

LETTER

Non-neutral patterns of species abundance in grassland communities

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Abstract

Although the distribution of plant species abundance in a Minnesota grassland was consistent with neutral theory, niche but not neutral mechanisms were supported by the ability of species traits to predict species abundances in three experimental grassland communities. In particular, data from 27 species grown in monoculture showed that species differed in a trait, R^* , which is the level to which each species reduced the concentration of soil nitrate, the limiting soil nutrient and which is predicted to be inversely associated with competitive ability for nitrogen (N). In these N-limited habitats, species abundance ranks correlated with their predicted competitive ranks: low R^* species, on average dominated. These correlations were significantly different than expected for neutral theory, which assumes the exchangeability of species traits. Additionally, we found that changes in relative abundance after environmental change (N-addition or disturbance) were not neutral but also were significantly associated with R^* .

Keywords

Cedar Creek, Konza, neutral theory, niche theory, nitrogen addition, nitrogen competition, R^* , species abundance, succession, traits.

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INTRODUCTION

Niche theory and neutral theory make diametrical assumptions about the necessity and importance of species traits in determining species abundance and diversity patterns (Hubbell 2001; Chave *et al.* 2002; Clark & McLachlan 2003). Niche theory assumes that species traits represent evolutionary adaptations to the physical and biotic environment (Ackerly *et al.* 2000; Gillespie 2004), that species face unavoidable tradeoffs, and that such tradeoffs are an essential mechanism allowing interacting species to coexist and determine the relative species abundances (Tilman 1982, 1988; Chesson 2000; Rees *et al.* 2001; Chase & Leibold 2003; Reich *et al.* 2003). Neutral theory has been proposed to be a simple yet sufficient explanation for observed relative species abundance patterns (Bell 2001; Hubbell 2001). The essence of neutral models of biodiversity is that all individuals are assumed to be functionally equivalent (Bell 2001; Hubbell 2001). Hubbell (2005) has asserted that functional equivalence does not require that species be identical in their traits, just that differences in traits do not lead to any differences in their per capita demographic rates. Because niche mechanisms and neutral processes are not mutually exclusive, the

question then is whether niche mechanisms are significantly more important than a null expectation of neutrality. Here, we test whether patterns of species abundances in midwestern USA prairie communities show a niche assembly signature beyond what would be expected from neutral processes. In addition we explore whether species composition changes in response to environmental change might be consistent with neutral expectations, an issue that neutral theory currently fails to address (Chase 2005).

Many tests of neutral theory have focused on attempts to distinguish differences between the goodness-of-fit of alternative expected distributions to observed species abundance distributions. There have been recent advances leading to analytical solutions to Hubbell's neutral model (Volkov *et al.* 2003; Etienne 2005) and superior methods for model comparison that can allow better discrimination between the potential importance of dispersal vs. niche mechanisms in structuring ecological communities (Etienne & Olf 2005). However, there have been few 'strong tests' of neutral theory, for example, tests using species traits to predict the identity of dominant vs. rare species (McGill 2003; Wootton 2005). Here, we emphasize this latter approach, although as a logical point of departure we first

ask: is the distribution of species abundances in these prairies consistent with neutral theory? Second, species abundance distributions might give the impression of neutrality that may or may not be supported by stronger tests asking what is the relationship between species traits and abundance – are species equivalent? We test this using data from three experiments at Cedar Creek, Minnesota (CDR) and Konza Prairie, Kansas (KNZ), each with very different assembly histories. Third, we ask do species abundance patterns change in a neutral manner in response to environmental change? We test this using data from a: (i) nitrogen (N) gradient; and (ii) post-disturbance successional gradient.

Because soil N is the major limiting resource in these grasslands (Tilman 1984a), we use an index of competitive ability for N as the primary plant trait we consider. In particular, we use R^* (Tilman 1982) which is predicted to be inversely related to competitive ability for N, where R^* is the level to which a species reduces soil nitrate when it is grown to equilibrium in monoculture. R^* summarizes and results from the full suite of morphological and physiological traits related to acquiring, transforming, conserving and losing resources (Tilman 1988, 1990). As an integrative index of a species' competitive ability, R^* correlates with multiple species traits associated with a low N environment (Craine *et al.* 2002), and has been shown to predict species dominance in terrestrial and aquatic systems (Tilman 1982; Wedin & Tilman 1993; Grover 1997; Fox 2002). This R^* rule has been shown to be robust even when strict model assumptions are not met (Fox 2002).

We used species R^* values from 27 perennial forb and grass species planted in monoculture to test whether species abundance patterns in multiple experiments at CDR and KNZ might be consistent with neutral theory. Specifically, if species are assumed to be competitively equivalent then there should be no relationship between a species trait such as R^* and species abundance. To test this hypothesis, we used species abundance data from three grassland experiments that were similar in that they were all N-limited communities and approximately equilibrial, but they differed greatly in how they were assembled: (i) old field grasslands at CDR that have undergone *c.* 60 years of succession following their abandonment from agriculture; (ii) experimentally assembled grassland communities at CDR in which all species were established at equal initial abundances thus allowing local interactions in the absence of regional dispersal processes to determine abundances over 5 years; and (iii) experimental grasslands at KNZ that have never been ploughed and thus may represent relict fragments of the tall-grass prairie ecosystem. KNZ is environmentally similar but spatially distant and isolated from CDR.

We tested two corollary hypotheses. (i) If neutrality holds and species are essentially functionally equivalent, then

species should respond equivalently to environmental changes such as N-deposition; there should be no directional change in the relative abundance of species with increasing levels of added N. Alternatively, if changes in relative abundance over time or space are because of deterministic sorting according to species traits (Clark & McLachlan 2003) then the importance of N-competition traits will decrease as N becomes less limiting. (ii) If species are functionally equivalent with respect to their traits, then successional changes in their relative abundances following disturbance should be stochastic. For instance, in successional old fields, after abandonment from agriculture, under the assumptions of neutrality, relative abundances of colonizing species should reflect their relative abundance in the regional species pool and migration; changes thereafter should be due to stochastic drift. Alternatively, immediately after abandonment from agriculture, fields would be dominated by a mixture of annuals and perennials associated with agriculture, mostly of Eurasian origin. If there are niche differences based on the N competitive abilities of these species, with native prairie perennials having lower R^* values (Tilman & Wedin 1991), then the Eurasian species should be replaced by native prairie perennials that have low abundance in the agricultural landscape, that may be slow colonists, but are superior N competitors.

METHODS

Study sites

We analysed data from multiple experiments conducted at the CDR Long-Term Ecological Research site (LTER) in East Bethel, Minnesota and at the KNZ LTER in Manhattan, Kansas. CDR soils derive from a glacial outwash sand plain (Grigal *et al.* 1974) for which N is the primary limiting resource (Tilman 1984b). Vegetation at CDR is a mix of successional and prairie-like oldfield grasslands, savanna, woodland and wetland (Pierce 1954). KNZ soils range from upland cherty silt loam to lowland silt clay loam (Knapp *et al.* 1998). Productivity at KNZ is also limited by N (Knapp *et al.* 1998). Grassland communities at KNZ, in contrast to CDR, have never been ploughed. Grassland vegetation at both sites is characterized as tall grass prairie (Knapp *et al.* 1998).

Monoculture gardens and species traits

To quantify species in terms of an index for competitive ability, we used species-level data from monoculture plots of common prairie plant species at CDR (Craine *et al.* 2002). These experimental plots were established in 1992 (CDR LTER experiment E111). Species, typically were planted in

Table 1 Monoculture species R^* values

Genus species	Group	Path	R^* soil nitrate (N) (mg kg ⁻¹)
<i>Achillea millefolium</i>	F	3	0.320 ± 0.029 (2)
<i>Agastache foeniculum</i>	F	3	0.183 ± 0.058 (2)
<i>Agropyron repens</i>	G	3	0.387 ± 0.197 (4)
<i>Agrostis scabra</i>	G	3	0.659 ± 0.206 (2)
<i>Andropogon gerardii</i>	G	4	0.144 ± 0.045 (4)
<i>Anemone cylindrica</i>	F	3	0.213 ± 0.085 (4)
<i>Asclepias syriaca</i>	F	3	0.458 ± 0.338 (4)
<i>Asclepias tuberosa</i>	F	3	0.288 ± 0.058 (4)
<i>Asclepias verticillata</i>	F	3	0.242 ± 0.006 (2)
<i>Aster azureus</i>	F	3	0.515 ± 0.132 (2)
<i>Aster ericoides</i>	F	3	0.266 ± 0.157 (3)
<i>Bouteloua curtipendula</i>	G	4	0.220 ± 0.120 (4)
<i>Calamovilfa longifolia</i>	G	4	0.297 ± 0.154 (4)
<i>Coreopsis palmata</i>	F	3	0.161 ± 0.204 (3)
<i>Koeleria cristata</i>	G	3	0.181 ± 0.060 (4)
<i>Liatis aspera</i>	F	3	0.102 ± 0.006 (2)
<i>Panicum virgatum</i>	G	4	0.381 ± 0.157 (4)
<i>Penstemon grandiflorus</i>	F	3	0.321 ± 0.084 (4)
<i>Poa pratensis</i>	G	3	0.226 ± 0.082 (3)
<i>Potentilla arguta</i>	F	3	0.384 ± 0.217 (2)
<i>Rudbeckia serotina</i>	F	3	0.521 ± 0.082 (3)
<i>Schizachyrium scoparium</i>	G	4	0.069 ± 0.026 (4)
<i>Solidago nemoralis</i>	F	3	0.133 ± 0.074 (4)
<i>Solidago rigida</i>	F	3	0.069 ± 0.024 (4)
<i>Solidago speciosa</i>	F	3	0.115 ± 0.089 (2)
<i>Sorghastrum nutans</i>	G	4	0.179 ± 0.060 (4)
<i>Stipa spartea</i>	G	3	0.440 ± 0.057 (4)

Functional group (G, grass; F, forb), photosynthetic pathway (3, C3; 4, C4). Values given are mean ± SD.

four replicate 2.4 or 1.2 × 1.5-m plots (Craine *et al.* 2002). As our index of competitive ability, we used R^* for soil nitrate (from 0.1 M KCl extractions, measured colorimetrically in 1997, Craine *et al.* 2002). Soil nitrate values are the average of 0–10 and 10–20-cm depth samples. We used species R^* data from 27 perennial grasses and forbs. We restricted our analyses to a functionally similar set of species. We excluded legumes from analyses because R^* as measured by soil nitrate does not apply to N-fixing species that can acquire N from the atmospheric N₂ pool. Annual and woody species were excluded because they were represented by only one or two species in monoculture. Species monoculture R^* values for the 27 species used in our analyses are summarized in Table 1.

Is the distribution of species abundances in CDR prairies consistent with neutral theory?

To address this question, we used species per cent cover data that were collected in 2002 from a chronosequence of

21 oldfields at CDR (100 plots per field, CDR LTER experiment E014, Inouye *et al.* 1987). These fields varied in age (time since abandonment from agriculture) from 6 to 76 years; here we used the oldest fields (fields 32, 35 and 72, all aged ≥ 60 years), which have composition typical of native prairie. Species percentage cover was estimated in 100 1 × 0.5-m plots per field: 25 plots 1.5 m apart along four transects per field (Inouye *et al.* 1987). Total plot cover was constrained to sum to ≤ 100%. To determine the relative abundance distribution expected by neutral theory, we used the sum of the cover of each species as a proxy for counts of individuals. In particular, we summed species' cover values across all 300 0.5 × 1-m plots for each species in these three oldfields, rounded up to the nearest integer value, and used this sum in lieu of counts of individuals. Our estimated total 'population size' was 9311, equivalent to *c.* 81 'individuals' per m², which is within the range of actual plant densities observed in other grasslands (Adler 2004). While our method for estimating species abundances is not equivalent to counting actual individuals, it is consistent with the spirit of the zero sum assumption used by Hubbell (2001) in which species compete for limited and equal units of a resource such as space. This approximation tends to standardize species whose individuals might differ in size or be clonal. Again, we use this approach solely for a qualitative assessment of neutrality that can then be contrasted to results from stronger tests. We used an implementation of Volkov *et al.*'s (2003) analytic solution to the neutral model (McGill, *et al.* in press) to fit a zero sum multinomial (ZSM) distribution to our estimated species abundance distribution (Preston log₂ binning). For comparative purposes we also fit a log-normal distribution to these data, a distribution often used as a niche-based null hypothesis. For this analysis we excluded species that could not be taxonomically resolved to the species level; our results were similar with the inclusion of these species.

What is the relationship between species traits and abundance – are species equivalent?

We used data from the three oldest fields at CDR, from a biodiversity experiment at CDR, and from the prairies at KNZ to test the null hypothesis that species are assumed to be ecologically equivalent, i.e. species traits are exchangeable and therefore species' R^* 's should not predict species abundances.

CDR oldfields

We used cover data from the three oldest fields at CDR described above to determine the Spearman correlation between species' monoculture R^* and species' relative cover in each plot. We then tested the likelihood that the observed mean correlation coefficient might occur by chance by

comparing it with the 95% confidence interval from 1000 bootstrapped resamplings in which species' R^* values were exchangeable (Good 1993). We excluded plots represented by fewer than three species for insufficient degrees of freedom.

CDR species assembly experiment

We used experimentally assembled communities in which all species were simultaneously established at equal initial abundances. A gradient of species richness from one to 24 species was experimentally established in 1994 (biodiversity 1, CDR LTER experiment E123) to determine the effect of biodiversity on ecosystem properties (Tilman *et al.* 1996). For our analyses, we used the proportional biomass of each species in each of the 24 plots planted to 24 species in this experiment and determined the correlation between species rank abundance and rank R^* in each plot and comparing their mean to a bootstrapped 95% confidence interval as above.

Konza prairie

We used plant cover data, sampled in 1999, from KNZ LTER experiment PVC02 (Collins & Glenn 1991). We used data from plots across all treatments in this analysis [i.e. soil type (upland = Florence, lowland = Tulley), fire (burned every 0, 1, 2 or 4 years) and grazing (bison and control)]. We additionally assessed the effects of these treatments (Collins *et al.* 1998). Cover was measured in each of 24 watersheds and along four transects in five 10 m² quadrats per transect. We converted the reported canopy cover classes to the midpoint of their per cent cover ranges and calculated the proportional cover of each species in each plot. Where multiple sample dates existed, we used the maximum cover of each species as representative of its peak production during the growing season. As above, we tested whether the mean correlation between species rank abundance and rank R^* in each plot fell within a bootstrapped 95% confidence interval.

Do species abundance patterns change in a neutral manner in response to environmental change?

Nitrogen gradient

To examine whether observed changes in the relative abundance of species along an experimental N gradient might be consistent with neutral theory, we analysed data collected in 2002 from all four fields of the nutrient addition experiment established at CDR in 1982 (CDR LTER experiment E001, Tilman 1987). Plots received 0, 1, 2, 3.4, 5.4, 9.5, 17 or 27 g m⁻² year⁻¹ of N added as ammonium nitrate. Each of these plots also received addition of P, K, Ca, Mg, S and trace metals; there was no significant response to these additional nutrients (Tilman 1987). Aboveground

biomass was clipped, sorted to species, weighed and the proportion biomass per species was calculated.

We determined the Spearman correlation between species' monoculture R^* values and species' average relative abundances within each N-addition level. The change in R^* -abundance correlations along this N gradient was best fitted using a Monod function. We then tested the likelihood that a nonlinear relationship such as this might arise under neutral assumptions. To do this we determined the 95% confidence region for the predicted values if species traits were assumed exchangeable (1000 bootstrap resamplings of species' R^* values, at each iteration we determined the resulting R^* -abundance correlation for each N-addition level and fit the Monod function).

Successional gradient

To test whether observed changes in species' relative abundance over time might be consistent with neutral theory, we used species relative cover data from all 21 CDR oldfields described above. We determined the Spearman correlation between species' monoculture R^* and species' average relative abundances within each field. The linear relationship between field age and R^* -abundance correlations represents the observed directional change in abundance associated with our species trait index, R^* . We then tested the likelihood that such a linear change with field age might be observed if species were assumed to be equivalent. We determined the 95% confidence region for the predicted values if species traits are exchangeable (1000 bootstrap resamplings of species' R^* values, at each iteration we determined the resulting R^* -abundance correlation at each field age and their linear relationship).

RESULTS

Is the distribution of species abundances in CDR prairies consistent with neutral theory?

The species abundance distribution for CDR old fields was fit well by both the ZSM and the log-normal (Fig. 1) showing that relative abundances were qualitatively consistent with neutrality. Parameter estimates for the fitted ZSM were: fundamental biodiversity number = 14.94 and probability of immigration = 0.37. The ZSM outperformed the log-normal in terms of χ^2 (12.7, $P = 0.31$ vs. 16.3, $P = 0.13$); however, the log-normal fit had a greater R^2 (0.82 vs. 0.69).

What is the relationship between species traits and abundance – are species equivalent?

CDR oldfields

Lower R^* species had, on average, greater abundance than higher R^* species in late successional old fields (>60 years

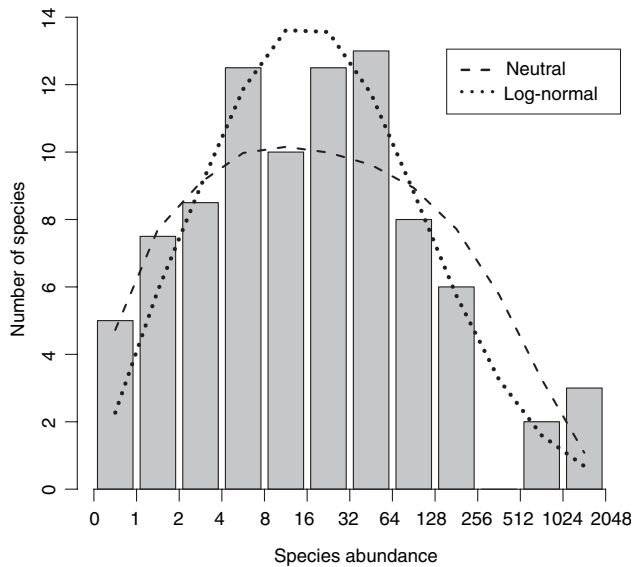


Figure 1 Both a log-normal distribution and a zero sum multinomial were fitted to the observed species abundance distribution for the three oldest Cedar Creek late successional grasslands (prairies).

old) at CDR (Fig. 2a). The mean of the correlations between species' rank abundance in each plot and their rank monoculture R^* values was significantly less than zero (Fig. 2b). While there was considerable variation in the correlations for these plots, most plots were dominated by low R^* species.

CDR species assembly experiment

We found that when we experimentally controlled for dispersal processes by planting all species at equal initial densities, species' relative abundances within communities assembled on a low N soil converged to a dominance pattern consistent with a nitrogen competitive hierarchy, as predicted by niche theory but not by neutral theory (Fig. 2c). If neutral processes predominated, then species should have remained more or less equally abundant and changes in abundance should have been stochastic. Rather, species with lower R^* values consistently dominated the 24-species plots in the biodiversity experiment; the mean correlation between species relative abundance and R^* in each plot of this experiment was significantly negative (Fig. 2d) and in fact no correlation was greater than -0.12 .

KNZ prairie

Similarly, species with lower R^* , as measured at CDR, dominated prairies at KNZ nearly 1000 km to the south (Fig. 2e). The mean correlation of species relative abundance with R^* was significantly negative (Fig. 2f). Grazing

and fire have been shown to affect the species composition of KNZ prairies (Collins *et al.* 1998), and although we found treatment differences (i.e. soil type, fire and grazing, results not shown) in mean correlations of species abundance at KNZ with CDR values for R^* , all treatment mean correlations were consistently and significantly negative.

Do species abundance patterns change in a neutral manner in response to environmental change?

Nitrogen gradient

Species rank abundance patterns reversed along a gradient of low to high N-addition, consistent with a competitive tradeoff correlated with a plant trait, R^* (Fig. 3). This shift is inconsistent with neutral theory. In particular, the correlation between relative abundance and R^* was negative at low rates of N addition, consistent with the most abundant species being better N competitors (lower R^* values). At higher rates of N-addition, the correlation between R^* and abundance became increasingly positive: plots became increasingly dominated by species with higher R^* values, which are predicted to be poorer N competitors, but presumably are superior competitors for some other factor, such as light, which becomes increasingly limiting as N becomes less limiting. Few of these individual N-addition level correlations were significant because of low power, but the overall trend (the focus of our hypothesis) as fit by a Monod function was highly significant. Either positive or negative relationships between R^* -abundance correlations and N-addition level could occur by chance if species traits are assumed to be exchangeable; however, the observed relationship (fitted curve) fell outside the 95% confidence region (Fig. 3). Thus it is highly unlikely that the observed changes in trait-abundance relationships across this N gradient were because of neutral processes.

Successional gradient

Species rank abundance patterns similarly reversed along a successional gradient (Fig. 4). During the early phases of succession (young field ages), fields were dominated by high R^* species; dominance shifted towards dominance by lower R^* species with increased field age. It is similarly highly unlikely that the observed changes in trait-abundance relationships across this successional gradient were because of neutral processes: the observed relationship fell outside the 95% confidence region predicted if R^* values were assumed exchangeable (Fig. 4).

DISCUSSION

The series of tests we performed supported niche mechanisms as the primary drivers structuring these prairie grasslands, even though the observed species abundance

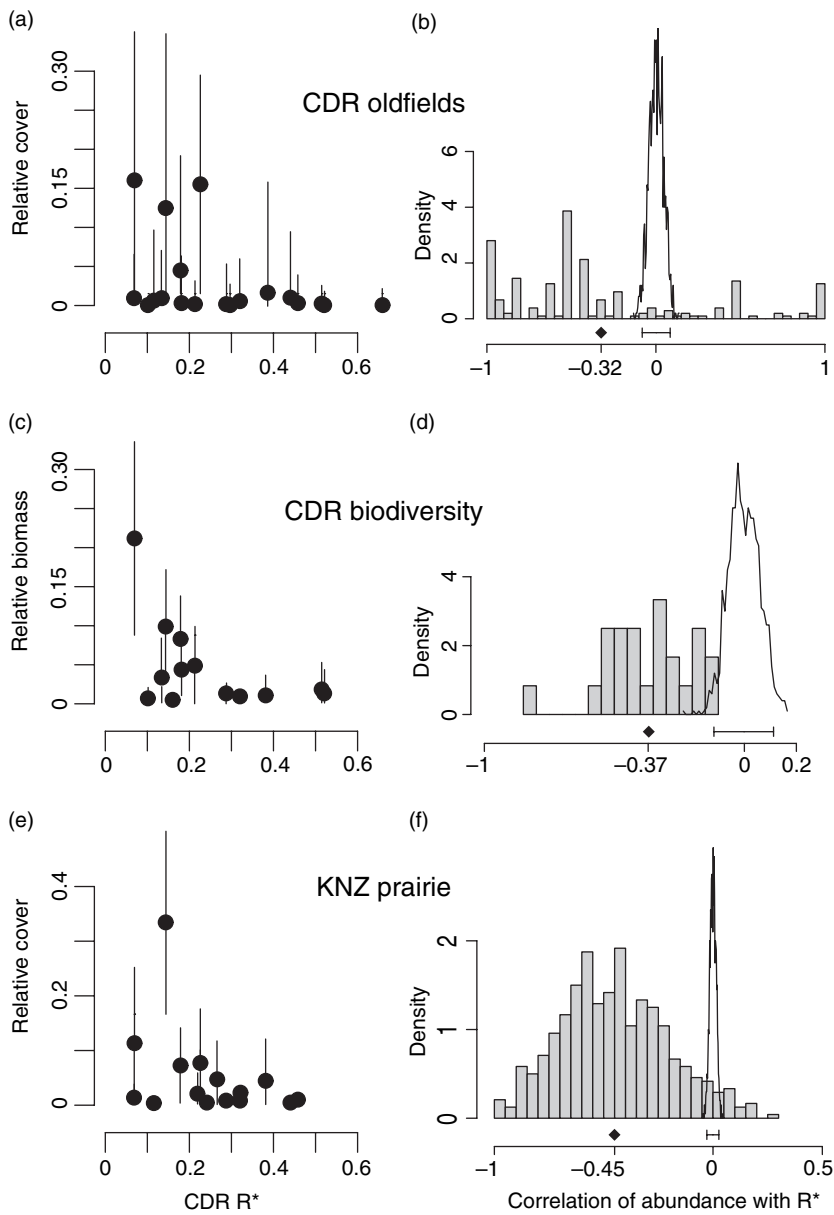


Figure 2 Species with low monoculture R^* values had greater mean relative abundance in: (a) the three oldest Cedar Creek (CDR) late successional grasslands; (c) CDR biodiversity experimental plots; (e) Konza Prairie (KNZ) prairies. Points represent the mean relative abundance across all experimental plots for each species, and error bars are 1 SD of the mean. The mean (diamond) and histogram of correlations between R^* and abundance within plots, in grey for: (b) CDR oldfields; (d) the CDR biodiversity experiment; (f) KNZ prairies. The results of the Monte Carlo simulations of neutrality are represented by the narrower black histogram [in panel (f) density scaled by 0.1 for clarity] and by its 95% bootstrapped confidence interval, also shown in black. In all three cases, the mean correlation was significantly different from the 95% confidence interval predicted by neutrality.

distribution at CDR was qualitatively consistent with neutral theory. These results illustrate that a distribution fitting approach could lead to incorrect assumptions of neutrality. Additionally, not only can niche and neutral models predict similar species abundance distributions (Chave 2004), but the distinction between the relative fit of alternative predicted distributions to species abundance distributions is contentious (McGill 2003; Volkov *et al.* 2003; Etienne & Olf 2005) and depends on which goodness-of-fit measurement is used (McGill 2003). Our ZSM fit outperformed the log-normal fit in terms of χ^2 , but not R^2 , which also suggests the need for better niche models that incorporate species traits such as R^* with dispersal limitation and stochasticity (Etienne & Alonso, in press; Tilman 2004; Etienne & Olf

2005), and methods to distinguish between the relative importance of these processes (Etienne & Olf 2005). Fitting a neutral distribution to observed species abundance data was proposed as a means of assessing the importance of neutral processes in ecological communities; deviations from this null expectation should indicate greater relative importance of other processes (Hubbell 2001). Because our observed species abundance distribution was consistent with neutrality while our stronger tests were not points out the potential limitation of using neutral distributions as a null expectation and test of neutral processes. We reassert that stronger tests are needed, including tests for relationships between abundance and ecologically relevant traits (McGill 2003; Chase 2005).

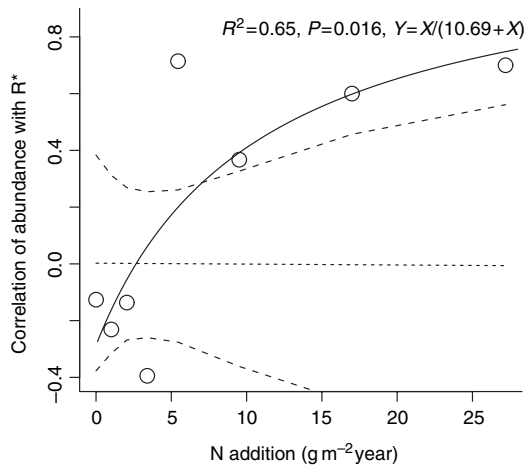


Figure 3 Relationship between R^* and abundance changes along an experimental N addition gradient: species ranking switches from dominance of good N competitors (low R^* values) to poor N competitors (high R^* values) with increasing rates of N addition. Each point is the treatment-level mean correlation of R^* indexes with species abundances. Dashed lines indicate the bootstrapped mean (short dash) and 95% confidence region (long dash) if species R^* values are exchangeable (neutrality).

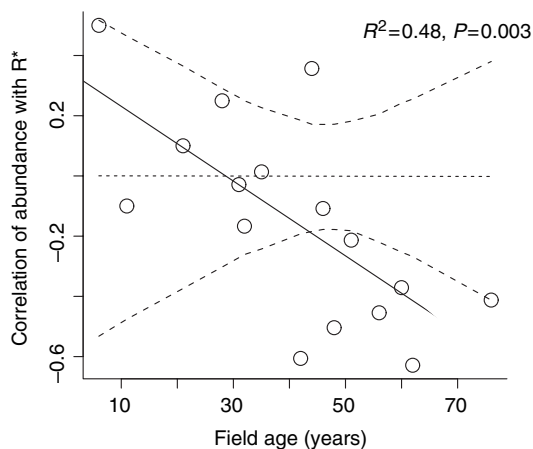


Figure 4 Relationship between R^* and abundance changes along a successional gradient; species ranking switches from dominance of poor N competitors (high R^* values) to good N competitors (low R^* values) with increasing field age. Each point is the treatment-level mean correlation of species abundances with their monoculture R^* indexes. A negative correlation means that good N competitors dominate (low R^* species). Dashed lines indicate the bootstrapped mean (short dash) and 95% confidence region (long dash) if species R^* values are exchangeable (neutrality).

In all three experimental communities (CDR oldfields, CDR biodiversity and KNZ), species abundance ranks correlated with their predicted competitive ranks: low R^* species, on average dominated. These three experiments

differed greatly in their assembly histories. CDR oldfields were colonized after agricultural abandonment via natural dispersal processes from the regional species pool over a period of 60 years, whereas species in the CDR biodiversity experiment were all seeded simultaneously at equal density and allowed to sort for 5 years, effectively decoupling community assembly from regional dispersal processes. Because KNZ Prairie has not been ploughed, it has undergone the longest continuous assembly process. Given that CDR and KNZ are isolated by a distance of almost 1000 km, and the relevant regional species pool is now dominated not by prairie species but primarily by corn and soya beans and the numerous exotic plant species associated with their cultivation, and by Eurasian pasture perennials, it is striking that low R^* species dominated in both naturally and experimentally assembled communities at both sites. Of the three experiments, the CDR oldfields showed the greatest variation in terms of the correlation between R^* and abundance suggesting that, even though niche mechanisms are a significant determinant of species abundance, dispersal processes may still be influencing these successional oldfields. The CDR biodiversity experiment provides the most compelling evidence that species assembly in these grasslands is not neutral. Species abundance patterns in all plots converged over time towards dominance by low R^* species, despite all species starting at equal density. This shows that local interactions rather than initial abundance (or species abundance in a regional pool) determined relative abundances.

Changes in relative abundance after environmental change (N-addition or succession) were not neutral but instead predicted by species traits. In particular, species that were predicted to be better N competitors at CDR because of their lower R^* values were more abundant (i) at low-N but not high-N ends of a N addition gradient, which is consistent with resource competition theory. Species with lower R^* were also more abundant (ii) in late but not early successional oldfields, consistent with native prairie perennials, which invade formerly farmed fields, being superior N competitors to the weedy annuals and Eurasian perennials that occurred in these fields at the time of abandonment from agriculture. Low R^* likely reflects a syndrome of traits associated with success in a low N environment, such as higher N use efficiency, slower maximal rates of vegetative growth, greater proportional root mass, shorter stature and perhaps greater resistance to herbivores or pathogens (Craine *et al.* 2002). Although our results may seem consistent with the competition–colonization hypothesis (Gleason & Tilman 1990; Tilman 1990), analysis of additional data on seed production we gathered in the monoculture plots showed no evidence for a competition–colonization tradeoff. In particular, seed

production (g m^{-2} of seed) in monoculture by each of the 27 species was independent of their R^* values ($R^2 = 0.02$, $P = 0.50$).

Our analyses focused on the monoculture R^* values of 27 perennial grasses and forbs and intentionally excluded other functional groups (i.e. annual, woody and N-fixing species). We found consistently significant patterns using such functionally similar species, which suggests that our conclusions are conservative, that assembly of these prairie communities may be primarily driven by niche mechanisms, and that the functional differences between species (even within functional groups) are important (Adler 2004). Other studies suggest that neutral processes may be less important in grasslands than in tropical forests (Adler 2004). Our ability to predict the relative abundance of dominant species in our system using species traits has important implications because these are the species that drive important ecosystem-level processes (Smith & Knapp 2003). While we agree that both niche and neutral processes may be important (Hubbell 2001) and act simultaneously to differing degrees (Tuomisto *et al.* 2003), our results suggest that mechanistic trait-based theory has the ability to predict, qualitatively, species-relative abundance patterns. Much of the variance in species relative abundances is not explained by such theory, but perhaps results from the stochastic processes associated with neutrality. Determining the relative contributions of niche mechanisms and neutral processes will require models that incorporate both simultaneously (e.g. Tilman 2004). Neutral and niche theories make very different predictions about how species abundances should change along fertility and disturbance gradients. An even deeper understanding of the actual mechanisms controlling the distribution and abundance of species will be needed to adequately address global change issues such as the impacts of N deposition, land use change, biological invasions and the loss of biodiversity (Chase 2005).

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REFERENCES

- Ackerly, D.D., Dudley, S.A., Sultan, S.E., Schmitt, J., Coleman, J.S., Linder, C., *et al.* (2000). The evolution of plant traits: recent advances and future directions. *BioScience*, 50, 979–995.
- Adler, P.B. (2004). Neutral models fail to reproduce observed species-area and species-time relationships in Kansas grasslands. *Ecology*, 85, 1265–1272.
- Bell, G. (2001). Neutral macroecology. *Science*, 293, 2413–2418.
- Chase, J.M. (2005). Towards a really unified theory for metacommunities. *Funct. Ecol.*, 19, 182–186.
- Chase, J.M. & Leibold, M.A. (2003). *Ecological Niches: Linking Classical and Contemporary Approaches*. University of Chicago Press, Chicago, IL.
- Chave, J. (2004). Neutral theory and community ecology. *Ecol. Lett.*, 7, 241–253.
- Chave, J., Muller-Landau, H.C. & Levin, S.A. (2002). Comparing classical community models: theoretical consequences for patterns of diversity. *Am. Nat.*, 159, 1–23.
- Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Ann. Rev. Ecol. Syst.*, 31, 343–366.
- Clark, J.S. & McLachlan, J.S. (2003). Stability of forest biodiversity. *Nature*, 423, 635–638.
- Collins, S.L. & Glenn, S.M. (1991). Importance of spatial and temporal dynamics in species regional abundance and distribution. *Ecology*, 72, 654–664.
- Collins, S.L., Knapp, A.K., Briggs, J.M., Blair, J.M. & Steinauer, E.M. (1998). Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science*, 280, 745–747.
- Craine, J.M., Tilman, D., Wedin, D., Reich, P., Tjoelker, M. & Knops, J. (2002). Functional traits, productivity and effects on nitrogen cycling of 33 grassland species. *Funct. Ecol.*, 16, 563–574.
- Etienne, R.S. (2005). A new sampling formula for neutral biodiversity. *Ecol. Lett.*, 8, 253–260.
- Etienne, R.S. & Alonso, D. (in press). A dispersal-limited sampling theory for species and alleles. *Ecology Letters*, 8, 1147–1156.
- Etienne, R.S. & Olf, H. (2005). Confronting different models of community structure to species-abundance data: a Bayesian model comparison. *Ecol. Lett.*, 8, 439–504.
- Fox, J.W. (2002). Testing a simple rule for dominance in resource competition. *Am. Nat.*, 159, 305–319.
- Gillespie, R. (2004). Community assembly through adaptive radiation in Hawaiian spiders. *Science*, 303, 356–359.
- Gleason, S. & Tilman, D. (1990). Allocation and the transient dynamics of succession on poor soils. *Ecology*, 71, 1144–1155.
- Good, P. (1993). *Permutation Tests*. Springer-Verlag, New York, NY.
- Grigal, D.F., Chamberlain, L.M., Finney, H.R., Wroblewski, D.W. & Gross, E.R. (1974). *Soils of the Cedar Creek Natural History Area*. University of Minnesota Agriculture Experiment Station, St Paul, MN.
- Grover, J.P. (1997). *Resource Competition*. Chapman & Hall, New York, NY.
- Hubbell, S. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ.
- Hubbell, S. (2005). Neutral theory in community ecology and the hypothesis of functional equivalence. *Funct. Ecol.*, 19, 166–172.
- Inouye, R.S., Huntly, N.J., Tilman, D., Tester, J., Stillwell, M. & Zinnel, K.C. (1987). Old-field succession on a Minnesota sand plain. *Ecology*, 68, 12–26.
- Knapp, A.K., Briggs, J.M., Hartnett, D.C. & Collins, S.L. (1998). *Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie*. Oxford University Press, New York, NY.
- McGill, B. (2003). Strong and weak tests of macroecological theory. *Oikos*, 102, 679–685.
- McGill, B.J., Maurer, B.A. & Weiser, M.D. (in press). Empirical evaluation of neutral theory, *Ecology*.

- Pierce, R.L. (1954). *Vegetation Cover Types and Land Use History of the Cedar Creek Natural History Reservation, Anoka and Isanti Counties, Minnesota*. University of Minnesota, St Paul, MN.
- Rees, M., Condit, R., Crawley, M., Pacala, S. & Tilman, D. (2001). Long-term studies of vegetation dynamics. *Science*, 293, 650–655.
- Reich, P.B., Wright, I.J., Cavender-Bares, J., Craine, J.M., Oleksyn, J., Westoby, M., *et al.* (2003). The evolution of plant functional variation: traits, spectra, and strategies. *Int. J. Plant Sci.*, 164, S143–S164.
- Smith, M.D. & Knapp, A.K. (2003). Dominant species maintain ecosystem function with non-random species loss. *Ecol. Lett.*, 6, 509–517.
- Tilman, D. (1982). *Resource Competition and Community Structure*. Princeton University Press, Princeton, NJ.
- Tilman, D. (1984a). Plant dominance along an experimental nutrient gradient. *Ecology*, 65, 1445–1453.
- Tilman, G.D. (1984b). Plant dominance along an experimental nutrient gradient. *Ecology*, 65, 1445–1453.
- Tilman, D. (1987). Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecol. Monogr.*, 57, 189–214.
- Tilman, D. (1988). *Dynamics and Structure of Plant Communities*. Princeton University Press, Princeton, NJ.
- Tilman, D. (1990). Mechanisms of plant competition for nutrients: the elements of a predictive theory of competition. In: *Perspectives on Plant Competition* (eds Grace, J.B. & Tilman, D.). Academic Press, San Diego, California.
- Tilman, D. (2004). Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proc. Natl. Acad. Sci.*, 101, 10854–10861.
- Tilman, D. & Wedin, D. (1991). Dynamics of nitrogen competition between successional grasses. *Ecology*, 72, 1038–1049.
- Tilman, D., Wedin, D. & Knops, J. (1996). Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*, 379, 718–720.
- Tuomisto, H., Ruokolainen, K. & Yli-Halla, M. (2003). Dispersal, Environment, and Floristic Variation of Western Amazonian Forests. *Science*, 299, 241–244.
- Volkov, I., Banavar, J.R., Hubbell, S.P. & Maritan, A. (2003). Neutral theory and relative species abundance in ecology. *Nature*, 424, 1035–1037.
- Wedin, D. & Tilman, D. (1993). Competition among grasses along a nitrogen gradient: initial conditions and mechanisms of competition. *Ecol. Monogr.*, 63, 199–229.
- Wootton, J.T. (2005). Field parameterization and experimental test of the neutral theory of biodiversity. *Nature*, 433, 309–312.

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