

Relative contributions of neutral and niche-based processes to the structure of a desert grassland grasshopper community

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Abstract Whether neutral or deterministic factors structure biotic communities remains an open question in community ecology. We studied the spatial structure of a desert grassland grasshopper community and tested predictions for species sorting based on niche differentiation (deterministic) and dispersal limitation (neutral). We contrasted the change in species relative abundance and community similarity along an elevation gradient (i.e., environmental gradient) against community change across a relatively homogeneous distance gradient. We found a significant decrease in pairwise community similarity along both elevation and distance gradients, indicating that dispersal limitation plays a role in structuring local grasshopper communities. However, the distance decay of similarity was significantly stronger across the elevational gradient, indicating that niche-based processes are important as well. To further investigate mechanisms underlying niche differentiation, we experimentally quantified the dietary preferences of two common species, *Psoloessa texana* and *Psoloessa delicatula*, for the grasses *Bouteloua eriopoda* and *Bouteloua gracilis*, which are the dominant plants (~75% of total cover) in our study area. Cover of the

preferred host plant explained some of the variation in relative abundances of the two focal species, although much variance in local *Psoloessa* distribution remained unexplained. Our results, the first to examine these hypotheses in arid ecosystems, indicate that the composition of local communities can be influenced by both probabilistic processes and mechanisms based in the natural histories of organisms.

Keywords Neutrality · Niche differentiation · Distance decay

Introduction

The study of mechanisms driving community assembly constitutes a central theme in ecology. Theories and hypotheses of community assembly fall into two broad classes. Deterministic models describe local communities as non-random sets of species, “sorted” based on their physiologically and competitively defined niches (Hutchinson 1957; MacArthur 1957; Tilman 1982; Brown 1995). In contrast, neutral models ignore species-specific traits and instead emphasize the role of random dispersal processes in structuring local communities, and speciation–extinction events in structuring large-scale metacommunities (MacArthur and Wilson 1963, 1967; Caswell 1976; Hubbell 1997, 2001). Evaluating which of these alternative theories best describes the assembly of biological communities is a source of debate (e.g., Etienne and Olff 2004; Hubbell 2006; McGill 2003; McGill et al. 2006; Ricklefs 2006; Volkov et al. 2003), although some synthesis of these paradigms has recently emerged (e.g., Karst et al. 2005; Adler et al. 2007).

Neutral and deterministic models each make unique predictions regarding spatial patterns of community assembly

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(Gilbert and Lechowicz 2004; Chase et al. 2005). Under a “species-sorting” (i.e., deterministic or niche-based) model, local-scale species composition and abundance should remain relatively constant across environmentally uniform distance gradients (e.g., transects through homogeneous space), but should change along gradients where environmental change is autocorrelated with distance (Condit et al. 2002; Chase et al. 2005). Under neutral models, where dispersal limitation dominates the spatial distribution of species, the similarity of species composition and abundance between two sample points is predicted to decrease as the distance between them increases, irrespective of any co-varying environmental factors (Chave and Leigh 2002; Condit et al. 2002; Chase et al. 2005). Examining spatial variation in community structure (i.e., species composition and abundance) is an increasingly popular approach to understanding the relative roles of neutral versus deterministic processes (e.g., Gilbert and Lechowicz 2004; Condit et al. 2002). However, identification of deterministic mechanisms (i.e., niche characteristics) requires further investigation, such as experimental manipulation of potential drivers of niche differentiation.

Our work focused on a local grasshopper (Orthoptera: Acrididae) community (22 species) in an arid grassland in central New Mexico, USA. Most studies of neutral theory have been based on tropical, plant communities (Chave 2004). Ours is the first, as far as we are aware, to test neutral predictions in an arid ecosystem and one of few to focus on arthropods (but see Novotny et al. 2002). We had two main objectives. First, we asked whether spatial patterns of grasshopper species composition and abundance across environmental and distance gradients were more consistent with neutral, dispersal-based predictions, or with deterministic, niche-based predictions. Given that grasshoppers can be influenced strongly by environmental conditions [e.g., microclimate (Anderson et al. 1979); host plant species and nutritional value (Joern 1979; Heidron and Joern 1984); and local plant diversity (Torrusio et al. 2002)], we predicted that composition of local communities would be influenced more by environment than by distance. Second, we experimentally investigated host-plant preference and statistically tested host plant availability as a potential driver of observed spatial occurrences of two dominant grasshopper species (*Psoloessa texana* and *Psoloessa delicatula*).

Materials and methods

Study area

This study was conducted at the Sevilleta National Wildlife Refuge (SNWR) in central New Mexico, USA, site of the

Sevilleta Long-Term Ecological Research program. The SNWR lies at the interface of the Chihuahuan Desert and Great Plains biomes (Kröel-Dulay et al. 2004) resulting in a patchwork transition between dominant plant species characteristic of these two biomes, most notably *Bouteloua gracilis* (blue grama) from the Great Plains and *Bouteloua eriopoda* (black grama) from the Chihuahuan Desert (Kröel-Dulay et al. 2004). Our study was located on the east side of the SNWR in an area of extensive desert grassland at the base of the Los Pinos Mountains spanning an elevation range from 1,680 to 1,820 m above sea level. *Bouteloua gracilis* and *Bouteloua eriopoda* together account for 75% of total plant cover in this area. Other common plant species include *Sporobolus cryptandrus*, *Opuntia imbricata* and *Sphaeralcea* spp. in the lowlands as well as *Agrostis gigantea*, and *Bouteloua curtipendula* on the mountain slopes.

Precipitation is highly variable, spatially and from year to year (Pennington and Collins 2007). As a consequence, annual aboveground net primary production is low (50–60 g m⁻²; Muldavin et al. 2008). The SNWR receives an average of 250 mm of precipitation annually, 60% of which occurs from July up to and including September (Báez et al. 2006). Average annual temperature is 13.2°C, with a low of 1.6°C in January and average high of 25.4°C in July (Moore 2006).

Sampling local grasshopper community structure

Data on species diversity and abundance were collected during July 2006 using 102 sampling points distributed across 25 km². Sampling points were divided into two groups: (1) 62 points (hereafter “elevation points”) were arranged along three ~1-km transects (one transect numbered 22 points) at 50-m intervals across an elevation gradient from 1,686 to 1,822 m; and (2) 40 points (hereafter “distance points”) were randomly scattered across a 20-km² area of desert grassland that was relatively homogeneous with respect to environmental variables (see below). Random points were generated by first selecting fixed reference points, and then by randomly selecting bearings (0°:360°) and distances (range: 50–1,000 m) to other points. Sampling points were established at the specified distance and bearing from the reference points. All sampling points were recorded using a Tremble GPS (Tremble GeoXT; Trimble Navigation, Sunnyvale, Calif.) with sub-meter accuracy.

Each sampling point consisted of a 1 × 5-m transect along which grasshoppers were flushed by the observer using a pole to disturb vegetation. These 1 × 5-m transects were placed to ensure consistency of microhabitat [defined by plant species composition, soil type (e.g., gravel or sand) and percent bare ground] within each sampling point. Surveys were conducted between 1000 and 1600 hours, and

weather conditions were consistent across surveys. Each point was surveyed weekly for grasshopper species diversity and abundance 3 times over the course of 3 weeks (11–26 July 2006). We quantified vegetation at each sample point during the census period using a 1 × 1-m quadrat to estimate percent cover by species (bare ground and percent rock cover were also estimated). All plant identifications were based on Allred (1997) and Ivey (2003).

Of the 62 elevation points, eight were removed due to a lack of grasshopper presence. To equalize the sample size of elevation and distance points we randomly added seven elevation points from below the altitude of 1,720 m to the 40 distance points resulting in a total of 47 distance and 47 elevation points. Because of gross habitat differences in vegetation as a function of elevation most environmental variation in this system was assumed to be due to elevation. Thus, points below the slope of the Los Pinos (i.e., <1,720 m) were expected to sample relatively homogeneous habitat. We used data from the elevation sampling points ($n = 47$) to test community response to environmental change co-varying with distance. To examine community responses to distance only, we used the distance sampling points ($n = 47$).

We did not sample grasshoppers by sweep-netting because, in preliminary sampling, most grasshoppers escaped capture (A. J. R., personal observation) and because sweep-netting has been questioned as an accurate means of estimating grasshopper community structure (Larson et al. 1999; Gardiner et al. 2005). Instead, grasshoppers were identified by sight in the field (as in Isern-Vallverdu et al. 1993; Gottschalk et al. 2003; Gardiner et al. 2005) and only immediately unidentifiable individuals were collected and taken to the laboratory for comparison against museum specimens. All grasshopper surveys were conducted by the same investigator (A. J. R.). All identifications were based on Otte (1981, 1984), and confirmed at the Orthoptera collection at the Museum of Southwestern Biology, University of New Mexico.

Correlation between environmental variation and geographic distance

To quantitatively evaluate whether the distance and elevation gradients provided an appropriate contrast for testing decay of grasshopper community similarity, we examined, for both gradient types, the correlations between distance and key environmental variables known to be important for grasshoppers: total plant cover (Anderson et al. 1979), total forb cover (Otte 1976; Joern 1979; Torrusic et al. 2002), *Bouteloua gracilis* cover and *Bouteloua eriopoda* cover (present study), shrub cover (see below), and proportion of rock (diameter ≥ 2 cm) in exposed soil (Isely 1938).

Shrub cover was calculated as percent cover over a 10-m radius circle centered at each sampling point. A 10-m radius was deemed necessary, as shrubs do not occur at high density, while individual shrubs, especially *Juniperus monosperma*, may span up to 5 m across, making estimation of cover problematic if single small-area samples were taken. GIS-enabled areal photographs available through Google Earth (photograph taken 4 September 2003; Google 2007) were used for calculating percent cover. Areal photography of our study area available for import into ArcView (ESRI, Redlands, Calif.) is not of as high a resolution as is that available through Google Earth; however, the accuracy of these projections is not publically available. To insure adequate accuracy (to within 5 m) sampling points were projected in both Google Earth and ArcView, and triangulation was used to evaluate the position of the first, middle and last sampling point along each elevation gradient relative to prominent rock outcroppings identifiable in both GIS programs. Areal photography from 2003 was deemed acceptable because of the slow growth rate of the dominant shrub species (*Juniperus monosperma*; USDA and NRCS 2004). No seedlings/saplings were observed during the 2006 field season. Shrub cover has been associated with changes in insect communities (Söderström et al. 2001) potentially as the result of changes in avian predator behavior in response to perch availability (Recher et al. 2002).

In order to compare independent variables related to vegetation, principle component analysis of plant cover (excluding shrub cover which was zero everywhere outside middle to high elevations) was used to create orthogonal axes describing *Bouteloua* cover (components 1, 2 and 3) and forb cover (component 4) which are uncorrelated with total plant cover. In regressing these principal components against distance, we used only components 1 and 4, as they had meaningful environmental interpretations. We posited that these variables would be more strongly related to distance for points along the elevation gradient than the distance-only gradient and we tested this hypothesis with linear regressions.

Analyses of grasshopper community structure

Due to low grasshopper abundances (average individuals per survey per point $n = 5$), we pooled data from the three sampling dates for each point, which ensured sufficient sample sizes for analyses of community structure (average individuals per sampling point $n = 14$). In order to mirror the replicated transects along the elevation gradient, three random subsets of the 47 distance points ($n = 17, 16, 14$, respectively) were generated to serve as “distance transects” through relatively homogeneous habitat. We quantified variation in community structure along both the distance and elevation transects using a variety of similarity

indices, all of which were highly correlated (data not shown); therefore, we report results only from Sorenson's quantitative index of similarity (an index which incorporates species relative abundance; Bray and Curtis 1957). Similarity was calculated between a base point (0 m for each of the elevation transects, and a random starting point for each distance transect) and each subsequent point along each replicate transect. We used analysis of covariance (ANCOVA) to test for the response of similarity to geographic distance (calculated using ArcView 3.3; ESRI) and any interaction between gradient type (elevation or distance) and geographic distance between points. The ANCOVA included transect replicates as a random effect. Under neutral processes, the slopes of these two regressions should be statistically indistinguishable; however, under deterministic processes, the slope of similarity decay along the elevation gradient should be significantly more negative than along the distance gradient.

To avoid any bias introduced by the selection of starting points, we also examined the distance decay of community similarity using all possible pairwise comparisons between points within each of the elevation and distance transects. However, using all possible pairwise comparisons violates the assumption of independence explicit in linear regression, and so we generated bootstrapped estimates (based on 1,000 bootstrap replicates) and 95% confidence intervals for the slopes of distance decay of community similarity across the elevation and distance gradients.

An important underpinning of neutral theory is that assemblages of species follow zero-sum dynamics (Hubbell 2001; Chave and Leigh 2002) in which any death or immigration is replaced by a birth or emigration. The fingerprint of zero-sum dynamics can be observed in a highly constrained linear accumulation of individuals with area sampled (Hubbell 2001). We therefore examined the relationship between numbers of individuals collected and area sampled.

Feeding trials

To further ascertain whether deterministic processes structure local grasshopper communities, we conducted feeding trials to quantify any dietary niche differentiation of the two common grasshopper species, *Psoloessa texana* and *Psoloessa delicatula* (Table 1), and determine whether food preference played a role in grasshopper distribution patterns. Together, these two species accounted for 46.67% of all grasshoppers sampled. In the feeding trials ($n = 36$ trials per species) individuals were presented a choice between a leaf of *Bouteloua gracilis* and of *Bouteloua eriopoda*. Additionally, *Ageneotettix deorum*, a known dietary generalist (Heidorn and Joern 1984, 1987), was tested ($n = 18$ trials) for comparison with the two *Psoloessa* species.

Table 1 All grasshopper species observed organized taxonomically by subfamily and alphabetically within each subfamily

	Subfamily	Species	Relative abundance ^a (%)
1.	Gomphocerinae	<i>Ageneotettix deorum</i>	5.152
2.	Gomphocerinae	<i>Amphitorus coloradus</i>	0.363
3.	Gomphocerinae	<i>Aulocara elliotii</i>	1.669
4.	Gomphocerinae	<i>Aulocara femoratum</i>	0.435
5.	Gomphocerinae	<i>Cordillacris crenulata</i>	1.234
6.	Gomphocerinae	<i>Eritettix simplex</i>	6.459
7.	Gomphocerinae	<i>Heliaula rufa</i>	1.742
8.	Gomphocerinae	<i>Opeia obscurua</i>	0.218
9.	Gomphocerinae	<i>Paropomala pallida</i>	26.415
10.	Gomphocerinae	<i>Phlibostroma puadrimaculatum</i>	0.145
11.	Gomphocerinae	<i>Psoloessa delicatula</i>	14.804
12.	Gomphocerinae	<i>Psoloessa texana</i>	32.003
13.	Gomphocerinae	<i>Syrbula montezuma</i>	0.726
14.	Oedipodinae	<i>Arphia conspersa</i>	0.073
15.	Oedipodinae	<i>Hadrotettix trifasciatus</i>	3.846
16.	Oedipodinae	<i>Trimopteris pallidipennis</i>	0.435
17.	Oedipodinae	<i>Xanthippus corallipes</i>	2.395
18.	Melanoplineae	<i>Aeoloplides rotundipennis</i>	0.073
19.	Melanoplineae	<i>Dactalotum bicolor</i>	0.073
20.	Melanoplineae	<i>Hesperotettix viridis</i>	0.145
21.	Melanoplineae	<i>Melanoplus arizonae</i>	0.943
22.	Melanoplineae	<i>Melanoplus sanguinipes</i>	0.653

^a Relative abundance is percentage of total grasshoppers counted in study area from 11 and 26 July 2006 ($n = 1,509$)

Feeding trials were conducted from 22 until 26 August 2006. Each day, four to ten replicates of the two *Psoloessa* species were tested; 18 replicates of *A. deorum* were tested on 25–26 August.

Grasshoppers of all three species were collected from across the entire study area. Collection of individuals of the same species was limited to three per sample point. Individuals were used in trials on the same day they were collected. For each trial, samples of the two *Bouteloua* species were collected within the same 20-m² area, but never from a grasshopper sample point. Between different trials, grass samples were collected from different sites in our study area, to ensure that our trials tested the effect of grass species and not grass collection site. Grass samples were collected on the same day as the trial in which they were used and kept in wet paper towels sealed in Ziploc bags until used.

In the lab, grasshoppers were placed in 7 × 9 cm clear plastic cylindrical containers with two grass leaves (one of each species) protruding from the bottom of the container. The base of each grass leaf was submersed in water. Feeding

trials lasted for 3 h between 1630 and 2100 hours. Leaf area of each grass species was measured before and after the trial using a 1.5×1.5 -mm grid. For each grasshopper species, we quantified the amount of leaf area eaten (mm^2) of each grass species.

For analysis, we first used a Fisher's exact test to compare the probabilities of each grasshopper species selecting either *Bouteloua gracilis* or *Bouteloua eriopoda*. This test included trials in which neither blades of grass were eaten (five *Psoloessa texana*, 13 *Psoloessa delicatula*, and two *A. deorum*). Instances of zero consumption were excluded from subsequent analyses. We quantified dietary preference as the difference in area (mm^2) eaten of each *Bouteloua* species (*Bouteloua gracilis*–*Bouteloua eriopoda*). We evaluated differences in dietary preference among *Psoloessa texana*, *Psoloessa delicatula*, and *A. deorum* using ANOVA. Effect of grasshopper body mass, collection site, time of collection, grass collection site, and day of experiment were initially tested in a factorial design but excluded in reported results because they did not explain a significant portion of the variance. We then tested the significance of each species' dietary preference (i.e., deviation from the null hypothesis: preference = 0) using a Student's *t*-test.

Correlations between *Psoloessa* and *Bouteloua* occurrence

To determine if results of the small-scale feeding trials could explain the spatial patterns in our local grasshopper community surveys, we analyzed whether *Psoloessa texana* and *Psoloessa delicatula* abundances and presence/absences were related to the abundances of their preferred host-plant species across the study area using linear and logistic regression models. Inference in the logistic model case was based on the χ^2 distributed likelihood ratio test statistic— $2\ln(L_{\text{full}}/L_{\text{reduced}})$ where L_{full} is the likelihood of the full model (i.e., with intercept and slope coefficients) and L_{reduced} is the likelihood of the model that considers only the intercept term. The grasshopper *A. deorum* was rare in our study area (5% of all grasshopper individuals sampled) and so was not

included in this analysis. Host-plant availability at each sample point was quantified as (% cover *Bouteloua gracilis*) – (% cover *B. eriopoda*). This simple index compressed the two variables (abundance of *B. gracilis* and *B. eriopoda*) onto one axis while still maintaining a strong linear association with the original variables ($R^2 = 0.6475$, and 0.807 for *B. gracilis* and *B. eriopoda* regressed against the index, respectively).

Sample points at which neither *Bouteloua* species occurred were excluded from this analysis. Two additional, outlying points with unusually high *P. delicatula* abundances (>20 individuals) were also excluded; however, the exclusion of these points did not substantially change the regression coefficients or their statistical significance. These points were not excluded from distance decay of similarity because they were not clear outliers in this analysis, the reason being that Sorenson's quantitative similarity, while potentially biased by dominant species, is based on the relative abundance of all species sampled, and so large absolute values for single species may be of little consequence.

Results

Correlation of environment and geographic distance

We found that two environmental factors—shrub cover and the principal component for *Bouteloua* cover—showed significant variation across the environmental gradient, but there was no significant variation across the distance gradient (Table 2). Also, proportion of rock in exposed soil varied (though not linearly) across the elevation gradient; rocks appeared abruptly above 1,720 m in elevation and averaged 54% of exposed soil ($t_{20} = 5.93$, $P \ll 0.001$, $H_A = \text{true mean not equal to } 0\%$). All points along the distance gradient shared 0% rock in exposed soil. These results indicate that the distance and elevation gradients provided a useful contrast for testing the predictions of neutral and niche-based theories.

Table 2 Summary of relationship between environmental variables and distance across the distance and elevation gradients

	Distance gradient			Elevation gradient		
	R^2	F (df)	P -value	R^2	F (df)	P -value
Component 1 ^a	0.048	2.275 (1,45)	0.138	0.189	12.36 (1.53)	<0.001
Component 4 ^b	0.027	1.269 (1,45)	0.265	0.026	1.46 (1.53)	0.232
Total plant cover	0.0008	0.039 (1,45)	0.843	0.008	0.44 (1.53)	0.508
Shrub cover ^c	NA	NA	NA	0.638	82.91 (1.47)	<0.001

^a Component 1 corresponds to a gradient from high *Bouteloua eriopoda* cover to high *Bouteloua gracilis* cover

^b Component 4 corresponds to increasing forb cover

^c No values for shrub cover are reported for the distance gradient as shrub cover was zero for all points along all transects

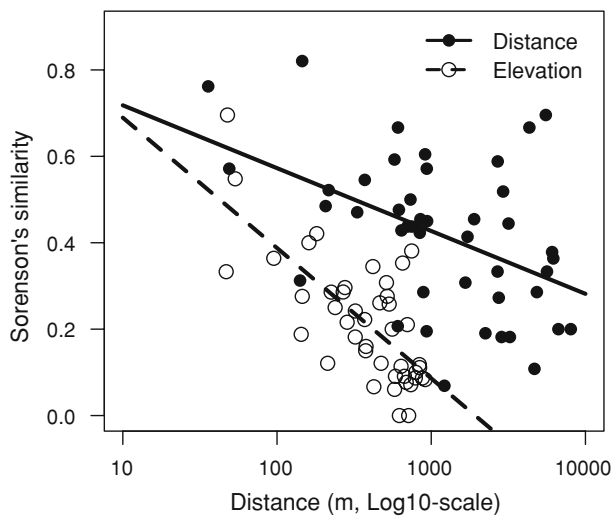


Fig. 1 Decay of community similarity with \log_{10} -transformed distance for points along the three distance and three elevation transects. Similarity and geographic distance were both calculated with respect to one “base” point for each transect, thus each point plotted represents the result of comparing a single sampling point to one base point. Both regressions are statistically significant, as is the difference between slopes (see text)

Local community spatial structure

A total of 22 grasshopper species and 1,360 individuals were recorded during the sampling period (Table 1). Using rarefaction with 1,000 randomized iterations, we observe that the accumulation of species with individuals sampled reaches an asymptote when surveys are pooled across time, but not for individual surveys. We also observe that the accumulation of individuals increased linearly with area sampled (slope = 2.7 ± 0.002 SE individuals per m^2 , based on 1,000 randomly ordered accumulations). Thus, this grasshopper community most likely satisfies a key assumption (zero-sum dynamics; Hubbell 2001; Chave and Leigh 2002) of neutral theory.

Similarity of local grasshopper communities decreased significantly across both elevation and distance gradients, relative to their base points (elevation, $R^2 = 0.52$,

$F_{1,42} = 44.77$, $P < 0.001$; distance, $R^2 = 0.21$, $F_{1,42} = 11.47$, $P = 0.001$; Fig. 1). However, the relationship was significantly steeper across the elevation gradient (slope = -0.30) than across the relatively homogeneous distance gradient (slope = -0.15 ; distance \times gradient type, $F_{1,84} = 5.06$, $P = 0.027$).

Patterns of distance decay from the bootstrap analysis that included all possible pairwise comparisons within a transect were qualitatively similar (Fig. 2). The decay of similarity across the elevation gradient was steeper than across the distance gradient, though the 95% confidence intervals for the two bootstrapped slopes do overlap slightly, indicating that the null hypothesis of no difference between the slopes cannot be rejected at the 0.05 confidence level (elevation gradient, -0.3119207 , -0.2113645 ; distance gradient, -0.2124661 , -0.1241878).

The large spatial extent of the distance transects relative to the elevation transects (~ 9 km compared to the ~ 1 km of the elevation transects) may have influenced our results. Truncating the distance transects to less than 1.5 km still resulted in detecting significant decay of similarity (slope = -0.20) although there were no longer significant differences between slopes of decay across distance and elevation gradients. However, truncating the data resulted in highly unbalanced sampling sizes, which made any differences in slope between the gradient types difficult to detect. The fact that spatial scale and sample size are confounded impedes our ability to differentiate their contributions to observed patterns and represents a limitation in our study design.

Feeding trials

Psoloessa texana was significantly more likely to select *Bouteloua eriopoda* than *Bouteloua gracilis* (Fisher's exact test: odds ratio = 0.234, $P = 0.007$). However, neither *P. delicatula* nor *Ageneotettix deorum* demonstrated a statistically significant probability of selecting one grass species over the other (odds ratio = 1.755, $P = 0.341$; and odds ratio = 1.63.1, $P = 0.725$, respectively).

Fig. 2 Bootstrapped estimates for the slope of decay in community similarity with \log_{10} -transformed distance based on re-sampling all possible pairwise distances. Gray shaded regions represent 95% confidence intervals with darker shading indicating overlap in confidence intervals

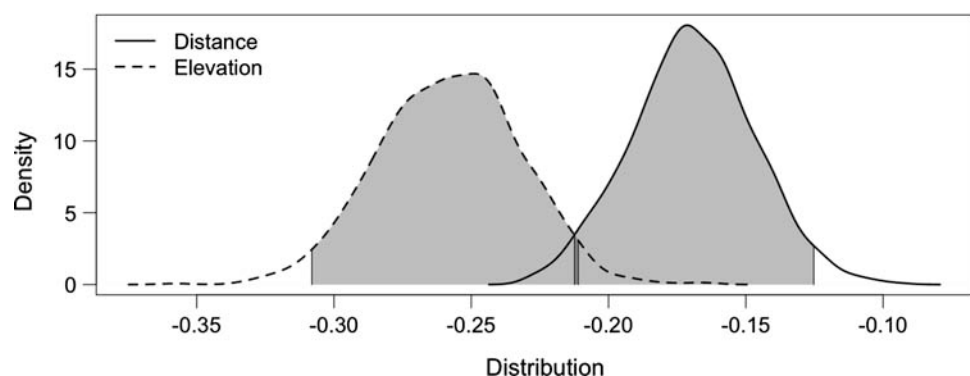
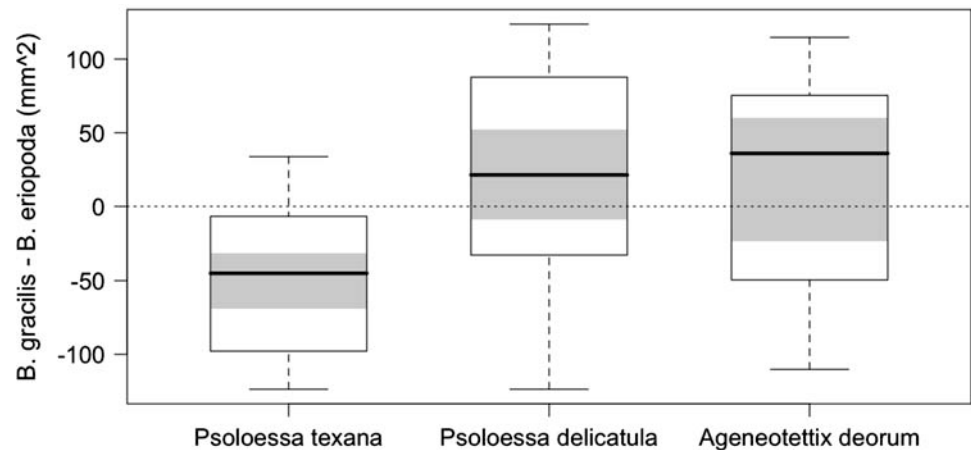


Fig. 3 Difference in amount eaten (*Bouteloua gracilis*–*Bouteloua eriopoda*) for three grasshopper species in laboratory feeding trials. Box plots represent medians (bold black horizontal line), 95% confidence intervals (gray shaded area), first and third quartiles (box perimeter), and outliers (whiskers)



We found similar variation among species in terms of amount eaten (ANOVA: $F_{2,66} = 10.11$, $P < 0.001$; Fig. 3). *P. texana* again showed a significant preference for *B. eriopoda* ($t_{30} = -5.43$, $P < 0.001$). *P. delicatula* showed a moderate preference for *B. gracilis*, though this trend was not statistically significant ($t_{23} = 1.46$, $P = 0.16$). *A. deorum* demonstrated no preference in either direction ($t_{14} = 0.94$, $P = 0.36$).

Local correlation between *Psoloessa* and *Bouteloua*

Abundance of *P. texana* showed no significant correlation with *Bouteloua* percent cover, measured as (% cover *B. gracilis*) – (% cover *B. eriopoda*) ($R^2 < 0.001$, $F_{1,92} = 0.0004$, $P = 0.983$). However *P. delicatula* showed a significant correlation with *Bouteloua* cover ($R^2 = 0.132$, $F_{1,90} = 13.95$, $P < 0.001$; Fig. 4) in the direction predicted by feeding trials: greater abundance with increasing cover of *B. gracilis*. Similarly, the probability of *Psoloessa texana* presence was not significantly related to *Bouteloua* cover (likelihood ratio = 0.29, $P = 0.59$), whereas the probability of *Psoloessa delicatula* presence was significant (likelihood ratio = 11.97, $P = 0.001$; Fig. 4).

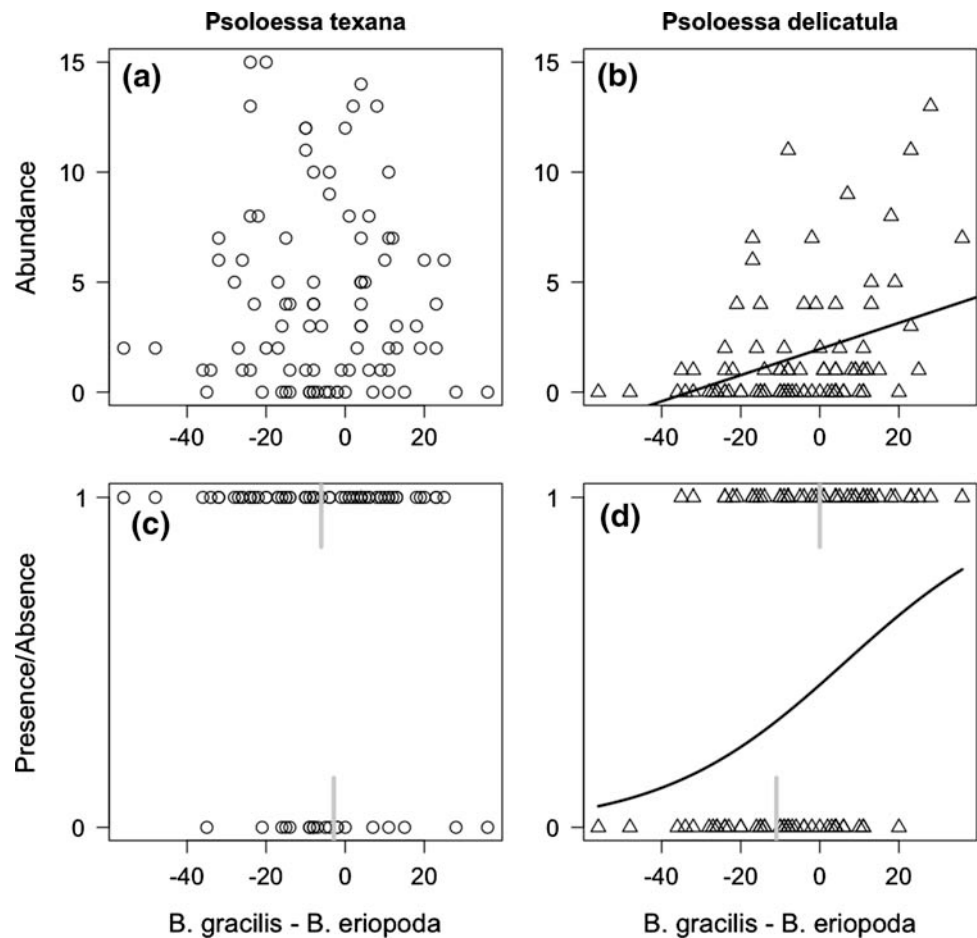
Discussion

We examined variation in grasshopper community structure to test competing predictions, based on neutral and deterministic niche processes, for change in community similarity with increasing spatial and environmental distance. We found that community similarity declined with distance across both elevation and distance gradient types (Figs. 1, 2), implicating dispersal limitation as an important factor in local community structure. However, according both to the analysis of covariance for pairwise comparisons (Fig. 1) and bootstrapped confidence intervals for all possible comparisons (Fig. 2), decay of similarity was steeper

across the elevation gradient, lending support for additional roles of environmental variables and ecological differences between species. Thus, our data indicate that the composition of local grasshopper communities in this desert grassland was influenced by a combination of neutral (dispersal limitation) and deterministic (niche-based) processes. Random dispersal could produce a “species rain” which is then “filtered” by the environment. We infer that patterns across the distance gradient were dominated by random dispersal effects, whereas the interaction of random dispersal and environmental filtering drove patterns across the elevation gradient.

Since Condit et al. (2002) first published results demonstrating the use of distance decay in testing neutral and niche-based theories of community assembly, others have sought to examine similar patterns towards that same end (Gilbert and Lechowicz 2004; Jones et al. 2006; Karst et al. 2005; Thompson and Townsend 2006; Lekberg et al. 2007). Condit et al. (2002) and Jones et al. (2006) take the approach of using a formal neutral theory of beta-diversity to model distance decay, finding that similarity declines with distance more rapidly than would be expected by chance. Their results imply that random dispersal, combined with speciation across large spatial scales, are not sufficient by themselves to explain patterns in distance decay of similarity; however, these neutral processes may still be important. This hypothesis is corroborated by several studies explicitly testing change in similarity due to environment and distance, separately and combined, which find that the most predictive phenomenological models of distance decay are those incorporating both environmental variation between sites, and distance (Karst et al. 2005; Thompson and Townsend 2006; Lekberg et al. 2007). Our study is consistent with these previous results, and contributes the novel approach of measuring decay in similarity across geographic gradients that incorporate either distance alone or environmental factors covarying with distance.

Fig. 4 Association of *Psoloessa texana* (a, c), and *Psoloessa delicatula* (b, d) with change in *Bouteloua* cover. a, b Grasshopper abundance in relation to *Bouteloua* percent cover. c, d Presence/absence in relation to *Bouteloua* percent cover. c, d Vertical gray lines represent means of plant cover corresponding to grasshopper presences and absences. The linear (b) and logistic (d) regression models (black lines) were statistically significant for *P. delicatula* only (see text)



The emerging pattern from these studies seems to be that dispersal limitation, a strictly neutral process, contributes in important ways to community structure and the maintenance of species diversity at local scales. For example, Hiltunen et al. (2006) showed through simulation that random dispersal can maintain species diversity and prevent complete dominance by one superior competitor. Environmental variation, while central to determining the identity of dominant species, may be insufficient to maintain diverse communities through time (Chesson and Huntly 1997).

Based on evidence for niche-based processes contributing to grasshopper community structure (Figs. 1, 2), we investigated a potential exemplar component of niche differentiation. Previous studies suggest that host-plant abundances are important environmental variables for grasshopper communities (Otte 1976; Joern 1979; Torrusic et al. 2002). Accordingly, we examined the preferences of three common grasshopper species for two dominant grasses and related these preferences to occurrence and abundance in the field. *Psoloessa texana* showed a significant preference for *Bouteloua eriopoda* over *Bouteloua gracilis*, while *Psoloessa delicatula* tended to consume more *B. gracilis* than *B. eriopoda*, though this difference

was not statistically significant. Based on these results, we predicted positive relationships between *Psoloessa texana* abundance/occurrence and *Bouteloua eriopoda* cover, and between *Psoloessa delicatula* abundance/occurrence and *Bouteloua gracilis* cover. While we found evidence for an association between *P. delicatula* and *B. gracilis*, there was a large amount of unexplained variance for both species (Fig. 4) indicating that factors other than these dominant grasses affect grasshopper species abundance and distribution in this desert grassland. Of the three analyses, the strongest relationship was between *P. delicatula* and *B. gracilis* (Fig. 4), which we predicted to be weaker based on the feeding trial.

There are several potential explanations for the weak predictive power of preferred resource availability: (1) the association of grasshoppers and their host plants could be scale-dependent; (2) other niche variables, or the autocorrelation of several variables, may be more important to spatial patterns; and (3) any apparent overlap of *Bouteloua* and *Psoloessa* species may be due to partial overlap of their niche spaces, not interdependence.

The scale at which *Psoloessa* species segregate based on *Bouteloua* gradients may be greater than what we examined

at the SNWR. Indeed, Pandolfi (2002) showed that the predictability of coral species composition increased with increasing spatial and temporal scale, and hypothesized that the pattern may be best explained by regional environments and species–environment interactions being more stable than local-scale processes. Apparent association of *Psoloessa texana* with *Bouteloua eriopoda* and *Psoloessa delicatula* with *Bouteloua gracilis* at the continental scale (continental data compiled from Otte 1981 and the PLANTS data base, www.usda.plants.gov, data not shown) supports the hypothesis that these species track preferred host-plant availability at a larger spatial scale. The northern, eastern and western range limits of *Psoloessa texana* conform to those of *Bouteloua eriopoda*, whereas the northern, eastern and western range limits of *Psoloessa delicatula* conform to those of *Bouteloua gracilis*. The effect of spatial scale on predictability of grasshopper communities warrants further study.

Perhaps it is not surprising that single niche variables cannot fully explain local species distribution and abundance given that numerous variables can contribute to a species' niche (Hutchinson 1957; Chase and Leibold 2003). Indeed, the autocorrelation of multiple niche variables is thought to be an important driver of species distributions and change in abundance across space (Brown 1995). This seems to agree again with the continental association of *Psoloessa* and *Bouteloua* species, as other variables (especially temperature) are likely correlated with *Bouteloua eriopoda* and *Bouteloua gracilis* distributions at the continental scale. The weak explanatory power of preferred host-plant availability may reflect the mobility of grasshopper individuals and their probably transient status at individual sampling points. Dispersal and random sampling effects could contribute, at local scales, to the unpredictability of observed patterns (Maurer 1999).

It is also possible that other environmental variables preferred by *P. delicatula* are also preferred by *B. gracilis*, accounting for the correlation between these two species. Such variables could include temperature and soil substrate type, both known to contribute to grasshopper habitat selection (Isely 1938; Anderson et al. 1979).

Evidence from our study, and from others (Hubbell 2001; Condit et al. 2002; Gilbert and Lechowicz 2004) indicates that both deterministic and neutral processes affect local community structure. Our study underscores the directions in which such work might proceed, and strongly suggests that deterministic and neutral processes may both be at play in structuring communities. We still face significant important challenges in identifying the taxonomic, environmental, geographic, and temporal scales over which neutral versus niche-based processes are expected to dominate.

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References

- Adler PB, HilleRisLambers J, Levine JM (2007) A niche for neutrality. *Ecol Lett* 10:95–104
- Allred KW (1997) A field guide to the grasses of New Mexico, 2nd edn. Agricultural Experiment Station, New Mexico State University, Las Cruces
- Anderson RV, Tracy CR, Abramsky Z (1979) Habitat selection in two species of short-horned grasshoppers. *Oecologia* 38:359–374
- Báez S, Collins SL, Lightfoot D, Koontz TL (2006) Bottom-up regulation of plant community structure in an aridland ecosystem. *Ecology* 87:2746–2754
- Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. *Ecol Monogr* 27:325–349
- Brown JH (1995) Macroecology. The University of Chicago Press, Chicago and London
- Caswell H (1976) Community structure: a neutral model analysis. *Ecol Monogr* 46:327–354
- Chase JM, Leibold MA (2003) Ecological niches: linking classical and contemporary approaches. University of Chicago Press, Chicago
- Chase JM, Amarasekare P, Cottenie K, Gonzalez A, Holt RD, Holyoak M, Hoopes MF, Leibold MA, Loreau M, Mouquet N, Shurin JB, Tilman D (2005) Competing theories for competitive metacommunities. In: Holyoak M, Leibold MA, Holt MA (eds) Metacommunities: spatial dynamics and ecological communities. University of Chicago Press, Chicago
- Chave J (2004) Neutral theory and community ecology. *Ecol Lett* 7:241–253
- Chave J, Leigh EG (2002) A spatially explicit neutral model of beta-diversity in tropical forests. *Theor Popul Biol* 62:153–168
- Chesson P, Huntly N (1997) The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *Am Nat* 150:519–553
- Condit R, Pitman N, Leigh EG, Chave C, Terborgh J, Foster RB, Núñez, Aguilar S, Valencia R, Villa G, Muller-Landau HC, Losos E, Hubbell SP (2002) Beta-diversity in tropical forest trees. *Sciences* 295:666–669
- Etienne RS, Olf H (2004) A novel genealogical approach to neutral biodiversity theory. *Ecol Lett* 7:170–175
- Gardiner T, Hill J, Chesmore D (2005) Review of the methods frequently used to estimate the abundance of Orthoptera in grassland ecosystems. *J Insect Conserv* 9:151–173
- Gilbert B, Lechowicz MJ (2004) Neutrality, niches, and dispersal in a temperate forest understory. *Proc Natl Acad Sci USA* 101:7651–7656
- Google (2007) Google Earth 4.1.7076.4458 (beta). earth.google.com
- Gottschalk E, Griebeler EM, Waltert M, Muhlenberg M (2003) Populations dynamic in the Grey Bush Cricket *Platycleis albopunctata* (Orthoptera: Tettigoniidae)—what causes interpopulation differences? *J Insect Conserv* 7:45–58
- Heidorn TJ, Joern A (1984) Differential herbivory on C3 versus C4 grasses by the grasshopper *Ageneotettix deorum* (Orthoptera: Acrididae). *Oecologia* 65:19–25
- Heidorn TJ, Joern A (1987) Feeding preference and spatial distribution of grasshoppers (Acrididae) in response to nitrogen fertilization of *Calamovilfa longifolia*. *Funct Ecol* 1:369–375

- Hiltunen T, Laakso J, Kaitala V (2006) Interactions between environmental variability and immigration rate control patterns of species diversity. *Ecol Modell* 194:125–131
- Hubbell SP (1997) A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs. *Coral Reefs* 16(Suppl 1):S9–S21
- Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton and Oxford
- Hubbell SP (2006) Neutral theory and the evolution of ecological equivalence. *Ecology* 87:1387–1398
- Hutchinson GE (1957) Homage to Santa Rosalia or why are there so many kinds of animals? *Am Nat* 93:145–159
- Isely FB (1938) The relationships of Texas Acrididae to plants and soils. *Ecol Monogr* 8:551–604
- Isern-Vallverdu J, Pedrocchi-Renault C, Voisin JF (1993) A comparison of methods for estimating density of grasshoppers (Insecta: Orthoptera) on alpine pastureland. *Rev Alp Ecol* II:73–80
- Ivey RD (2003) Flowering plants of New Mexico, 4th edn. Ivey, Albuquerque
- Joern A (1979) Feeding patterns in grasshoppers (Orthoptera: Acrididae): factors influencing diet specialization. *Oecologia* 38:325–347
- Jones MM, Tuomisto H, Clark DB, Olivas P (2006) Effects of meso-scale environmental heterogeneity and dispersal limitation on floristic variation in rain forest ferns. *J Ecol* 94:181–195
- Karst J, Gilbert B, Lechowicz MJ (2005) Fern community assembly: the roles of chance, and the environment at local and intermediate scales. *Ecology* 86:2473–2486
- Kröel-Dulay G, Ódor P, Peters DPC, Hochstrasser T (2004) Distribution of plant species at a biome transition zone in New Mexico. *J Veg Sci* 15:531–538
- Larson DP, O'Neill KM, Kemp WP (1999) Evaluation of accuracy of sweep sampling in determining grasshopper (Orthoptera: Acrididae) community composition. *J Agric Urban Entomol* 16:207–214
- Lekberg Y, Koide RT, Rohr JR, Aldrich-Wolfe L, Morton JB (2007) Role of niche restrictions and dispersal in the composition of arbuscular mycorrhizal fungal communities. *J Ecol* 95:95–105
- MacArthur RH (1957) On the relative abundance of bird species. *PNAS* 43:293–295
- MacArthur RH, Wilson EO (1963) An equilibrium theory of insular zoogeography. *Evolution* 17:373–387
- MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton
- Maurer BA (1999) Untangling ecological complexity: the macroscopic perspective. University of Chicago Press, Chicago
- McGill BJ (2003) A test of the unified neutral theory of biodiversity. *Nature* 422:881–885
- McGill BJ, Maurer BA, Wiser MD (2006) Empirical evaluation of neutral theory. *Ecology* 87:1411–1423
- Moore D (2006) Met Central (2006). <http://sev.lternet.edu/modules.php?op=modload&name=News&file=index&catid=4>
- Muldavin EH, Moore DI, Collins SL, Wetherill KR, Lightfoot DC (2008) Above ground net primary production dynamics in a northern Chihuahuan Desert ecosystem. *Oecologia* 155:123–132
- Novotny V, Basset Y, Miller SE, Welbien GD, Brenner B, Cizek L, Drozd P (2002) Low host specificity of herbivorous insects in a tropical forest. *Nature* 416:841–844
- Otte D (1976) Species richness patterns of New World desert grasshoppers in relation to plant diversity. *J Biogeogr* 3:197–209
- Otte D (1981) The North American grasshoppers volume I; Acrididae: Gomphocerinae and Acridinae. Harvard University Press, Cambridge, MA
- Otte D (1984) The North American grasshoppers volume II; Acrididae: Oedipodinae. Harvard University Press, Cambridge, MA
- Pandolfi JM (2002) Coral community dynamics at multiple scales. *Coral Reefs* 21:13–23
- Pennington DD, Collins SL (2007) Response of an aridland ecosystem to interannual climate variability and prolonged drought. *Landsc Ecol* 22:897–910
- Recher HF, Davis WE, Calver MC (2002) Comparative foraging ecology of five species of ground-pouncing birds in western Australian woodlands with comments on species decline. *Ornithol Sci* 1:29–40
- Ricklefs RE (2006) The unified neutral theory of biodiversity: do the numbers add up? *Ecology* 87:142–1231
- Söderström B, Svensson B, Vessby K, Glimskär A (2001) Plants, insects and birds in semi-natural pastures in relation to local habitat and landscape factors. *Biodivers Conserv* 10:1839–1863
- Thompson R, Townsend C (2006) A truce with neutral theory: local deterministic factors, species traits and dispersal limitation together determine patterns of diversity in stream invertebrates. *J Animal Ecol* 75:476–484
- Tilman D (1982) Resource competition and community structure. Princeton University Press, Princeton
- Torrusio S, Cigliano MM, de Wysiecki ML (2002) Grasshopper (Orthoptera: Acrididae) and plant community relationships in Argentine pampas. *J Biogeogr* 29:221–229
- USDA, and NRCS (2004) PLANTS profile: *Juniperus monosperma*. In USDA, and NRCS (2004) The PLANTS database, version 3.5. National Plant Data Center, Baton Rouge. www.plants.usda.gov
- Volkov I, Banavar JR, Maritan A, Hubbell SP (2003) Neutral theory and relative species abundance in ecology. *Nature* 424:1035–1037