Local and regional-scale responses of ant diversity to a semiarid biome transition

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The locations of biome transitions and ecotones are frequently defined by the rapid shift from one form of dominant vegetation to another. The composition of animal taxa is predicted to shift in parallel with that of dominant plants and species diversity is predicted to be greater in transitional zones than in adjacent areas. We asked whether ant species diversity and composition supported these predictions across a biome transition between shortgrass steppe and Chihuahuan desert vegetation. Neither species richness nor diversity was highest at the biome transition region as a whole, or within habitats in the biome transition. The biome transition region was not intermediate in ant species composition or in the representation of different faunal complexes. The community similarity between matched habitats shared between the biome transition zone and adjacent regions was less than that between distinct habitats occurring within regions. A zoogeographic transition for ants may occur to the north of the phytogeographic transition and may be coincident with the northern limits of monsoonal precipitation patterns. In contrast, the phytogeographic transition may be related to less extreme climatic variation within the monsoonal region occurring further south.

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At the scales of regions and continents, biotic assemblages exhibit a mosaic pattern in which characteristics of local communities may change abruptly in space. Documenting and understanding the processes underlying such transitions are key to explaining local and regional patterns in species diversity (Gosz 1992). At broad spatial scales, biome transitions are often defined by a shift in the dominance of particular life forms or generalist taxa in response to climatic variation across a region (Gosz and Sharpe 1989). The location of this shift, or tension zone (Curtis 1959, Gosz and Sharpe 1989), may be determined by the steepness of climatic gradients or because of nonlinear, threshold responses of taxa to changing interactions between climate and other environmental variables across a region.

At a finer spatial scale, similar transitions (traditionally termed ecotones) may be produced by variations in soil texture, microtopography, or moisture availability (Gosz 1993, Kent et al. 1997). While ecotones have received considerable attention from ecologists and wildlife managers (e.g. Leopold 1933, Hansen and di Castri 1992) transitions between biomes at the biogeographic scale are less well documented.

Biome transitions and ecotones are usually recognized by the responses of plant communities, but ecosystem properties and animal communities are believed to respond in parallel due to the great influence of dominant plants on ecosystem structure (Gosz 1993, Risser 1995). However, animal communities vary in their responses to changes in plant communities depending upon the characteristics of constituent species (Elton 1927). Many bird species forage and nest in vegetation, and small mammals may depend upon particular plant life forms, such as shrubs, for food or

cover. Thus, their assemblages might be expected to covary spatially with changing plant-community structure in transitional areas. On the other hand, some animal groups, such as soil-dwelling invertebrates, might respond to environmental variation, including soil texture, independently of plant composition.

Like ecotones, biome transitions are predicted to exhibit plant and animal communities with higher species diversity than those in adjacent areas because they harbor species from two or more community types (Odum 1971, Risser 1995). This is due to an increase in the number of distinct habitat types in an area, and to increases in the number of species within habitats due to dispersal from distinct habitats (i.e. mass effects; Shmida and Wilson 1985, Nekola and White 1999) emerging from the proximity of these habitats. For some taxa, transitional areas may represent distinct habitats and may favor some species found in lower abundance in adjacent habitats (Hansen and Urban 1992). There have been few studies of species diversity patterns across biome transitions (Risser 1995), so it is unclear how different taxa compare in their responses to changing environmental conditions across landscapes and regions.

Krasnov and Shenbrot (1998) addressed these issues by examining the response of different animal taxa to a desert-steppe phytogeographic boundary in two stages. First, they asked whether the assemblages found on either side of the boundary differed. If they differed, they then evaluated whether the assemblages belonged to different faunal complexes (i.e. have similar geographic ranges that are distinct from those of other complexes) or if the assemblages represented different groupings within the same faunal complex. They sought to determine how well phytogeographic classification represented the zoogeographic patterns of different animal groups.

In this study, we use a similar approach to investigate the response of ant assemblages to a biome transition between North American shortgrass steppe and Chihuahuan desert biomes. Ants were examined because they are abundant and diverse animals in these environments. Furthermore, ants are an interesting group with which to consider how animals respond to phytogeographic transitions because ants share certain characteristics with plants. Both plants and ant colonies occupy a fixed position and capture resources through the ramification of foraging modules (Andersen 1991). Thus, ants and plants may respond to similar environmental variables, such as soil texture (Johnson 1992) and microclimate (Perfecto and Vandermeer 1996).

The Sevilleta (SEV) Long-Term Ecological Research (LTER) site in central New Mexico, USA, contains a phytogeographic boundary between the shortgrass steppe and Chihuahuan desert biomes. The shortgrass steppe biome extends north and east from this point through northwest Texas, western Kansas, eastern Col-

orado, to southern Wyoming (Fig. 1). The Chihuahuan desert extends south and east from SEV through western Texas into the Mexican states of Chihuahua, Durango and Coahuila. The biome transition has been recognized by the shift in the dominant vegetation from blue grama *Bouteloua gracilis* grasslands that characterize the shortgrass steppe to the black grama *Bouteloua eriopoda*-dominated grasslands interspersed with more xeric creosotebush *Larrea tridentata* shrublands that characterize the Chihuahuan desert. Within the SEV, blue and black grama co-dominate (Minnick and Coffin 1999). At the regional scale, the location of the biome (vegetation) transition in central New Mexico is believed to be caused by changes in temperature and
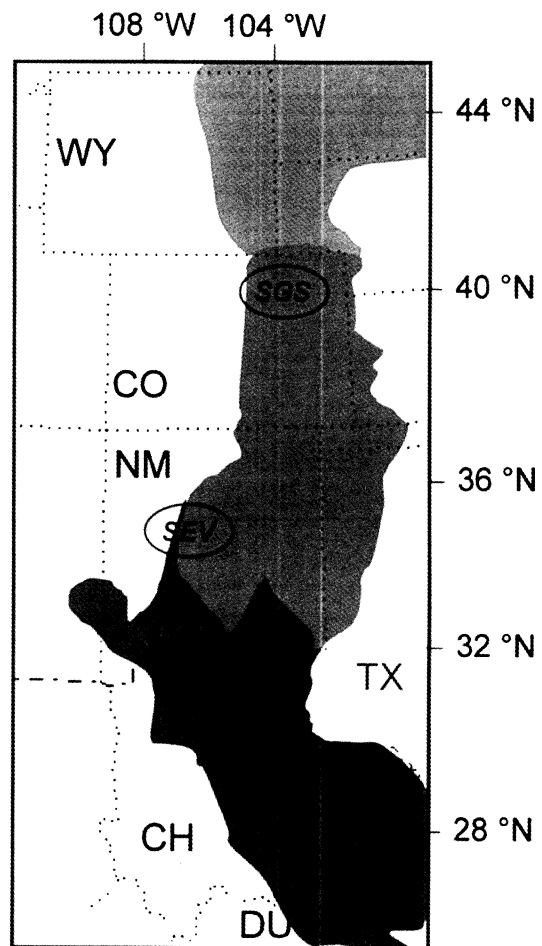

Fig. 1. Approximate distribution of northern mixed prairie vegetation (top), shortgrass steppe vegetation (middle) and Chihuahuan desert vegetation in Wyoming (WY), Colorado (CO), New Mexico (NM), United States, and Chihuahua (CH), Coahuila (CO), and Durango (DU), Mexico. Detail in WY and CO adapted from Lauenroth and Milchunas (1991) and within NM from Gosz (1992). The locations of the study sites are also given: SGS = Shortgrass Steppe Long-Term Ecological Research (LTER) site, SEV = Sevilleta LTER, and JRN = Jornada LTER.

the timing and amount of precipitation (see Minnick and Coffin 1999). The location of the biome transition within the boundaries of the SEV may be determined by the local impedance of spring storms caused by local topography (Gosz 1992).

Here, we examined the response of ant assemblages to the biome transition at SEV, and predicted that SEV would represent a zoogeographic transition for ants. We tested the hypothesis that SEV would have greater ant species diversity than adjacent sites occurring entirely within the shortgrass steppe and Chihuahuan desert biomes. We compared matched habitat types occurring within the biome transition zone with the same habitats occurring in regions away from the transition to determine if local habitats, in the context of a biome transition, would have greater ant diversity due to the mixing of faunal complexes. Thus, we will determine whether the transition affects ant diversity both locally (habitat scale) and regionally (site scale).

We then asked whether the ant fauna of the biome transition was intermediate in species composition and in the representation of different faunal complexes at a regional scale. We hypothesized that matched habitats occurring in different regions would be more similar to one another in species composition than to distinct habitats within the same region, and that these communities would represent distinct faunal complexes.

Materials and methods

Study areas

Field work was conducted within the SEV and two other LTER sites located well within the shortgrass steppe and Chihuahuan desert biomes (Fig. 1). SEV is located in the Sevilleta National Wildlife Refuge in Socorro County, New Mexico. The area receives ca 265 mm precipitation yr^{-1}. We sampled areas in the eastern half of this refuge, which has been ungrazed since 1973. Black grama grasslands in the MacKenzie Flats area, blue grama grasslands near the foot of the Los Piños range, and creosotebush stands and mixed areas of creosotebush and black grama grassland were sampled in the Five-Points area.

To represent the shortgrass steppe, we examined ant assemblages within the Shortgrass Steppe (SGS) LTER site located in the USDA-ARS Central Plains Experimental Range near Nunn, Weld County, Colorado. This area is wetter than SEV, receiving ca 320 mm of precipitation yr^{-1}, and is dominated by blue grama grassland. In order to represent blue grama grasslands under similar conditions to those found at SEV, we sampled within 1-ha exclosures that had not been grazed since 1939. Creosotebush shrublands do not occur at SGS, so we sampled the two most common shrubland types to balance the effects of landscape

heterogeneity among regions for overall region-scale comparisons. The shrublands constituted patches of saltbush *Atriplex canescens* that typically occupy low-lying areas (Stapp 1997), and soapweed yucca *Yucca glauca*-dominated patches often found on stony hillocks or ridges.

Chihuahuan desert was represented by the Jornada (JRN) LTER site, located in New Mexico State University's Chihuahuan Desert Rangeland Research Center (CDRRC; elsewhere referred to as the College Ranch), and in the USDA-ARS Jornada Experimental Range (JER) near Las Cruces, Doña Ana County, New Mexico. This area is slightly drier than SEV, receiving ca 232 mm of precipitation yr^{-1}. Black grama/mesa dropseed *Sporobolus flexuosus* grasslands are abundant here and were sampled within grazing exclosures (1–2 ha) that had been ungrazed since 1946. These grasslands also included shrubs such as honey mesquite *Prosopis glandulosa* and *Yucca elata*. We also sampled creosotebush shrublands along a gently-sloping bajada near Mount Summerford, as well as in honey mesquite-dominated coppice dunes that represent an irreversible transformation from grassland to shrubland due to a combination of grazing and drought (Hennessy et al. 1983, Schlesinger et al. 1990).

Ant sampling

Ant species composition and abundance were sampled using 10 stations along 90-m transects (10-m spacing). Within each habitat type in each region, four transects were randomly located in areas accessible by roads. Pitfall traps were polypropylene sample containers (65 mm diameter, 100 mm deep) filled with 40 ml of a propylene glycol/ethanol mixture. Traps were buried in the soil with lids on for at least 72 h prior to operation in order to allow the ants to reestablish foraging trails and become accustomed to the disturbance (Greenslade 1973). Traps within a region were operated simultaneously for 72 h during a trapping session. Trapping was performed at two times per year to coincide with the driest and wettest months during which temperatures would be sufficiently high for ants to be active. Dry periods were October/November at SGS, and April at SEV and JRN. Wet periods were June at SGS, and July/August at SEV and JRN. This sampling design ensured that ants with different seasonal activity would be recorded. Ants were sampled over two years (1996–98; four samples per region) to improve our estimates of ant-community composition at the regions, given annual variation in ant activity above ground in arid environments (Whitford 1978).

Following trapping, pitfall traps were capped and removed to the laboratory for processing. Ant specimens in each trap were counted and identified to species or morphospecies. Most species identifications were

verified by Roy R. Snelling of the Los Angeles County Museum, James Trager of the Shaw Arboretum, and William MacKay of the Univ. of Texas, El Paso. Nomenclature follows Bolton (1995).

For each sampling period, ant abundances were ln-transformed at the trap level in order to reduce the wide variance in capture rates due to differences in the proximity of traps to nests, differences in capture rates due to the effects of varying substrate on forager movement, and differential species responses to traps (Bestelmeyer et al. 2000). Furthermore, species that are poorly sampled by pitfall trapping techniques due to their foraging behaviour, including legionary (*Neivamyrmex*), obligate slave-making (*Polyergus*), and subterranean ants (*Hypoponera*), were excluded from analyses. The ln-transformed trap abundance values were summed across sampling periods and traps to obtain transect values that were the units of analysis. These values represent scaled estimates of ant activity that are likely to provide less biased comparisons between samples than those based on raw abundance values (Andersen 1991). Summing across seasons results in a sample that is less affected by seasonal or weather-induced differences in ant foraging activity than a single-season sample and thus better represents ant community characteristics at points in space (see Krasnov and Shenbrot 1998).

Characterization of faunal complexes and biogeographic analysis

Common ant genera occurring within the three study areas were classified into three faunal complexes based upon previous studies of biogeographic patterns in North American ants (Gregg 1963, Brown 1973, A. N. Andersen pers. comm.). These were 1) holarctic genera that are restricted to the north temperate and boreal regions of the United States, Canada, Europe, and Asia; 2) New World xeric genera that inhabit arid and semiarid regions within the Neotropical (e.g. western Chaco woodlands and Monte/Atacama deserts of South America) and/or Nearctic biogeographic realms (in the Great Basin, Mojave, Sonoran, and Chihuahuan deserts), and 3) tropical and/or cosmopolitan genera that are abundant throughout the warmer areas of the world. The distribution of congeneric species within this latter group exhibit a great deal of heterogeneity, nonetheless, they are treated at the generic level here for consistency.

To broaden our consideration of biogeographic patterns between the shortgrass steppe and Chihuahuan desert regions, we documented the regional distributions of ant species found within our study areas and tallied the number of species per ant genus in a belt encompassing both biomes as well as the northern mixed prairie found to the north of shortgrass steppe

(Lauenroth and Milchunas 1991). We considered records in prairie and steppe in eastern Wyoming, eastern Colorado, and northwestern Texas, and in Chihuahuan desert-dominated regions in western Texas and a site in the state of Durango, Mexico, using previously published species lists. Distribution data for Wyoming were recorded at the county level (Wheeler and Wheeler 1988), so the eastern counties in which prairie exists were divided into three groups based upon differences in their latitude. Colorado records included mapped locations of collection localities (Gregg 1963), so records in areas dominated by shortgrass steppe were divided into 1°-latitude blocks extending from the eastern border to the foothills of the Rocky Mountains. Texas records were also mapped (Moody and Francke 1982, Cokendolpher and Francke 1990) and shortgrass steppe records (referred to as Great Plains grassland; Moody and Francke 1982) and Chihuahuan desert records (located in the Trans-Pecos region of west Texas) were determined using regional maps and habitat records found within the publications. All records for the Mapimi Biosphere Reserve in Durango were in Chihuahuan desert vegetation (Rojas-Fernandez and Fragoso 1994). In all cases, we attempted to ascertain from the publications whether the species occurred within the appropriate habitat type.

Data analysis

Species diversity was characterized as both species richness and logseries-α diversity, which includes a measure of the distribution of abundance among species (Magurran 1988). Richness and diversity values at the transect level, for which there were four replicates per habitat, were compared between regions using Wilcoxon rank-sum tests and Kruskal-Wallis tests where appropriate. Richness and diversity at the habitat level within regions and at the level of the entire region were unreplicated and were compared directly. We also report incidence-based coverage estimators (ICE; EstimateS 5.01; Colwell 1997) of region-scale and habitat-scale richness to compare estimates of true species richness, given that there may have been differences in sampling efficiency among the regions (Colwell and Coddington 1994).

We directly compared the scaled abundances of individuals within genera that belonged to different faunal complexes among each of the study regions by summing the transect scores of each genus within each region. These measures were unreplicated. We then compared patterns of species composition between matched habitat pairs using correspondence analysis (CA; ter Braak and Smilauer 1998). This analysis was used to test whether patterns of association of species with particular habitats were stronger than between-region variation in species composition. According to our

Fig. 2. Species richness (S) and logseries-α diversity (α) patterns in a) blue grama, b) black grama, and c) Larrea habitats at the SEV and SGS or JRN. Measured richness/diversity values at transects (n = 4; solid circles), at the habitat scale (solid square), and a habitat-scale richness estimate (incidence-based estimator; open square) are presented.
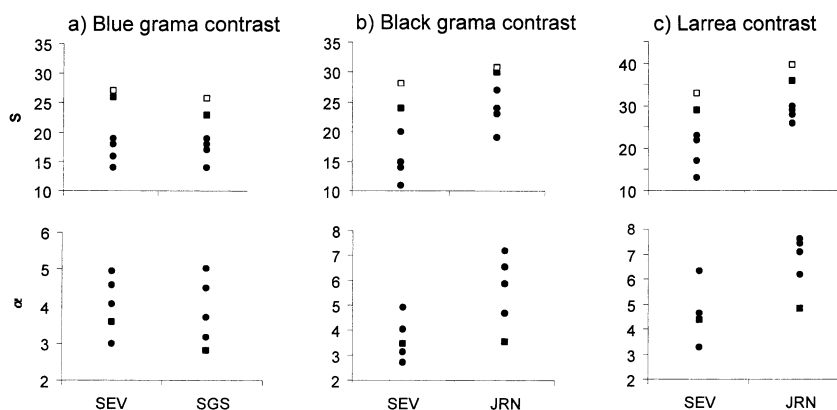
hypothesis, we expected that axis 1 should segregate transects located in different habitat types, and variation due to between-region differences might be apparent on axis 2.

We used Bray-Curtis ordination to examine species turnover from SGS to JRN within a group of ant species that were found within the study regions and that had also been recorded in areas between the SGS and SEV. We defined SGS and JRN as endpoints in the ordination (McCune and Mefford 1999) and plotted the Bray-Curtis axis 1 scores against latitude to look for discontinuities, in particular an increase in slope, along the north-south latitudinal gradient from shortgrass steppe to Chihuahuan desert. The presence of SEV at such a discontinuity would support its characterization as a zoogeographic transition for ants (e.g. Gosz and Sharpe 1989). In addition, we compared the number of species belonging to different faunal complexes along the gradient using all records from the literature sources, provided that the species were believed to occur in the appropriate habitats.

Results

Diversity patterns

We recorded 33, 39, and 40 ant species within the dominant, ungrazed grassland type together with the two other most dominant habitat types at SGS, SEV and JRN, respectively. Estimated total richness values (ICE) were similar (SGS, 41.7; SEV, 42.7; JRN, 40.6). Within the blue grama habitat, neither transect-scale richness (Wilcoxon rank sum = 18.5; n = 4, 4; p = 1.00) nor logseries-α (Wilcoxon rank sum = 18.0; n = 4, 4; p = 1.000) differed between SGS and SEV (Fig. 2a). Observed habitat-scale richness and diversity were higher at SEV, although estimated richness was only slightly so. Within the Chihuahuan desert habitats, transect-scale richness (Wilcoxon rank sum = 11; n = 4, 4; p = 0.06) and logseries-α (Wilcoxon rank sum = 11;

n = 4, 4; p = 0.06) within black grama grassland were greater at JRN than at SEV (Fig. 2b). Habitat-scale richness, both observed and estimated, was higher in JRN, although habitat-scale logseries-α was not. In creosotebush shrubland, transect-scale richness was also higher at JRN than SEV (Wilcoxon rank sum = 20; n = 4, 4; p = 0.03), but logseries-α was not (Wilcoxon rank sum = 24; n = 4, 4; p = 0.11; Fig. 2c). Estimated and observed habitat-scale richness and logseries-α followed this pattern. Thus, at a regional scale, at a habitat scale, and at a transect scale within habitats, SEV did not possess a more diverse ant fauna than either the SGS or JRN.

Patterns of species composition

Holarctic genera (Formica, Lasius, and Myrmica) were abundant at SGS (Fig. 3) but were completely absent from SEV and only one occurrence of Formica was recorded at JRN (F. perpilosa; Appendix). In particular, the abundance of Formica at SGS was greater than that of any genus at any region in this study. The abundance of xeric genera increased from SGS to JRN. Forelius was found only once at SGS and Myrmecocystus was absent. Abundances of Dorymyrmex and Pogonomyrmex were similar at SGS and SEV, but were greater at JRN. Results for the cosmopolitan genera were mixed. Some genera (Leptothorax and Tapinoma) decreased in abundance from SGS toward JRN, whereas others were absent at SGS and abundant at SEV and JRN (Aphaenogaster and Crematogaster), or were least abundant at SEV (Solenopsis). Pheidole was abundant in all regions and increased from SGS to SEV and JRN. Overall, the SGS region differs strongly from SEV and JRN by the abundance of holarctic genera, whereas SEV and JRN are comparatively similar to one another, and are dominated by the genus Pheidole.

Consequently, the SGS region was most distinct in species composition from the others, sharing only 7 species with SEV (19.4% of species; Jaccard's index)

and 3 species with JRN (8.2%). On the other hand, SEV and JRN shared 26 species (65.8%). Within the blue grama habitat, only four species were shared between the SGS and SEV (16.5%), demonstrating the great importance of variation in species composition between these regions (thus a CA comparison was not used to compare blue grama habitats within them). The CA of the habitats shared between SEV and JRN showed that the primary axis separated the regions, and the second axis separated black grama from creosotebush habitats within regions (Fig. 4). This indicates that variation between regions was greater than between-habitat variation. Further, differences in species composition between the habitats were stronger at SEV than at JRN along axis 2.

Species turnover within the ant fauna recorded in study regions revealed a smooth gradient from SGS to JRN (Fig. 5). The amount of variance in the original
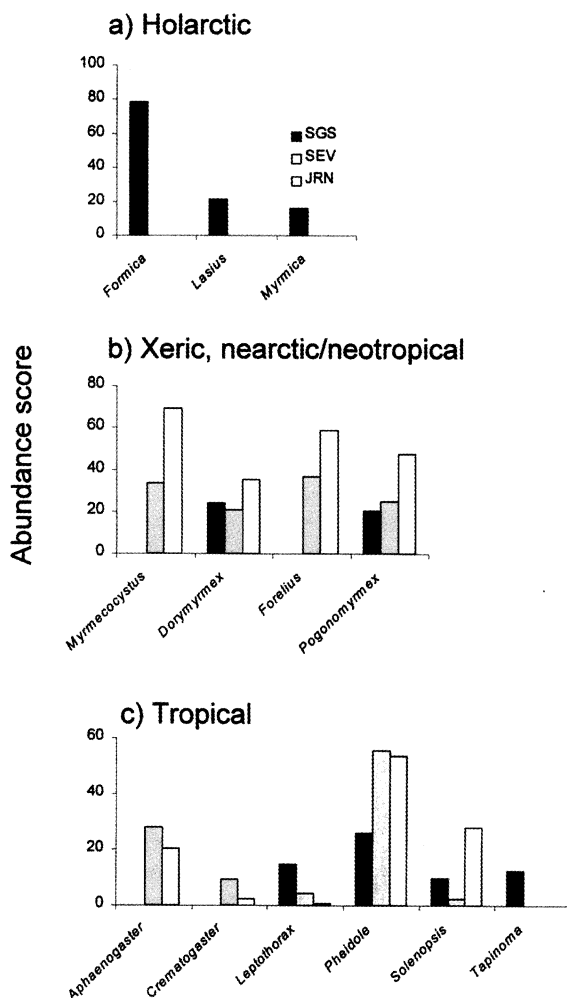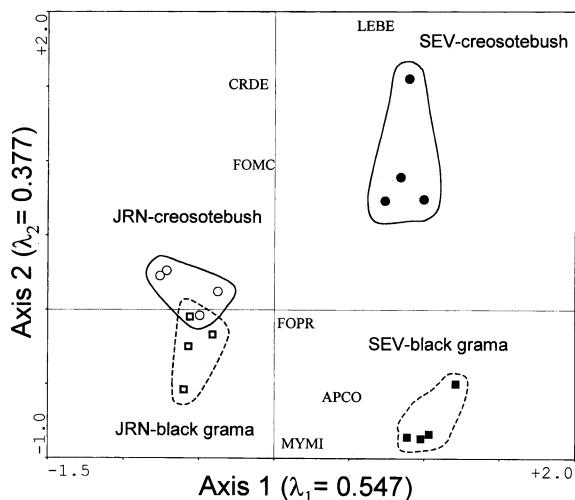

Fig. 4. Correspondence analysis of ant species composition at transects located in creosotebush shrubland and black grama grassland at the SEV and JRN sites. Species found in both SEV and JRN and that drive covariation on axis 2 are shown: apco = *Aphaenogaster cockerelli*, crde = *Crematogaster depilis*, doin = *Dorymyrmex insanus*, fomc = *Forelius mccooki*, fopr = *F. pruinosus*, lebe = *Leptothorax bestelmeyeri*, mymi = *Myrmecocystus mimicus*.

distance matrix that was explained by the first Bray-Curtis axis was high (87.7%), indicating that much of the variation in the ant composition was represented in the axis 1 scores. If SEV were located at a compositional threshold, we would expect it to have a lower, more intermediate Bray-Curtis score and to be flanked by much higher and much lower scores on each side. In fact, SEV is not intermediate in composition and is instead most similar to JRN.

The proportion of the species belonging to different faunal complexes also exhibited continuous change from north to south along the latitudinal gradient (Fig. 6). Throughout Wyoming and northern Colorado, hol-

Fig. 3. The abundance of genera, pooled across all transects, belonging to different faunal complexes at the three study sites.
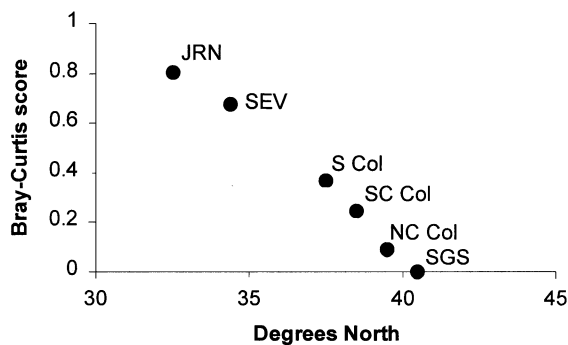

Fig. 5. Variation in Bray-Curtis axis 1 scores based upon an ordination of presence-absence data of the distribution of ant species (see text) among areas between and including the SGS and JRN. Latitude values are at the center of geographic areas.
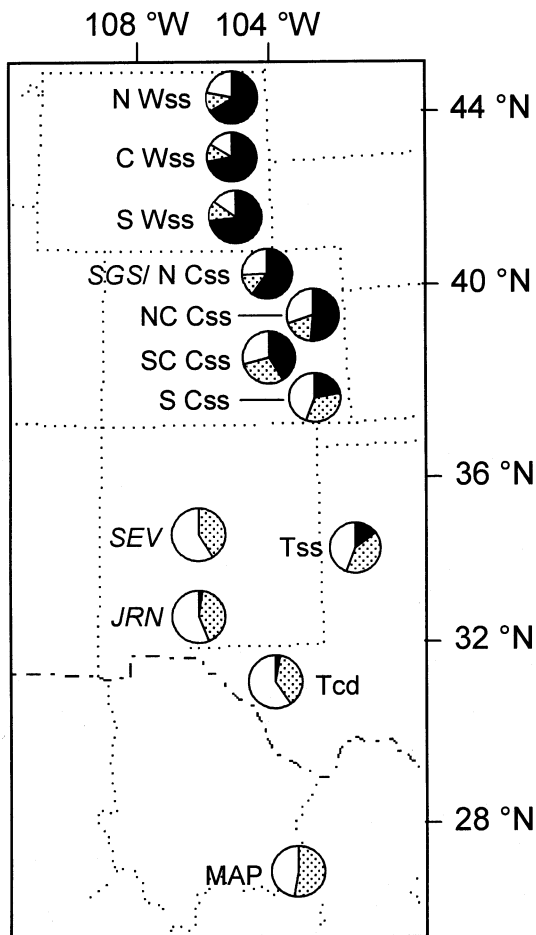
Fig. 6. The proportion of shortgrass steppe and Chihuahuan desert ant species occurring in each geographic area that belong to holarctic (black), xeric (stippled), and tropical (white) faunal complexes. N, NC, C, SC, S = north, north-central, central, south central, and south, respectively. Prefix W, C, T = Wyoming, Colorado, and Texas, respectively. Suffix ss = shortgrass steppe habitat, and cd = Chihuahuan desert habitat. MAP = Mapimi Biosphere Reserve.

SEV and JRN, but estimated richness values were similar across the sites. This is surprising considering that ants are thermophilic animals. Cold temperatures have been identified as an important stress affecting ant composition and limiting richness at local (Gregg 1963, Andersen 1997) and global (Brown 1973, Andersen 1995) scales, and the duration of freezing temperatures decreases from SGS to JRN. Precipitation, however, also decreases from north to south, and aridity may also limit ant richness (Davidson 1977, Marsh 1986). It is possible that these factors act antagonistically and lead to similarities in regional ant richness among the sites.

Within the blue grama habitat, richness did not differ between the SGS and SEV. The pool of species available to colonize blue grama habitats is almost completely different between SGS and SEV, so a potential role for regional-scale faunal mixing or mass effects in increasing richness in. SEV's blue grama habitat does not apply. The large species turnover between SGS and SEV is likely due to the relatively large distance between these sites (Fig. 5). Local richness levels in the two regions may be governed by similar factors.

In both Chihuahuan desert habitats, however, richness decreased from JRN to SEV. It is possible that, because these habitats at SEV are located at the extreme northern extent of their distribution, they may be less suitable for many Chihuahuan ant species found deeper within the biome. Ant distributions may be more strongly limited by the changing environmental factors that also ultimately limit the northward distribution of dominant plant taxa. This process, coupled with a lack of faunal mixing or mass effects, may lead to a depression in within-habitat richness at a plant-defined biome transition. Whitford (pers. comm.) also recorded unusually low ant richness at a Chihuahuan desert-oak savanna transition zone in eastern New Mexico, and this may be due to a similar combination of processes.

arctic species predominate, and their representation declines rapidly through Colorado. By the time SEV is reached, all but one holarctic species has disappeared. A few holarctic taxa persist in the shortgrass steppe of Texas.

Discussion

Diversity patterns

Contrary to the hypothesized peak in richness expected at a biome transition, species richness was not greatest at SEV at the regional scale, nor within habitats that are shared with adjacent regions. Along the north-south gradient, measured richness increased from SGS to

Patterns of species composition

SEV was not intermediate in either the abundance of different faunal complexes (Fig. 3) or consequently, in species composition. Community change along the regional gradient was continuous (Fig. 5) and illustrative of the distance-decay of similarity noted by Nekola and White (1999). Thus, the shift in the composition of dominant types observed among the plants that determines the physical structure of these environments is not reflected in a shift in the composition of ants, and the spatial relationships among the regions and habitats determined relationships in species composition. Within the SEV, we (Bestelmeyer and Wiens in press) found strong differences in species composition among the blue grama, black grama, and *Larrea* shrubland habi-

tats (see also Fig. 4). These fine-scale differences are not related to biogeographic patterns. The ants inhabiting blue grama habitats at SEV are largely distinct from those found at SGS, indicating that the environmental features governing the distributions of ants and blue grama differ and do not covary between regions. For example, of several species that were abundant in blue grama grasslands at SEV, only *D. smithi* was also recorded in the blue grama habitat at SGS (Bestelmeyer and Wiens in press). Other species that were present within blue grama at the SGS site, including *Pheidole longula*, *Leptothorax olbiquicanthus*, and *Dorymyrmex insanus*, were most abundant at SEV in black grama grassland, the creosotebush-grass ecotone, or creosotebush shrubland, respectively (Bestelmeyer and Wiens in press). Even when regional pools are more similar, such as between SEV and JRN, regional differences in species composition continue to predominate (Fig. 4, axis 1). Species such as *P. longula* that were abundant in black grama at SEV (in fact, this ant was the most abundant species at SEV) were completely absent from JRN (Appendix).

In studies comparing the relationship between local and regional determinants of diversity patterns, it is common to witness an overriding influence of regional variation on features of local community structure (Cornell and Lawton 1992, Medel 1995, Caley and Schluter 1997). Many of these results are likely due to the fact that regional variation also includes a great deal of unmeasured local variation, depending upon how "habitat" is defined. Bestelmeyer (2000) showed that habitat types defined by vegetation, such as creosotebush shrubland, may include areas that differ in soil characteristics between regions, to which ant species may respond directly. The use of incorrect criteria to define the habitat of a taxon (Kolasa and Rollo 1991) will confound regional comparisons; insofar as human-defined habitats occurring in different regions differ in other important ways, controlled comparisons of the role of local versus regional effects will be difficult.

Despite the overall importance of regional differences, some species present at both SEV and JRN responded to the contrast between grassland and *Larrea* shrubland in parallel (Fig. 4; axis 2). This effect is due to the influence of species such as *Crematogaster depilis*, *Forelius mccooki*, and *Leptothorax bestelmeyeri* that were associated with creosotebush plants in both regions, as well as species such as *Aphaenogaster cockerelli* and *Myrmecocystus mimicus* that were associated with grasslands across the regions. This suggests that the definition of habitat should vary among species within higher taxa, further complicating generalizations about regional patterns of community structure.

The response of ant-community composition to variation between grasslands and shrublands was greater at SEV than at JRN. This is consistent with the suggestion that the sensitivity of assemblage structure to local environmental variation is heightened at biome transitions due to an increased variability in climate, and thus an increasing role for climate-by-environment interactions (Gosz and Sharpe 1989). As noted above, however, the habitats vary in soil texture between the regions, so it is not possible to isolate the effects of climatic and local environmental variation.

Where is the zoogeographic transition?

Our results are similar to those of Krasnov and Shenbrot (1998). There are differences in ant composition among habitats at SEV, but SEV does not harbor a zoogeographic transition for ants. Where, then, might there be a transition for ants, if one exists? Patterns of variation in species composition (Fig. 3), and the proportion of species belonging to different faunal complexes (Fig. 6), suggest that an important transitional zone for ants occurs north of SEV. Unfortunately, ant distributional data are lacking for northern New Mexico, but it is likely that nearly all holarctic species occurring in southern Colorado west of the eastern New Mexico border terminate their distributions in extreme southern Colorado or northeastern New Mexico.

The location of the postulated zoogeogeographic transition in ant faunal complexes at the Colorado/New Mexico border is concordant with a climatic transition from a monsoonal precipitation pattern (summer rainfall peak) to a Midwestern pattern (spring rainfall peak) in southern Colorado that has been identified by Comrie and Glenn (1998; Fig. 7). This threshold is based upon a multivariate regionalization of precipitation patterns in the southwestern United States and northern Mexico. While such a regionalization imposes an artificially discrete structure to continuous variation in climate, the analysis nonetheless suggests the presence of a relatively steep gradient in climate across the northern New Mexico-southern Colorado region that may be an important determinant of ant composition. A similar transition may occur within the panhandle of Texas (Figs 6, 7). More detailed surveys of ant abundance and precipitation patterns across these regions will be necessary to test this proposition.

Comrie and Glenn (1998) also identified a secondary set of climatic subregions within the large monsoonal region (Fig. 7). The junction of three of these subregions corresponds roughly with the location of SEV. Thus, major shifts in the life-forms of plants and ants appear to occur in response to different kinds or scales of climatic variation. A threshold response of recruitment to climate may determine the location of a grass transition at SEV (Minnick and Coffin 1999), but ants may exhibit a threshold response to distinct climatic features occurring farther to the north. This threshold

may constitute a direct response to climate, independent of the influence of plant distribution. At this point, little information is available to suggest potential mechanisms for such a threshold in ants. One possibility is that seasonal variation in precipitation patterns affect ant distributions by determining the timing of reproduction and the successful establishment of ant colonies (Hölldobler and Wilson 1990). Another possibility is that changing temperature regimes coincident with the northern limit of the monsoon affect the distribution of ant faunal complexes via physiological tolerances.
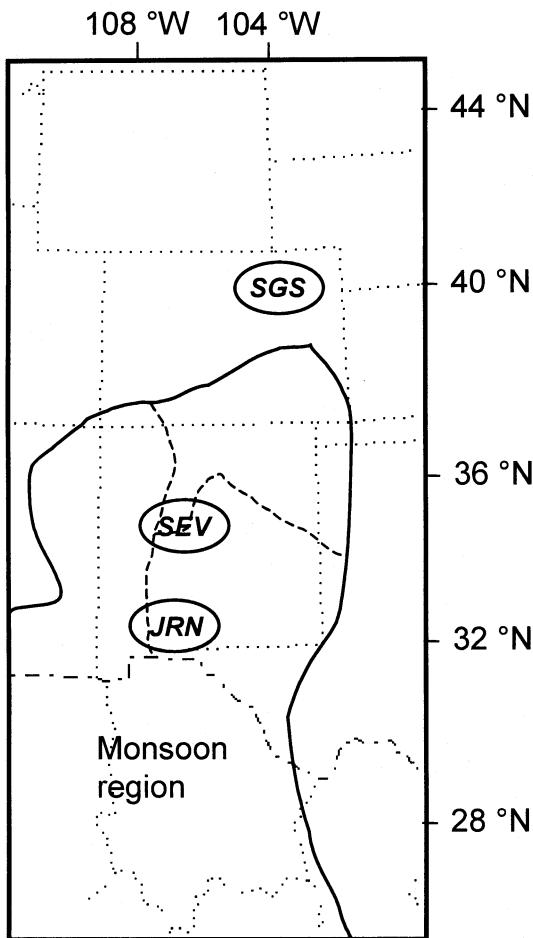

Fig. 7. The northern limit of the monsoonal precipitation region (solid line) and the division between three subregions within the monsoonal region of New Mexico (dashed lines), based upon a multivariate (principal components analysis) regionalization of precipitation seasonality and annual variability in the southwestern United States and northern Mexico (adapted from Comrie and Glenn 1998). In this plot, regional delineations were defined by different principal components, and depict the maximum-loading approach in which each of the 309 weather stations studied was assigned to the component upon which it loaded most highly (Fig. 4b in Comrie and Glenn 1998). All of the regionalization methods Comrie and Glenn tried yielded similar results.

Our results illustrate that vegetation-animal relationships and the spatial patterns that they create vary depending upon the characteristics of the study organisms (Wiens 1989, Conroy and Noon 1996). Parallel studies of other animal taxa along the biogeographic gradient considered here have yet to be performed. We expect that these studies will find that in some cases, the abiotic processes determining the distribution patterns of different taxa are similar and covary in space, but in other cases, they are not. Given the variability of species characteristics and the environmental variables to which they respond (e.g. van Jaarsveld et al. 1998, Woinarski et al. 1999), untangling and documenting patterns of biodiversity will likely require detailed surveys of different kinds of organisms (Haila and Margules 1996) using organism-specific definitions of habitats and ecoregions.

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Appendix. Ant species recorded in all the habitat types examined at the Shortgrass Steppe, Sevilleta, and Jornada LTER sites. OT = Pitfall trapped in a habitat other than that examined in this study, incuding grazing treatments within in dominant grassland types. HC = hand collected only.

Subfamily / Species	SGS	SEV	JRN
Ponerinae			
Hypoponera opacior (Forel)	OT		
Ecitoninae			
Neivamyrmex carolinensis (Emery)	HC		
Neivamyrmex nigrescens (Cresson)		x	
Neivamyrmex texanus Watkins		x	x
Myrmicinae			
Aphaenogaster cockerelli André		x	x
Aphaenogaster huachucana Creighton		HC	
Crematogaster depilis Wheeler		x	x
Crematogaster larreae Buren			x
Crematogaster navajoa Buren		x	HC
Crematogaster punctulata Emery		x	HC
Crematogaster sp. S1		x	
Leptothorax bestelmeyeri		x	x
Leptothorax carinatus Cole		x	x
Leptothorax olbiquicanthus Cole	x	x	x
Leptothorax schmitti (Wheeler)	x		
Leptothorax sp. C1	x		
Leptothorax sp. S1		x	
Monomorium minimum (Buckley)	x	x	x
Myrmica emeryana Cole	x		
Myrmica sp. C1	x		
Myrmica sp. C2	HC		
Pheidole cerebrosior Wheeler		x	x
Pheidole coloradensis Emery	x		
Pheidole crassicornis Emery		x	x
Pheidole desertorum Wheeler		HC	
Pheidole hyatti Emery		x	x
Pheidole longula Emery	x	x	
Pheidole militicida Wheeler			x
Pheidole rugulosa Gregg			x
Pheidole sciophila Wheeler			x
Pheidole soritis Wheeler		x	
Pheidole sp. C1	x		
Pheidole sp. J1		x	x
Pheidole sp. J2			x
Pheidole sp. S1		x	
Pheidole tepicana? Pergande		x	
Pheidole tucsonica Wheeler		x	x
Pheidole xerophila Wheeler		x	x
Pogonomyrmex apache Wheeler		x	HC
Pogonomyrmex californicus (Buckley)			x
Pogonomyrmex desertorum Wheeler		x	x
Pogonomyrmex imberbiculus Wheeler		x	x
Pogonomyrmex maricopa Wheeler		x	x
Pogonomyrmex occidentalis (Cresson)	x		
Pogonomyrmex rugosus Emery		x	x
Pogonomyrmex texanus Francke&Merickel		x	x
Solenopsis amblychila Wheeler			x
Solenopsis krockowi Wheeler			x
Solenopsis molesta sp.	x	x	
Solenopsis sp. J1			x
Solenopsis xyloni McCook			x
Tetramorium spinosum (Pergande)			x
Trachymyrmex smithi Buren		x	x
Dolichoderinae			
Dorymyrmex c.f. *flavus* McCook			x
Dorymyrmex insanus (Buckley)	x	x	x
Dorymyrmex smithi Cole	x	x	
Dorymyrmex sp. S1		x	
Dorymyrmex bicolor Wheeler			x
Forelius mccooki McCook		x	x
Forelius pruinosus (Roger)	x	x	x
Tapinoma sessile (Say)	x		

Appendix (Continued)

Subfamily Species	SGS	SEV	JRN
Formicinae			
Acanthomyops coloradensis (Wheeler)	HC		
Brachymyrmex sp. S1		x	
Camponotus festinatus (Buckley)			x
Camponotus noveboracensis (Fitch)	x		
Camponotus vicinus Mayr		x	
Formica argentea Wheeler	HC		
Formica bradleyi Wheeler	x		
Formica dakotensis Emery	x		
Formica densiventris Viereck	x		
Formica fossaceps Buren	x		
Formica integroides sp.	x		
Formica lasiodes Emery	x		
Formica limata Wheeler	x		
Formica mucescens Wheeler	x		
Formica neoclara Emery	HC		
Formica neogagates Viereck	x		
Formica obscuripes Forel	x		
Formica obtusopilosa Emery	x		
Formica occulta Francouer	x		
Formica oreas Wheeler	x		
Formica perpilosa Wheeler			OT
Formica wheeleri Stitz	x		
Lasius crypticus Wilson	x		
Lasius neoniger Emery	x		
Lasius pallitarsus (Provancher)	HC		
Lasius sitiens Wilson	x		
Lasius sp. C1	OT		
Lasius subumbratus Viereck	HC		
Myrmecocystus depilis Forel		x	x
Myrmecocystus mexicanus Wesmael		x	x
Myrmecocystus mimicus Wheeler		x	x
Myrmecocystus navajo Wheeler		x	x
Myrmecocystus placodops Forel		x	
Myrmecocystus romainei Snelling			x
Paratrechina terricola (Buckley)			HC
Polyergus breviceps Emery	OT		