

NEUTRAL MODELS FAIL TO REPRODUCE OBSERVED SPECIES–AREA AND SPECIES–TIME RELATIONSHIPS IN KANSAS GRASSLANDS

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Abstract. In contrast to competing explanations of species–area relationships (SARs), neutral theory is dynamic, meaning that it should explain patterns in both space and time. However, most empirical tests of neutral theory have relied on snapshots, such as comparisons of observed and simulated SARs observed at one point in time. I used 35 years of data from permanent plots in Kansas grasslands to test the ability of strict and modified neutral models to reproduce observed species–area and species–time relationships (STRs). Holding species density to observed values, the models could generate realistic SARs or STRs, but not both simultaneously. Parameter combinations that simulated realistic STRs led to SARs with extremely steep slopes. To examine the consequences of relaxing neutrality, I incorporated plant functional types into the model. More realistic dominance produced only limited improvement in the simulated results, and indicates that the models' primary flaw is their failure to reproduce rapid but spatially correlated changes in species composition. In these grasslands, characterized by large interannual variation in resources and many short-lived species, functional differences among species play a strong role in driving macroscopic patterns. The results emphasize the need to test neutral models, and other dynamic community models, with spatiotemporal data.

Key words: *mixed-grass prairie; neutral theory; shortgrass prairie; simulation model; species–area relationship; species–time relationship.*

INTRODUCTION

The species–area relationship (SAR), arguably one of the few laws of ecology (Lawton 1999), has greatly influenced ecological application and theory. In conservation biology, it has provided a basis for identifying biodiversity hotspots (Myers et al. 2000) and predicting extinctions as a function of habitat fragmentation (Pimm and Askins 1995). Theorists have invested considerable effort trying to identify the mechanisms underlying the typical power-law form of the SAR (reviewed in Rosenzweig 1995), attempting to explain the SAR as a result of various statistical distributions (May 1975, Harte et al. 1999), environmental variation (Harner and Harper 1976), or, at some spatial scales, niche-based interactions (Shmida and Wilson 1985). Recently, neutral theory has emerged as a potential explanation of the SAR. Random fluctuations in birth, death, immigration, and dispersal can reproduce observed patterns of dominance among species and, in turn, realistic macroscopic patterns such as the SAR (Bell 2001, Hubbell 2001). The implication is that functional differences among species need not play an important role in generating these patterns.

In contrast to many of the competing explanations of SARs, neutral community models are based on dy-

namic biological processes. Their dynamic nature means that neutral models can make testable predictions about patterns in space and time simultaneously. However, empirical tests of neutral theory have relied on snapshots, comparisons of observed and simulated SARs or species abundance distributions observed at one point in time (Hubbell 2001, McGill 2003a, Tuomisto et al. 2003; but see Clark and McLachlan 2003). This failure to take advantage of the predictive power of neutral theory is important given the presence in the models of parameters essentially impossible to estimate from observational data, such as immigration to local sites from a regional species pool. Because these parameters are unconstrained, they can be tuned to improve the simulations (McGill 2003b). Although recent work (Volkov et al. 2003) has reduced the number of parameters needed to produce neutral predictions of species abundance distributions, generating other patterns such as SARs still requires simulation using the full set of parameters. Confronting neutral models with spatial and temporal data simultaneously would provide a more rigorous test, perhaps revealing unexpected consequences of tuning free parameters.

More than 40 years ago, Preston (1960) proposed that the relationship between species number and time should take the same form as the species–area relationship. While the SAR describes the increase in species number with increasing area sampled for a given time period, the species–time relationship (STR) describes increases in species number with increases in the time period of sampling for a fixed area. Preston

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PLATE 1. A view of the little bluestem community at Hays, Kansas, USA. Photo credit: P. B. Adler.

suggested that the biological mechanisms underlying the various phases of the STR are analogous to those invoked for SARs. At the finest spatial and shortest temporal scales, species accumulation is due primarily to sampling and saturates in log-log space. At “ecological” scales, ranging from tens of square meters to square kilometers, and decades to centuries, SARs and STRs should be linear in log-log space. Here, species accumulate due to changes in community composition as new habitats are added. Spatial sources of habitat heterogeneity might include topography and edaphic conditions, while temporal sources include climatic variation, disturbance, and succession. Steeper slopes of SARs and STRs thus indicate more rapid species turnover in space and time, assuming that species density remains relatively constant. The available evidence supports Preston’s conjecture of time–space equivalence. STRs at decadal scales for birds (Preston 1960, E. P. White, *in press*), lepidoptera (Preston 1948, Rosenzweig 1995, 1998), small mammals (Hadley and Maurer 2001), and vascular plants (Adler and Lauenroth 2003) are fit well by the power-law functions frequently used for SARs (Arrhenius 1921), though the slope of the relationship depends on the spatial scale of observation (Adler and Lauenroth 2003).

Extending the SAR into the temporal dimension has important implications for theory since it requires a dynamic mechanistic explanation. Neutral theory meets this criterion, but testing neutral models against empirical SARs alone is insufficient; the models must generate realistic SARs and STRs simultaneously. Here, I use long-term data from permanent plots in Kansas grasslands to show that neutral models fail to reproduce observed species–area and species–time relationships. I begin by documenting the empirical patterns. Next, I describe the strict neutral model and its simulation results. Finally, I present simulations using

a modified neutral model to diagnose the reason for the strict neutral model’s failure.

EMPIRICAL PATTERNS

Site and data description

The data set was collected by Albertson and colleagues from 1938 through 1972 at a field site near Fort Hays State University in western Kansas (see Albertson and Tomanek 1965). During the period of record, the mean annual temperature was 12°C, and annual precipitation, concentrated from April through September, averaged 577 mm. This mixed-grass prairie contains distinct plant communities corresponding to specific topographic positions. Level uplands, characterized by deep, heavy-textured soils derived from loess deposits, support a shortgrass community dominated by the short-statured warm-season perennial grasses *Bouteloua gracilis* and *Buchlöe dactyloides*. Forbs contribute the majority of species diversity but only a fraction of the biomass in this community. The mid-stature perennial bunchgrass little bluestem (*Schyzachyrium scoparium*) dominates shallow limestone soils on hill-brows and slopes (see Plate 1). Species richness is higher in this community. Permanent 1-m² quadrats were established in livestock exclosures in each community type, and the identity, size, and location of every individual plant in the quadrats was mapped using pantographs (Hill 1920). Adler and Lauenroth (2003) report parameters of STRs calculated for each quadrat. To construct SARs, I sampled a modified Whittaker plot (Stohlgren et al. 1998) in each community in July 2002, counting species number in 10 1-m² subplots, two 10-m² subplots, and one 100-m² subplot nested within a 1000-m² subplot. I then performed a linear regression of the log of the mean species number at each sampling scale on log area.

Species–area and species–time relationships

Parameter values of the observed SAR and STR were the standard for comparison with the neutral model simulations. The power-law equation fit the data slightly better (higher r^2) than did an exponential function. The empirical SAR for the shortgrass community had an intercept of 2.17 and a slope of 0.23 ($r^2 = 0.98$, $P = 0.011$), while the SAR for the little bluestem community had an intercept of 2.79 and a slope of 0.22 ($r^2 = 0.97$, $P = 0.014$). I found a total of 40 species in the shortgrass compared to 71 in the little bluestem plot.

Observed STRs, best fit by log-log regressions, had steeper slopes, ranging from 0.39 to 0.45 with an average of 0.42 for individual quadrats in the shortgrass community ($n = 7$) and ranging from 0.34 to 0.42, with an average of 0.38 in little bluestem ($n = 3$) (Adler and Lauenroth 2003). Species density, the number of species occurring in one quadrat in one year, averaged 5.6 in shortgrass and 8.2 in little bluestem over the 35-yr record.

STRICT NEUTRAL COMMUNITY MODELS

Model description

Neutral models were first used in evolutionary research to tease apart the influence of selection pressures and genetic drift on changes in allele frequencies. Their ecological analogues, first used by Caswell (1976), are meant to separate the influence of adaptation and ecological drift on the relative abundance of species. If a neutral model (neutral because all species have the same demographic parameters) can replicate an observed pattern, then there is no need to invoke explanations for the pattern based on functional differences among species, such as niche partitioning. The model applies to communities of “trophically similar sympatric species that actually or potentially compete in a local area for the same or similar resources” (Hubbell 2001:5). Vascular plant species occurring in the Hays grasslands fit this description.

The neutral community model that I used is based on those described by Bell (2000, 2001). This discrete-time model features a lattice of interacting local communities and contains seven parameters: the dimension of the lattice, L ; the number of species in the species pool, N ; the number of individuals in each local community, K ; the probability of birth, b , and death, d ; the probability that a newborn individual will disperse to a neighboring local community, u ; and the probability of immigration from any species in the regional pool, m . For each time step, birth occurs first. Second, each newborn individual disperses to one of four nearest neighbor cells with probability u , and continues this random walk until a random number greater than u is drawn. Third, species from the regional pool immigrate to local cells. When immigration occurs, only one individual from a given species colonizes a given cell.

If the fourth operation, mortality, does not reduce the total population of the cell to K , then individuals are removed at random. At the end of the time step, the model outputs the abundance of every species in each cell.

My model differs from Bell’s in only one detail: immigration from the regional pool is possible to all cells, not only the marginal cells. At the high rates of immigration I found necessary to produce realistic STRs, immigration to only marginal cells resulted in strong gradients of diversity from the edges towards the center of the lattice, even with high rates of dispersal. Because this model does not include speciation (as in Hubbell 2001), meaning that the regional species pool is static, it would be inappropriate to simulate STRs over long time spans. Therefore, I ran simulations for 2000 time steps to reach equilibrium, then analyzed output from an additional 35 time steps (2035 total time steps), matching the length of the Hays empirical record.

Nonspatial simulations

In order to understand which parameters have the most important effects on the STR, and thus would be useful for fitting the observed data, I first worked with models of just one local community ($L = 1$). I explored the parameter space by factorially varying N (100, 500), K (20, 100, 1000), $b = d$ (0.2, 0.5, 0.8), and m (0.1, 0.01, 0.001). Dispersal of newborns, u , does not appear in this nonspatial version of the model. I then used a multiple regression with the parameters as the independent variables and the slope of the STR as the dependent variable. For all simulations, I initialized the model by seeding the community with K/N individuals of each species. For simulations with $K < N$, I added one seed from each species with probability K/N until reaching K . The calculation of STRs was exhaustive, meaning that for a time period x , I averaged species number in all possible periods of x time steps occurring in the 35-generation output.

The simulations showed that the size of the species pool, N , and the immigration rate, m , had positive effects on the slope of the STR, while the size of the local community, K , had a negative effect on the STR slope (Table 1). For $K \gg N$, the slopes of the STRs were less than 0.1. Birth rate, set equal to death rate, had no significant effect on the slope. This result justifies fixing birth and death rates in the subsequent exploration of the full, spatial model.

Simulations with a spatial neutral model

To evaluate the ability of the standard NCM to reproduce observed STRs and SARs, I ran a spatial version of the model on a 40 by 40 lattice (results were equivalent on a larger landscape), with cells linked by dispersal, u , as in Bell (2001). I calculated SARs by counting species number in 100 unique but possibly overlapping randomly selected blocks of cells for pro-

TABLE 1. Influence of neutral model parameters on the slope of the species–time relationship.

Parameter†	Unstandardized coefficient	Standard error	Standardized coefficient	<i>t</i>	<i>P</i>
Constant	0.252	0.022		11.55	<0.0001
<i>N</i>	0.00034	<0.0001	0.356	9.36	<0.0001
<i>K</i>	−0.00027	<0.0001	−0.630	−16.56	<0.0001
<i>b = d</i>	0.023	0.030	0.029	0.77	0.442
<i>m</i>	1.317	0.164	0.305	8.01	<0.0001

Notes: The regression shown here is based on an exploration of parameter space in a non-spatial neutral model. For the overall model, adjusted $R^2 = 0.61$, $F_{4,256} = 106.7$, $P < 0.0001$.

† Definitions of variables: *N*, no. species; *K*, no. individuals per species; *b*, birth rate; *d*, death rate; *m*, immigration.

gressively larger sampling areas, and then regressed the log of the mean species number on log area. The time-step of sampling for each square was randomly chosen from the 35-generation output period. STRs were also calculated based on a sample of 100 cells, regressing log of the mean species number on log time.

I chose $K = 100$ (Table 2), close to the observed mean density of plants in each quadrat in the shortgrass community. Each local community in the NCM thus represents 1 m² of natural vegetation. I set $N = 500$, an estimate of the number of vascular plant species in the central grasslands region that could potentially colonize Hays. This estimate is generous, making it easier for the neutral model to generate a steep STR. I simulated three levels of dispersal ($u = 0.02, 0.1, 0.5$) at three levels of immigration ($m = 0.000001, 0.00001, 0.0001$). I could not test higher levels of immigration, since all species in the species pool then occurred in the local communities, causing the SAR to saturate. Based on the results of the nonspatial neutral model, which showed that birth and death rates had little influence on the slope of the STR, I arbitrarily set $b = d = 0.5$. (In the spatial version of the model, birth rate has a greater effect on the STR since increasing birth rate increases dispersal as well; varying birth rate is therefore similar to varying dispersal rate.) I simulated only three repetitions at each parameter combination since variability in the species–time and—area relationships was low.

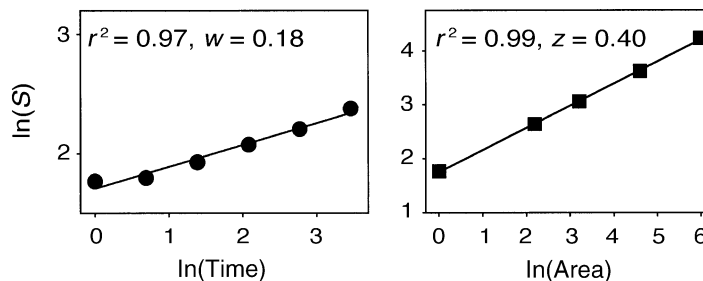
Although simulations using this spatial version of the neutral model generated STRs and SARs that were highly linear in log-log space (Fig. 1), no parameter combination could simultaneously reproduce the observed SAR slope, STR slope, and species density (similar to the untransformed SAR intercept). In fact, most parameter combinations produced a SAR with a slope much steeper than observed, and a STR with a slope far below the observed (Fig. 2). Increasing dispersal rate helped lower the SAR slope by increasing spatial autocorrelation in composition, and increased the STR slope by accelerating species turnover in time, but had the undesirable effect of greatly increasing species density (Fig. 2). For example, the parameter combination ($m = 1 \times 10^{-6}, u = 0.5$) that best simulated the SAR slope for the shortgrass community ($z_{\text{sim}} = 0.21, z_{\text{obs}} = 0.23$) resulted in species density almost five times the observed value ($S_{\text{sim}} = 28.9, S_{\text{obs}} = 5.6$) and a STR slope far below observed ($w_{\text{sim}} = 0.26, w_{\text{obs}} = 0.42$). Increasing the rate of immigration from the regional pool helped increase the slope of the STR, but also increased the SAR slope and species density (Fig. 2). As a result, the parameter combination ($m = 1 \times 10^{-6}, u = 0.5$) that best matched the observed STR slope ($w_{\text{sim}} = 0.37, w_{\text{obs}} = 0.42$) produced a SAR with a very steep slope ($z_{\text{sim}} = 0.39, z_{\text{obs}} = 0.23$) and grossly elevated species density ($S_{\text{sim}} = 44.5, S_{\text{obs}} = 5.6$).

Although dominance at the regional scale did emerge under the neutral model, it did not match the degree

TABLE 2. Parameters of the strict and modified neutral models used in the simulations.

Plant functional type	No. species (<i>N</i>)	No. individuals per species (<i>K</i>)	Birth (<i>b</i>)	Death (<i>d</i>)	Immigration (<i>m</i>)	Dispersal (<i>u</i>)
Strict neutral model						
All species	500	100	0.5	0.5	0.0001–0.000001	0.02–0.5
Functional type model, shortgrass community						
Dominant grasses	2	61	0.5	0.5	0.0001	0.5
Other grasses	24	10	0.5	0.5	0.0001	0.5
Forbs and annuals	300	19	0.6	0.6	0.0001	0.5
Functional type model, little bluestem community						
Dominant grasses	4	17	0.5	0.5	0.0001	0.5
Other grasses	22	10	0.5	0.5	0.0001	0.5
Forbs and annuals	300	15	0.6	0.6	0.0001	0.5

FIG. 1. Examples of a species–time relationship (STR) and a species–area relationship (SAR) simulated by one run of the spatial neutral model. Model parameters were: size of the species pool (N) = 500, size of the local community (K) = 100, birth rate (b) = death rate (d) = 0.5, immigration rate (m) = 0.000001, and dispersal rate (u) = 0.1.



of dominance present in the Hays data. In the Hays shortgrass plots, the two dominant species were present in almost every plot in every year, while more than 40% of all species in the record occurred in less than 1% of all possible quadrat–year combinations (Fig. 3A). The neutral model generated fewer rare species and no truly dominant species, producing instead a distribution of frequency data with a stronger central tendency than the observed pattern (Fig. 3B).

MODIFIED NEUTRAL MODELS

Model description

After finding that the strict neutral model failed to reproduce the observed patterns, I modified it to test whether more realistic relative abundances would improve the simulated patterns. The modification introduces plant functional types, sacrificing neutrality in order to simulate stronger dominance. If lack of dominance is the primary reason for the strict neutral model's failure, this change would greatly improve the simulated results. The functional-type model is actually a set of neutral models running simultaneously but independently, each one corresponding to a specific plant functional type. Therefore I could model the dominant perennial grasses, of which there are few species (N) in the species pool but many individuals (K) in each local community, separately from the forbs, of which there are many species but few individuals. This version of the model is appealing since the concept of plant functional types assumes neutrality among species within each type and complementarity between functional groups. Though each functional type is modeled independently, I analyzed their combined output, enabling comparison with the results from the strict neutral model.

For the functional-type models, I simulated shortgrass and little bluestem communities separately. I divided each of these communities into three functional types: dominant grasses, other perennial grasses, and forbs and annuals. Since my objective was to test how adding functional types and thus dominance might improve the simulations, and not to demonstrate a method for defining functional types, I chose the dominant grasses based on the abundance data, not on a priori trait differences. K and N for each functional type were based on the observed data for the mean number of

individuals of each functional type in quadrats of each community, and the number of species in each group at Hays, although for the forbs and annual functional type I set N to 300 to reflect potential immigrants. The total species pool (N) in the functional-type model is thus lower than in the strict neutral model, since introducing functional groups allowed the model to generate realistic STRs with fewer species in the model. Decreasing N helped decrease the unrealistically steep slopes of the simulated SARs.

Since with three functional types there are three times the parameters of the strict neutral model, systematic search of the parameter space is extremely difficult. Therefore, I used the analysis of the strict neutral model as a starting point, and experimented with changes in m , u , and $b = d$. I found that I could increase immigration rates more than in the strict neutral model without overestimating species density because the population size of the most diverse functional group, the forbs, was limited. To further simplify the model analysis and interpretation, I held parameter values constant across all functional groups with one exception: $b = d$ was higher for the forb and annuals group to reflect the higher turnover of these species (Table 1). Increasing this parameter led to a slight improvement in the simulated patterns. Results are the means of three simulation runs.

Simulation results using the modified neutral model

The functional-type model reduced the difference between simulated and observed patterns. For the shortgrass community, the simulations produced realistic values of the STR slope ($w_{\text{sim}} = 0.39$, $w_{\text{obs}} = 0.42$) and species density ($S_{\text{sim}} = 8.0$, $S_{\text{obs}} = 5.6$), but the slope of the SAR was much too steep ($z_{\text{sim}} = 0.49$, $z_{\text{obs}} = 0.23$). The results were similar for the little bluestem community ($w_{\text{sim}} = 0.35$, $w_{\text{obs}} = 0.38$; $S_{\text{sim}} = 7.7$, $S_{\text{obs}} = 8.2$; $z_{\text{sim}} = 0.48$, $z_{\text{obs}} = 0.22$). The distribution of frequency data from the functional-type model matched the observed data better than the output from the strict neutral model, as designed, with more extremely rare species and, in the case of the shortgrass community, two dominant species (Fig. 3C).

DISCUSSION

The strict neutral could simulate either a SAR or a STR, but failed to generate realistic SARs and STRs

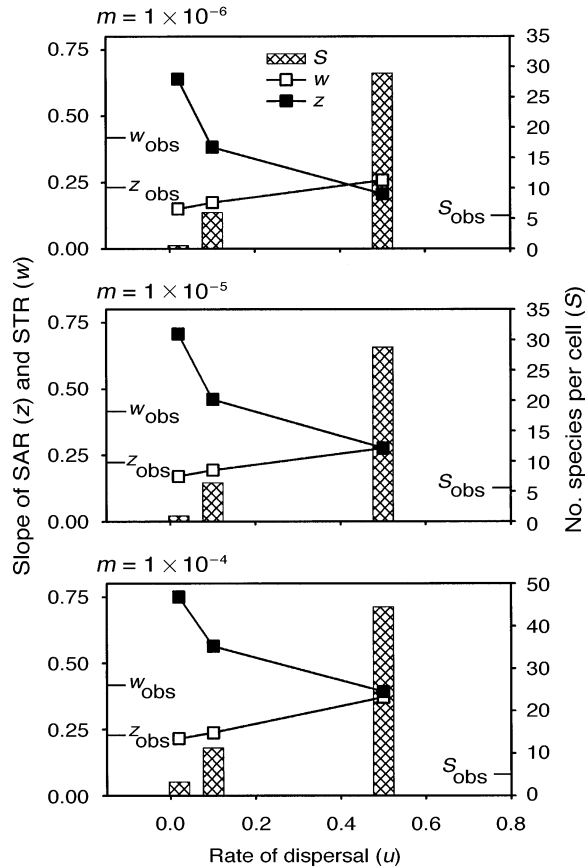


FIG. 2. Species density (species per cell) and the slope of the species–area relationship (SAR; z) and the species–time relationship (STR; w), simulated by the neutral model. For all simulations $N = 500$, $K = 100$, $b = d = 0.5$, and immigration (m) and dispersal (u) were varied factorially. Values are the means of three simulations for each parameter combination. The observed values of w , z , and S (species density) for the shortgrass community are indicated on the corresponding axes of each panel. The parameter combination that best matches the observed z (top panel) produces an extremely low w and high S , while the combination that best matches the observed w (bottom panel), produces an extremely high z and high S .

simultaneously. Even though N and K were the only model parameters constrained by data, giving me freedom to explore wide ranges in the values of the remaining parameters, I could not force the model to reproduce the observed patterns. In the empirical data, species turnover in space, represented by the slope of the SAR, was much slower than species turnover in time, represented by the slope of the STR. Under most parameter combinations, the neutral model produced the opposite result. Increasing the rate of temporal turnover required very high immigration rates, but had the undesirable effects of increasing the rate of spatial turnover and also species density. Higher dispersal rates, homogenizing the local communities, helped reduce the rate of spatial turnover, but further increased species density.

The functional-type model was somewhat more successful at reproducing observed patterns, primarily because it limited the population size of the most diverse functional type, the forbs and annuals. Limiting this group to a few individuals in each local community limited species density as well, permitting the use of models with higher immigration and dispersal rates. Making the size of the regional forb species pool very large relative to the size of the forb local population successfully increased temporal turnover. Finally, the presence of the dominant species in virtually all local

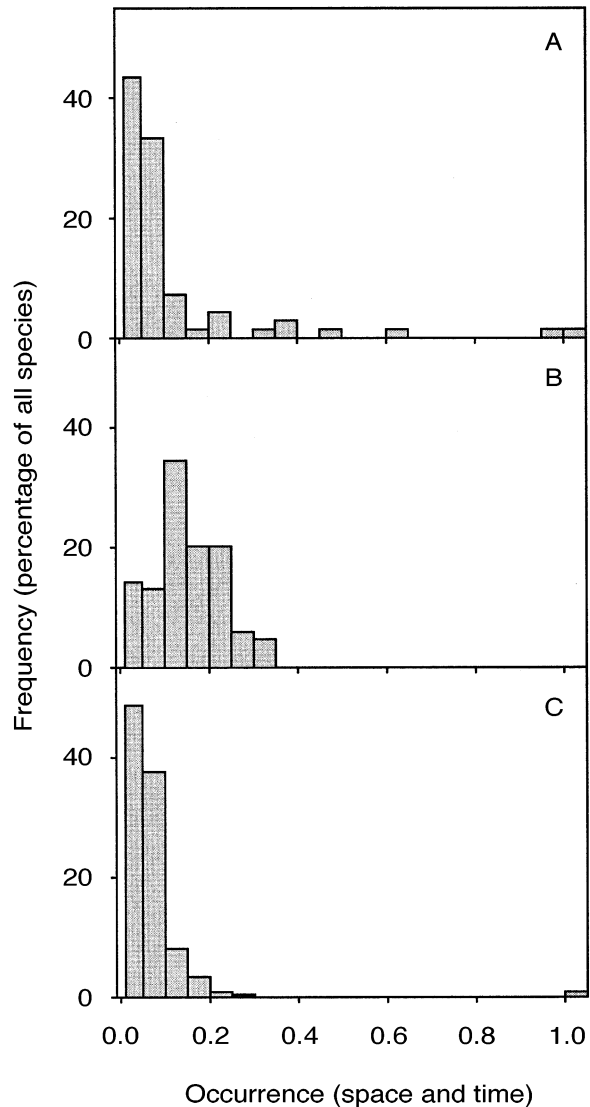


FIG. 3. Dominance (A) in the Hays shortgrass community, (B) in one simulation of the strict neutral model, and (C) in the shortgrass functional-type model. Occurrence is the proportion of all quadrat-year combinations in which a species was present. The histograms show the percentage of all species occurring in the record at each level of occurrence. Parameters for the strict neutral model are the same as in Fig. 2. Parameters of the functional-type model are shown in Table 2.

communities in every time step contributed to greater spatial correlation, helping to lower spatial turnover.

The improvement gained by introducing functional types, however, was unimpressive, especially since the number of model parameters tripled. The functional-type model generated strong dominance, but still failed to match the observed patterns, suggesting that reproducing the dominance hierarchy may not be the answer. For example, grouping species into five functional types, instead of three, caused little change in the parameters of the simulated species–area and species–time relationships (not shown). Improving the models would require simulating temporally synchronized changes in species composition across the landscape. Increasing dispersal rate would strengthen spatial correlations, but because it leads to unacceptably high species density in the presence of the large regional species pools and high immigration rates necessary to generate steep STRs, an alternative solution is needed. Differences among species in their response to environmental variation could solve the problem: in certain years, some species will become common across the entire landscape while others will disappear. In the empirical record, uncommon species often occur in many plots in certain years but are absent from all plots in most years. This kind of synchrony in dynamics also has been observed for broader temporal and spatial scales using fossil pollen data (Clark and McLachlan 2003), and explains how temporal turnover can be rapid while spatial turnover remains relatively low.

Ricklefs (2003) predicted that a major challenge for the neutral model would be generating sufficient change through time. My results show that while the model could generate rapid local changes, it could not reproduce the rapid landscape-level changes apparent in the empirical data. The only mechanism in the model that can link dynamics among local communities is dispersal. Even if increasing dispersal rate did not increase species density unacceptably, it may not be a sufficiently powerful synchronizing mechanism. Reproducing the observed dynamics may be impossible without a year-by-species interaction in birth and death rates, or some other form of a temporal niche or storage effect (Hutchinson 1961, Chesson and Warner 1981, Pake and Venable 1995). Understanding these mechanisms will require better knowledge of how individual species “disperse” through time (Rosenzweig 1998): to what environmental cues do propagules of different species respond? How important is the seed bank relative to underground perennial organs?

Rather than classify tests of the neutral model as successes or failures, however, we should ask at what spatial scales and in what ecosystems is neutrality most important (Hubbell 2003). At present, we have few guidelines about the spatial scale at which neutral theory applies. How big is a local or metacommunity? One approach is to define these scales based on the number of individual organisms in a certain area. Un-

fortunately, existing work on neutral models suggests that the number of individuals in a local community is arbitrary; simulations have included from 10 to 10 000 (Bell 2000) and 16 to 1024 individuals (Hubbell 2001). Since dispersal plays a central role in driving ecological drift, we might better define the local community as a function of mean dispersal distance. Dispersal might occur on the order of tens or hundreds of meters in a forest, whereas in a grassland it might range from centimeters to meters. In the absence of clear definitions, however, we can at least ensure that tests of neutral theory in different ecosystems are consistent in scale. The 50-ha forest plots that Hubbell (2001) used contain ~20 000 trees greater than 10 cm diameter at breast height (dbh). The 1000-m² plots that I sampled to construct SARs in the little bluestem and shortgrass communities, given a density of 50 and 100 plants per m² respectively, contained ~50 000 and 100 000 individuals, within one order of magnitude of the forest plots. Testing neutral theory at broader spatial scales will be extremely difficult because of the lack of empirical data.

Perhaps grasslands are farther from neutrality than the tree-dominated communities that inspired neutral theory (Hubbell 1979, 2001). Compared to tropical forests, Kansas grasslands have extremely variable environments and many species with short life spans. The combination of large interannual changes in resources and short-lived species may increase the importance of functional differences relative to the effects of dispersal and random demographic variation. In fact, interannual variability would lead to a departure from zero-sum dynamics in high resource years that follow poor years, violating an assumption of neutral models (Bell 2000, Hubbell 2001). Therefore, we might envision a gradient extending from variable environments populated by short-lived species to stable environments dominated by long-lived species along which the importance of neutral processes increases. Recent tests in forest ecosystems, however, also question the importance of neutrality (Clark and McLachlan 2003, McGill 2003a, Tuomisto et al. 2003).

Conclusion

My results demonstrate the failure of neutral models to simultaneously reproduce observed spatial and temporal patterns in a grassland ecosystem and highlight the important role that functional differences among species play in generating community-level patterns. This analysis also emphasizes the need to confront neutral models, and other dynamic explanations of community dynamics, with spatiotemporal data. Especially when some parameters of the candidate models are unknown, tests of spatial or temporal predictions alone may not impose sufficient constraints. Moreover, since tests in isolated ecosystems cannot illustrate how hypothetical mechanisms vary in importance across environmental and biotic gradients, it is vital that we

collect long-term, spatially extensive data from a broad range of ecosystems.

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