2001). PERMANOVA provides a nonparametric MANOVA that utilizes permutation methods to evaluate differences between treatment groups (levels of seed addition and N fertilization in our case) on the basis of any multivariate distance measure. PERMANOVA calculates multivariate distances between each pair of experimental units to generate a distance matrix. An *F*-statistic is then calculated as dictated by the particular experimental design. To test for statistical significance among groups, the calculated *F*-statistic is compared to a null distribution of *F*-values generated by randomly reshuffling the data many times and then recalculating a new *F*-value with each permutation. We conducted PERMANOVA for each year of the study separately using Bray–Curtis distances. Species cover data were standardized to proportional cover prior to analysis and data were permuted 10 000 times for each analysis. Preliminary analyses showed no effects of P on composition in any year, consistent with earlier evaluations of the data that showed little influence of P fertilization on individual species abundances and measures of species diversity. As a result, all analyses presented in this paper reflect data pooled across P levels and focus on effects of sowing and N fertilization only. In these analyses a significant N effect is interpreted as evidence of deterministic species sorting and community differentiation along the N gradient.

Because the *F*-value from PERMANOVA expresses the variance in composition among different levels of a treatment relative to residual variation, the value can be used a measure of treatment effect magnitude. To examine how the effects of seed sowing and N fertilization on species composition varied in magnitude over time, we plotted the *F*-values from PERMANOVA against year for the sowing main effects, the N fertilization main effects and for the interaction terms. We then used simple linear regression to assess relationships. Because we found significant interactions between sowing and N fertilization, we also conducted PERMANOVA to assess effects of N fertilization on species composition for the non-sown and sown subplots separately and then plotted the resulting *F*-values against year as described above.

PERMANOVA was also performed using 2008 data to examine effects of seed sowing and N fertilization on functional guild composition in the last year of the study. Functional guilds used in the analysis grouped species as: Annual Graminoids; Annual Forbs; Biennials; C_3 Perennial Graminoids; C_4 Perennial Graminoids; Perennial Forbs; Perennial Legumes; Woody Plants. PERMANOVA was performed using the PERMANOVA+ for PRIMER-E statistical package – Version 6 (Anderson, Gorley & Clarke 2008).

Using data from the last year of the study (2008) we used Indicator Species Analysis (ISA; Dufrene & Legendre 1997) to identify the individual species and functional guilds underlying compositional differences that had emerged by the last year of the study in response to N fertilization. For each species or guild, ISA assigns an indicator value (IV) for each N treatment that can range from 0 to 100% of perfect indication. An IV is calculated as the product of species relative frequency (the proportion of sample units at a given N level that contain the given species) and species relative abundance (average cover of a given species at a given N level expressed as a proportion of the species' mean cover summed across all N levels), expressed as a percentage. Statistical significance for the observed maximum indicator value with respect to N level was conducted for each species or functional guild using a Monte Carlo test with 5000 iterations. ISA was conducted for non-sown and sown subplots separately to identify significant indicators of N fertilization under ambient and enhanced seed pool conditions. ISA was conducted using PC-ORD (McCune & Mefford 1999).

Results

The first two axes generated by Detrended Correspondence Analysis (DCA) performed on the entire data set (all subplots in all years) explained 74% of the total variation in species composition (56% and 18% for DCA axis 1 and DCA axis 2,

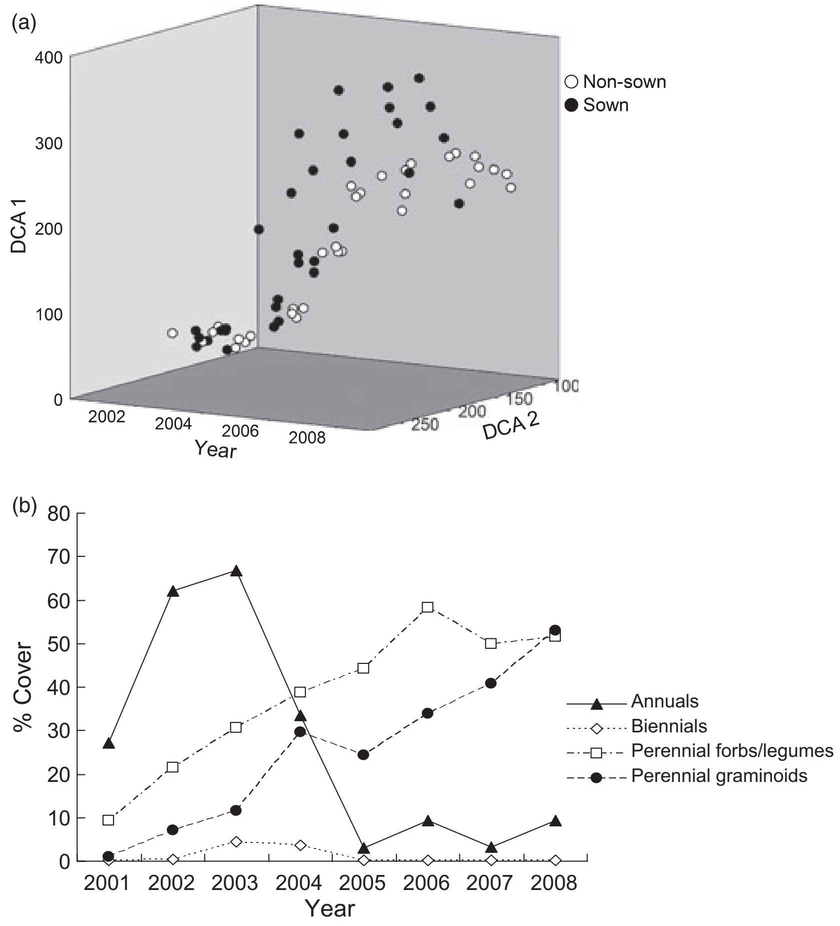

Fig. 1. (a) Detrended Correspondence Analysis (DCA) ordination scores plotted against year of succession and shaded by sowing treatment. Each point represents the mean DCA axis 1 and DCA axis 2 scores for each nitrogen (N) treatment in each year. DCA axis 1 and 2 explain 56% and 18% of the total variance in species composition, respectively. (b) Successional change in the abundance of dominant functional guilds (mean % cover calculated across all treatments).

respectively). The resulting ordination revealed a strong signal of temporal change and a strong influence of the sowing treatment on community composition that became more evident over time (Fig. 1a). Axis 1 of the ordination was significantly correlated with year in both the non-sown subplots ($r = 0.85$, $P < 0.0001$) and the sown subplots ($r = 0.87$, $P < 0.0001$). Axis 2 was also significantly correlated with year, although the relationships were weaker (non-sown subplots: $r = -0.21$, $P < 0.001$; sown subplots: $r = 0.15$, $P < 0.001$). Difference between non-sown and sown plots in the sign of the correlation between axis 2 and year indicate some degree of community divergence over time between the sowing treatments. Correlations of the DCA axes with year reflect a typical pattern of old-field succession (Fig. 1b) progressing from initial dominance by annual plants in 2001 to replacement by perennials by 2008. Axis 1 was also correlated with N fertilization level, but only in sown subplots (non-sown subplots: $r = -0.07$, $P > 0.05$; sown subplots: $r = -0.23$, $P < 0.001$), consistent with our prediction that community differentiation along the N fertilization gradient would be more evident in sown subplots.

Using PERMANOVA to evaluate community responses more formally we found that species composition varied significantly with the main effects of sowing and N fertilization in each of the last 4 years of the study (Fig. 2a,b). The *F*-values from PERMANOVA for the sowing and N main effects increased significantly over time (Fig. 2a,b) indicating an increased influence of sowing on species composition and increased correspondence between the plant community and the experimental N gradient over time as predicted.

The sowing × N fertilization interaction was also found to be significant for the last 4 years of the study and increased significantly in magnitude over time (Fig. 2c), indicating that the effects of N fertilization on species composition depended on sowing level and that the extent of this dependence increased as succession proceeded. When examining species composition in non-sown subplots only, the effect of N fertilization was insignificant in all years except the last one (2008; Fig. 2d). However, in sown subplots the effect of N was highly significant in each of the last 4 years of the study (2005–2008; Fig. 2d), indicating a much greater strength of association between community composition and the N gradient in sown than non-sown subplots in later years of the study. *F*-values for the N effect increased significantly over time in both the non-sown and sown subplots (Fig. 2d), but as indicated by a homogeneity of slopes test, the *F*-values for sown subplots increased with time more rapidly (sow × year interaction: $F_{2,13} = 16.25$; $P < 0.0001$).

The stronger influence of N enrichment on community composition in sown than non-sown subplots over time is evident visually in the partitioned DCA ordination diagrams of Fig. 3. In non-sown subplots (Fig. 3a), the visual correspondence of the community to the N fertilization gradient is relatively

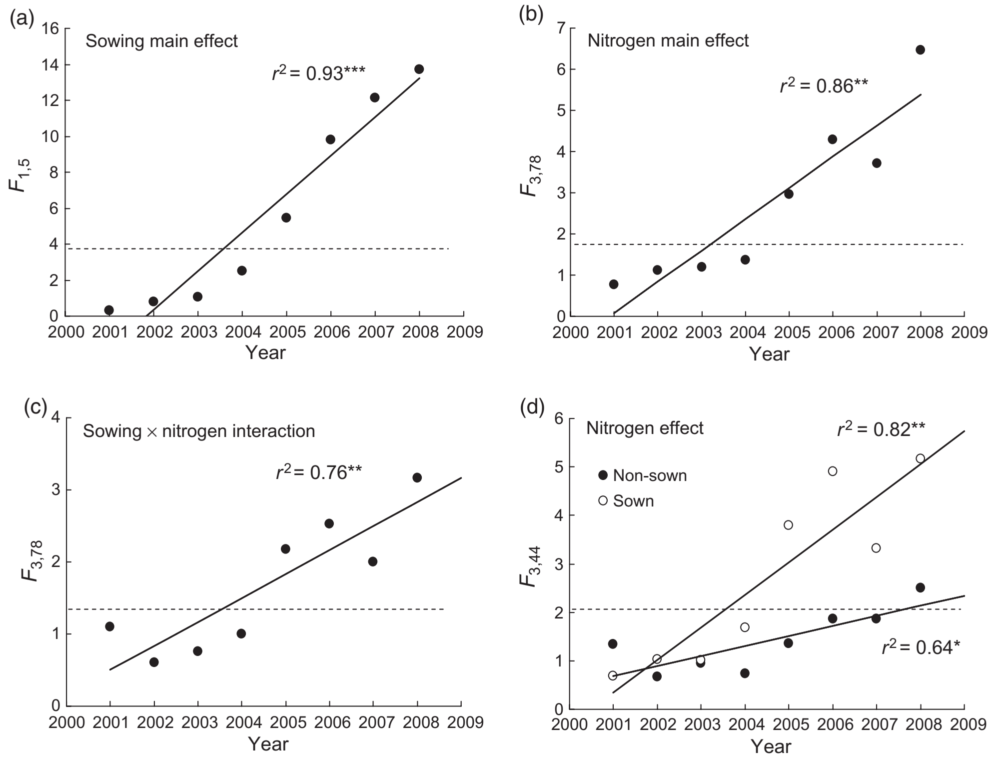

Fig. 2. PERMANOVA results evaluating effects of sowing and nitrogen (N) fertilization on species composition in each year of the study: (a) *F*-values for the sowing main effect on species composition (pooled across N fertilization levels); (b) *F*-values for the N fertilization main effect on species composition (pooled across sowing levels); (c) *F*-values for the sowing × N fertilization interaction; (d) *F*-values for the fertilization effect on species composition, calculated for non-sown and sown treatments separately. The dashed horizontal line in each pane represents the threshold of statistical significance: all *F*-values above this line are significant at $P < 0.05$. Significance levels for r^2 values: $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

weak. In contrast, in sown subplots (Fig. 3b), community differentiation along the N gradient is readily apparent in each of the last 4 years of the study (2005–2008) when the effects of N enrichment on community composition were found to be highly significant with PERMANOVA (Fig. 2d).

In non-sown subplots ISA found only two species (4.3% of all species recorded across all non-sown subplots) to be significant indicators of N fertilization: *Lespedeza stipulacea* (non-native annual legume) was a significant indicator of low-N subplots (0 g N; IV = 32; $P = 0.01$); *Setaria faberi* (native annual grass) was a significant indicator of high-N subplots (16 g N; IV = 29; $P = 0.039$). However, in sown subplots 14 species (16.5%) were found to be significant indicators of N fertilization. The majority of these species were sown native prairie species, eight of which reached peak abundance and were significant indicators of low-N sown subplots (0 g N). Prominent among these native sown indicator species are the perennial C_4 tall-grasses: *Andropogon gerardii* (IV = 48; $P = 0.001$), *Sorghastrum nutans* (IV = 40; $P = 0.013$) and *Schizachyrium scoparium* (IV = 35; $P = 0.02$); prairie legumes: *Lespedeza capitata* (IV = 54; $P = 0.001$), and *Amorpha canescens* (IV = 42; $P = 0.015$). Two sown prairie species were significant indicators in sown subplots of intermediate N supply: *Bouteloua curtipendula* (native C_4 grass: significant indicator of 4 g N m^{-2} year^{-1}; IV = 43; $P = 0.01$) and *Aster novae-angliae* (native forb: significant indicator of 8 g N m^{-2} year^{-1}; IV = 28; $P = 0.026$). The only individual species found to be significant indicators of the highest fertility level (16 g N m^{-2} year^{-1}) in sown subplots were three N-demanding, non-sown species that established naturally in the subplots: *Solanum carolinense* (native perennial forb; IV = 55; $P = 0.001$), *Ambrosia artemisiifolia* (native annual forb; IV = 53; $P = 0.015$) and *S. faberi* (native annual grass; IV = 27; $P = 0.026$).

To further illustrate the effects of sowing and N fertilization on the plant community we examined treatment responses at the functional guild level in the last year of the study (2008) using PERMANOVA and ISA, substituting species with functional guild designations. PERMANOVA revealed significant main effects of sowing ($F_{1,5} = 24.68$; $P < 0.01$) and N fertilization ($F_{3,78} = 12.71$; $P < 0.001$) on functional guild composition along with a significant sowing × N fertilization interaction ($F_{3,78} = 4.70$; $P < 0.001$), reflecting greater functional differentiation across the N gradient in sown than in non-sown subplots (Fig. 4).

Indicator species analysis identified the functional guilds underlying functional differentiation across the N gradient. The C_3 perennial graminoid guild was the only significant indicator of N fertilization in non-sown subplots, indicating the highest level of N fertilization (IV = 34; $P = 0.03$; Fig. 4a). In sown subplots: C_4 perennial graminoids (IV = 43; $P = 0.002$) and perennial legumes (IV = 52; $P = 0.001$),

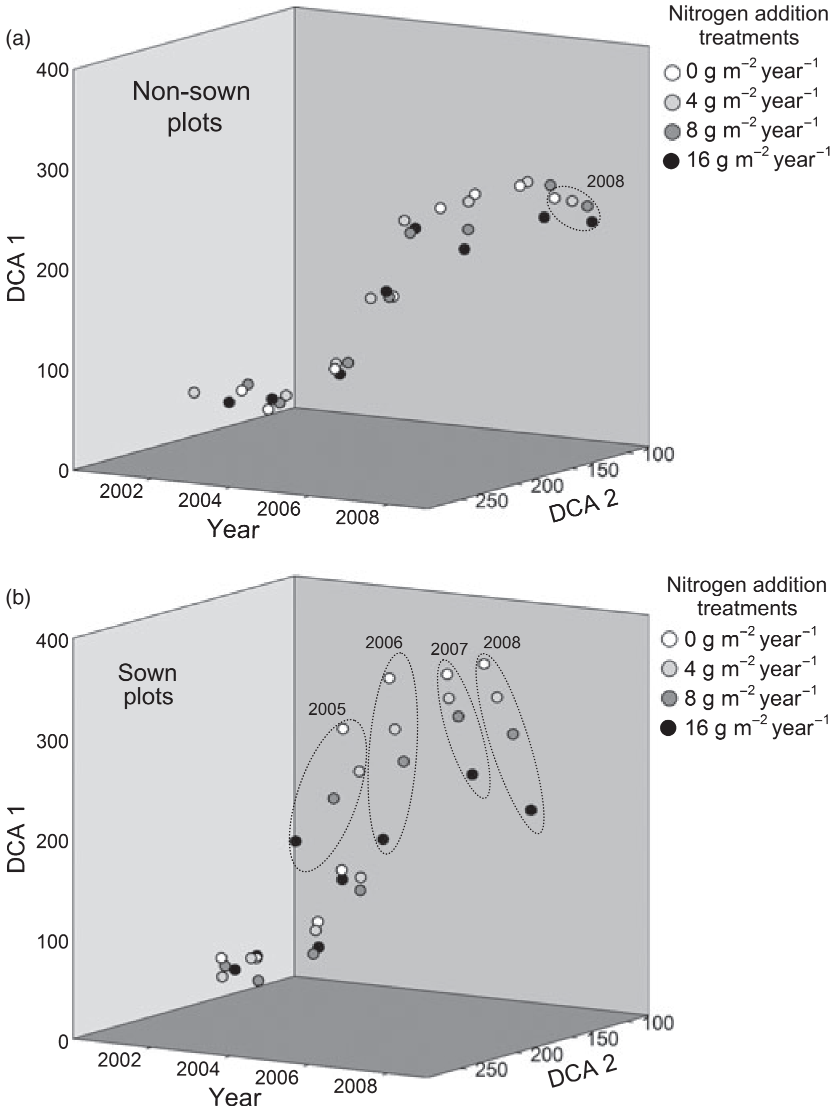

Fig. 3. The same Detrended Correspondence Analysis (DCA) ordination reported in Fig. 1, but partitioned by sowing treatment: (a) non-sown subplots; (b) sown subplots. Each point represents the mean DCA axis 1 and DCA axis 2 score for each nitrogen (N) treatment in each year. Points within an ellipse indicate a year when species composition was significantly affected by N fertilization as determined by PERMANOVA.

which were both comprised almost entirely of native sown prairie species, were significant indicators and most abundant at low N (Fig. 4b). Perennial forbs were marginally significant indicators and were most abundant at intermediate N (IV = 30; $P = 0.059$). Annual Forbs (IV = 55; $P = 0.008$) and C_3 graminoids (IV = 42; $P = 0.011$) were significant indicators and were most abundant at high N.

Discussion

Our study showed that plant community differentiation across an experimental nitrogen gradient increased over time as the community assembled and became more pronounced in subplots that received experimental multi-species seed additions. These findings are consistent with the notion that the importance of deterministic species–environment sorting to community development, and the degree to which underlying environmental gradients become expressed as spatial patterns of community composition, should be contingent upon the availability of species as influenced by factors such as habitat connectivity, dispersal constraints and size of local species pools.

In recent decades there has been an increasing effort in community ecology to understand the contributions of species pools, dispersal constraints and spatial stochastic processes to the regulation of community structure (Zobel 1997; Leibold *et al.* 2004; Cottenie 2005). A number of studies have sought to assess the relative contributions of dispersal limitation and species–environment sorting to community variation within a meta-community context (Shurin 2000; Cottenie 2005; Questad & Foster 2008). One approach to do this has been to survey variation in community composition across a range of localities and apply statistical approaches to decompose community spatial variation into environmentally determined versus purely spatial components, the latter of which is assumed to reflect the influence of dispersal limitation and species availability. Using this approach, Cottenie (2005) conducted a meta-analysis of 158 observational data sets encompassing a wide range of terrestrial and aquatic taxa. That study found that both species–environment sorting and dispersal limitation

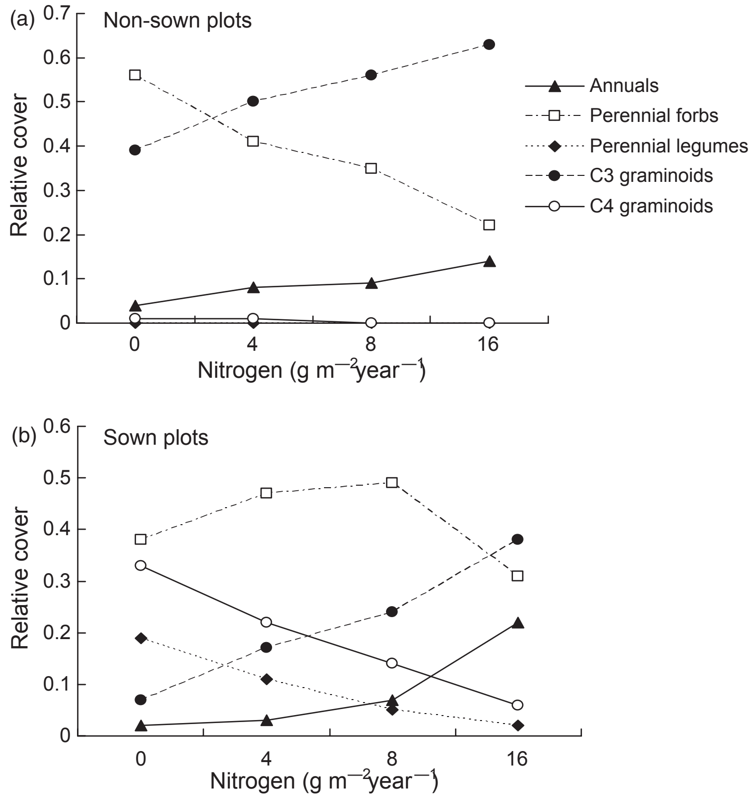

Fig. 4. Relative cover (Mean) of functional guilds at each level of nitrogen (N) fertilization in non-sown subplots (a) and sown subplots (b). Annual Forbs and Annual Graminoids were combined for simplicity in this figure. Abundances of Biennials and Woody Plants are not included in the figure due to low abundance overall.

influence patterns of community structure, but that their relative contributions depend upon the attributes of meta-communities that influence connectivity and species availability to localities (organism size and dispersal mode, spatial scale).

An alternative approach has been to directly manipulate dispersal and species availability to localities using propagule addition experiments, as was done in our study. Experimental manipulations of dispersal to investigate meta-community processes have commonly been conducted in aquatic systems and/or microcosms focused on small taxa where dispersal is easily manipulated and community dynamics can be resolved relatively quickly (Amezcua & Holyoak 2000; Shurin 2000; Cottenie & De Meester 2004; Holyoak & De Meester 2005). Several of these experiments have highlighted the role of dispersal in regulating the arrival of species to appropriate sites and in regulating the capacity of communities to track changing environmental conditions (Amezcua & Holyoak 2000; Shurin 2000; Cottenie & De Meester 2004; Leibold & Norberg 2004).

Although many community-level propagule addition studies have been conducted in plant communities (Myers & Harms 2009), our study is one of only two from plant communities that we are aware of that have used propagule additions to investigate the influence of seed availability and species pools on the expression of species–environment sorting. The other such study (Questad & Foster 2008) found that experimental seed additions to grassland increased spatial community turnover by enhancing opportunities for niche-based species sorting in response to spatio-temporal gradients of disturbance. In that experiment, seed additions enhanced species sorting and diversity to a greater extent when communities were exposed to a functionally rich propagule pool than when exposed to a functionally redundant propagule pool, indicating the importance of trait variation in the available species pool for exploiting environmental heterogeneity.

Although our findings are consistent with one key prediction of meta-community theory regarding species sorting, it is important to note that the theory also predicts that weak or diffuse sorting should occur not only in the case of limited dispersal and limited species availability, but also when dispersal rates and species availability are extremely high. Thus it is at intermediate levels of dispersal and species availability where sorting is predicted to be most expressed (Leibold & Norberg 2004). Weak sorting at high levels of dispersal occurs when mass effects that maintain many species as sink populations in suboptimal localities swamp the selective influence of the environment in structuring communities.

In our study we added large quantities of seed for 53 species over a 2-year period. This was not done to mimic natural seed arrival rates, but rather to saturate the community with propagules early in succession and greatly increase the probability that the local abundances of added species and their distributions along the N gradient would not be limited by a lack of propagules. It is under such conditions of uniformly high seed input across localities that we would most expect to observe mass effects. However, if mass effects occurred in our study they were clearly too weak to overcome the clear signal of deterministic species sorting observed in response to N fertilization in later years of the study. Indeed, our N fertilization gradient (0–16 g N m^{-2} $year^{-1}$) represents a rather severe environmental gradient that likely minimized the influence of mass effects in sown subplots by imposing a strong selective filter on the available species pool. Our findings then are consistent with the notion that the expression of species sorting along an environmental gradient depends on the degree of dispersal limitation and species availability, but may also depend on the magnitude or 'steepness' of the environmental gradient (spatial niche dimensionality) and thus the selectivity of the ecological filter. It could be argued that mass effects explain the lack of correspondence between the plant community and N fertilization observed in sown subplots early in the study, particularly in 2002 and 2003 when seeds were added. This is unlikely because: (i) we also found no correspondence between the community and N fertilization in the non-sown subplots in early years of the study and (ii) in initial years of the study most sown species were represented in subplots as small seedlings and juveniles and contributed very little to vegetative cover and thus to overall patterns of community differentiation.

In our study the greater level of species sorting and community differentiation observed along the N fertilization gradient in sown subplots largely reflects the responses of native sown prairie species that were made available early in succession. These native species, which remained absent from the non-sown subplots throughout the entire study, are members of the regional species pool and are represented by viable populations in nearby remnant prairie habitats (Foster 2001). In later years of the study, sown low fertility subplots (0 g N m^{-2}) were dominated by native C_4 tall-grasses, which are known to be efficient below-ground competitors in habitats of limited N supply (Parrish & Bazzaz 1982; Tilman & Wedin 1991), and by native prairie legumes which are favoured in N-limited habitats due to their capacity to fix N. A variety of native prairie forbs became established at all levels of N supply in sown subplots, but as a group these species were most abundant at intermediate levels of N fertility. Although a number of native prairie species were common in sown subplots at the highest levels of N fertility, these subplots were dominated by C_3 perennial graminoids and annuals. It is interesting to note that although the C_3 perennial graminoid guild was the most abundant guild at the highest level of N and was a highly significant indicator of high-N fertility, no individual C_3 perennial graminoid species emerged as a significant indicator species. This is explained by the fact that replicate high fertility subplots tended to be dominated by different species of C_3 grass (either *B. inermis*, *L. arundinaceum* or *Poa pratensis*), reflecting community convergence of functional guild composition, but community divergence of species composition at the highest level of N fertility.

The fact that native prairie species established in our experiment only when experimentally sown highlights the importance of dispersal limitation in governing succession and recovery of native vegetation in our system. The rapid rise to dominance by sown native species in the absence of N enrichment indicates that dispersal limitation is the primary barrier to restoration of native vegetation on upland N-limited soils in this region. Many native prairie species may be dispersal limited because of inherently poor dispersal ability resulting from limited allocation to seed production and/or the lack of adaptation for long-range dispersal (Tilman 1994). Dispersal limitations of native prairie species that delay arrival to sites undergoing succession may be particularly acute in human-dominated landscapes such as eastern Kansas and where habitat destruction and fragmentation have reduced habitat connectivity and diminished the availability of prairie seed sources in the landscape (Jog *et al.* 2006).

To conclude, our findings support the hypothesis that dispersal limitations and species pools mediate the contribution of niche-based species sorting to community development and thereby govern the capacity of ecological systems to attune deterministically to underlying environmental gradients. We suggest that continued habitat destruction and fragmentation in this former prairie landscape will further reduce native species pools and habitat connectivity, diminishing opportunities for species–environment sorting and compromising the capacity of these grassland systems to respond to environmental change.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Table S1. List of species sown into the experiment with information pertaining to functional guild classification, origin and subplot relative frequency within the sown main plots as a function of nitrogen fertilization level.

Figure S1. Diagram of the experimental plot array.