

## ANT BIODIVERSITY IN SEMIARID LANDSCAPE MOSAICS: THE CONSEQUENCES OF GRAZING VS. NATURAL HETEROGENEITY

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**Abstract.** The conservation of biodiversity in landscape mosaics requires an understanding of the impacts of human land use within mosaic elements and an evaluation of the biological uniqueness of different elements. We address these issues by examining patterns of ant diversity in three semiarid rangeland landscapes used predominantly for grazing. These landscapes lie along a regional gradient from shortgrass steppe through a transitional zone to desert grassland, along which climate and ant species composition vary. Within each landscape, we compared the effects of grazing and natural variation in soils and vegetation on ant diversity and community composition. Grazing had little effect on ant richness, diversity, or composition at the transitional zone or the desert grassland site, but ungrazed areas at the shortgrass steppe site had a higher overall richness and favored the abundance of some species. Some samples of saltbush (*Atriplex canescens*) shrubland were similar to ungrazed samples in richness and species composition. In both the transitional zone and the desert grassland, creosotebush (*Larrea tridentata*)-dominated habitats harbored comparatively species-rich and distinct ant communities. In addition, mesquite (*Prosopis glandulosa*) coppice dunes at the desert grassland site favored the abundance of several species that were rare across the site. Canonical correspondence analysis revealed that variation in soil strength and texture best explained community variation at the shortgrass steppe site, whereas soil texture and associated differences in shrub density best explained differences in composition at the transitional and desert grassland sites. The characterization of habitats based upon vegetation classification did not adequately reflect environmental variation that was important to ants in shortgrass steppe, but reflected important soil textural variation in the transitional and desert grassland sites. These results suggest that ant conservation in these semiarid rangelands should emphasize patterns of variation in soil properties. The results add to a growing consensus that a variety of variables determined by the responses of several focal taxa may be needed to characterize biodiversity patterns.

**Key words:** ants; canonical correspondence analysis; desert grassland; diversity; Formicidae; grazing; habitat classification; shortgrass steppe; soil texture.

### INTRODUCTION

In a world increasingly dominated by human activities, a central focus of modern conservation biology is the maintenance of species diversity in landscape mosaics composed of areas of varying land use and natural habitat features (Lubchenco et al. 1991, Steffen et al. 1992). Two objectives supporting this broad goal include the identification and preservation of mosaic elements that maximize biodiversity (Prendergast et al. 1993, Wagner et al. 2000) and the evaluation and minimization of negative impacts to biodiversity within mosaic elements that are exploited by humans (Pimentel et al. 1992, Wiens 1994).

Livestock grazing is one of the most extensive forms of land use. About 26% of the Earth's land surface

(FAO 1996) and 70% of land in the 11 western United States (Fleischner 1994) is used primarily for grazing. Where grazing pressure is poorly managed, desertification can result in the loss of grasslands and associated species (Graetz 1994). Mabbutt (1984) estimates that 62% of the world's grasslands, and 42% of grasslands in North America, are desertified. At both regional and global scales, the magnitude of grazing-induced environmental change may be great (Wright 1990, Fleischner 1994, Wuerthner 1994), and Cooperrider (1991) considered grazing to be "one of the primary threats to biological diversity."

Ecologists and environmentalists, however, have recently debated the impacts of grazing (Brussard et al. 1994, Noss 1994, Brown and McDonald 1995, Curtin 1995, Fleischner 1995, Wuerthner 1995). For example, some authors (Milchunas et al. 1998, Perevolotsky and Seligman 1998) contend that "undergrazing" carries negative consequences for biodiversity in some situations. Several points have emerged from this debate. First, the response of biodiversity to grazing is not

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easily generalizable; species respond in different ways depending upon their adaptations and the environmental and historical context in which these adaptations evolved (Milchunas and Lauenroth 1993). Second, the effects of grazing on the environmental variables that underlie species' responses vary among ecosystems (Lauenroth and Milchunas 1991, Perevolotsky and Seligman 1998). Finally, comparisons of biodiversity responses to grazing are often complicated by such factors as the size, position, availability, and representativeness of grazing treatments, temporal variability in grazing effects, the methods used to select study sites, the methods used to assess grazing intensity, and the measurements used to characterize biodiversity (Fleischer 1994, Brussard et al. 1994, Brown and McDonald 1995). Clearly, there is an urgent need for carefully designed studies of grazing impacts on different taxa in different regional settings (e.g., Landsberg et al. 1997). These studies should consider the range of grazing intensities most often observed in a region and employ a variety of measures to characterize the responses of species communities.

Anthropogenic effects upon biodiversity operate within a context of naturally occurring landscape variation in soils, vegetation, and topography. Such variation may have important consequences for the distribution of biodiversity and its management (e.g., Tuomisto et al. 1995), yet we know very little about them or their relationships to human influences in most ecological systems. Because grazing management and conservation decisions are implemented at relatively broad scales (Turner et al. 1995), management areas often include habitats other than the economically important rangeland vegetation. These habitats may contain unique biotic communities that complement the overall biodiversity of landscape mosaics (Wagner et al. 2000). Rangeland conservation strategies should explicitly consider the conservation value of less exploited habitats adjacent to areas of more intense economic use (Forman 1995).

A landscape perspective may also aid our understanding of the indicator properties of focal taxa. The use of focal taxa to characterize the effects of human activities on other, unconsidered species (Kremen et al. 1993) has been necessary because exhaustive biodiversity studies are usually impossible within reasonable time frames (Scott et al. 1993). Such focal or indicator taxa should be sensitive to a wide range of environmental variation and their ecology should be relatively well understood. If a potential indicator taxon reveals little response to anthropogenic environmental change, this may be due to its general insensitivity to environmental variation in a region (Whitford et al. 1999). Alternatively, a small response by an otherwise sensitive focal taxon may suggest that an anthropogenic change is relatively unimportant to other, similar kinds of organisms at that site. Comparing the responses of focal taxa across a range of environmental variation

occurring at a site can assist in our evaluation of a focal taxon's utility (e.g., Haila and Margules 1996).

Here, we address these issues by examining the effects of different grazing regimes on ant communities (Hymenoptera: Formicidae) at three Long-Term Ecological Research (LTER) sites in shortgrass steppe and desert grassland biomes of the United States. Ants have been used extensively as focal taxa in studies of human impacts throughout the world (e.g., Perfecto and Snelling 1995, Bestelmeyer and Wiens 1996, Andersen 1997, Majer and Nichols 1998) because they are abundant and their responses may indicate environmental patterns that determine the distribution of other organisms over a wide range of scales and environments (Andersen 1997). This may be especially true for invertebrates (Andersen et al. 1998), which constitute the bulk of animal biodiversity but seldom enter into conservation decision making (Dingle et al. 1997). Furthermore, ants are important components of ecosystems in their own right (Elmes 1991, Catangui et al. 1996).

Previous studies have demonstrated that ants respond in ecologically interpretable ways to grazing impacts and other variation (Scougall et al. 1993, Abensperg-Traun et al. 1996, Bestelmeyer and Wiens 1996, Landsberg et al. 1997, Nash et al. 1998). These studies have indicated that the direct effects of differences in microclimate (Andersen 1991a, Bestelmeyer and Wiens 1996, Perfecto and Vandermeer 1996), and the abundance of nesting microhabitats (Abensperg-Traun et al. 1996) and food resources (Nash et al. 1998) are important mechanisms that mediate ant community responses. Because surface-dwelling ant species are often highly territorial, a strong indirect effect of changing environments can be mediated by changes in the activity of dominant ant species (Scougall et al. 1993). Ant species may also respond directly to soil properties (Johnson 1992, Crist and Wiens 1996) although this is seldom documented.

Our approach was to examine the consequences of grazing activities in relation to natural sources of heterogeneity in soils and vegetation that may contribute to diversity patterns across landscapes (Forman 1995). In contrast to some other studies, grazing treatments were chosen to reflect the dominant rangeland management that we observed in each landscape rather than selecting highly degraded but spatially limited areas (see Brussard et al. 1994, Brown and McDonald 1995). We compared these treatments to one another, to ungrazed areas, and to other, previously recognized vegetation types occurring within each LTER site. Instead of relying solely on land-type categorizations, we also measured the effects of grazing and natural processes on several environmental variables that are believed to affect ant distributions. Specifically, we asked (1) do general measures of ant diversity and community composition change with grazing and how do these effects vary between regions, (2) is variation in ant diversity or composition due to grazing more or less important

than that generated by natural processes acting at landscape scales, and (3) do vegetation-type categorizations correspond well to the primary sources of environmental variation affecting ant community structure?

#### STUDY AREAS AND METHODS

##### *Study sites, grazing treatments, and vegetation types*

This work was conducted in and around the Shortgrass Steppe (SGS), Sevilleta (SEV), and Jornada (JRN) LTER sites. These sites span a transition from the shortgrass steppe biome (SGS) to the Chihuahuan Desert biome (JRN). Grassland is the dominant vegetation type in these regions and cattle grazing is the dominant land use (Lauenroth and Milchunas 1991, Holechek et al. 1994). At each site, we sampled ants and environmental variables along 20 transects, located in areas of different grazing management within the dominant grassland type and in other, less dominant vegetation types (mostly shrublands) that were recognized in previous studies at each site. Four transects were located in each of five grazing or vegetation types (collectively referred to as "habitats") in each site. To maintain control over variables such as climate and to facilitate regional comparisons, all transects were distributed within a 100-km<sup>2</sup> area in each site.

Sufficient replication, and thus precise statistical inference, is difficult at broad spatial scales (Hargrove and Pickering 1992). In order to maximize the generality of our assessments within each site, grazing and vegetation types considered in this study were selected to represent the dominant categories of vegetation and grazing management recorded by maps as well as the prevalent conditions that we observed while driving all roads in and around the 100-km<sup>2</sup> areas. Elevation at the transects within a site varied by no more than 58 m and we located transects away from the confounding influences of major topographic relief and watercourses. Overall, grazing types fell into the following categories: (1) ungrazed areas in enclosures or reserves, (2) moderate-managed grazed areas as determined by rangeland research protocols in U.S. Department of Agriculture-Agricultural Research Service sites (USDA-ARS; see Holechek et al. 1994, Milchunas et al. 1998), and (3) public-leased or private lands with varied grazing management. Study areas situated in public-leased and private lands were located as near as possible to other grazing types.

Areas along networks of roads passing through the study areas were categorized according to the five habitats we studied at a site. Within a habitat, the four transects were allocated among road sections (~0.5–5 km) so that the sections were as evenly distributed as possible within the study area. Most transects were then placed 100 m from the road at a randomly determined location along each section. Transects located on the other side of cattle fences from the road were placed 300 m from the fenceline in order to avoid the influence

of the fence on cattle activity patterns. Transect locations that fell upon unusual terrain, such as in flooded depressions or areas near to water points (see Brown and McDonald 1995), were avoided because they represented a minute area within the habitat and were likely to experience atypical grazing pressures. Ungrazed enclosures were selected to be interspersed with transects located in moderate-grazed treatments. Interspersion was not possible for treatments found exclusively in different administrative units, such as private land, or for other vegetation types. The grazing and vegetation types sampled in each LTER site are described below.

SGS was located in the USDA-ARS Central Plains Experimental Range (CPER) and Pawnee National Grasslands (PNG) near Nunn, Weld County, Colorado. The area receives ~320 mm precipitation/yr. The shortgrass steppe vegetation is dominated by blue grama grass (*Bouteloua gracilis*). Within the CPER, we sampled moderately summer-grazed pastures and 1-ha enclosures that had not been grazed since 1939. The stocking rate in the moderate-grazed treatment at CPER has averaged 6.5 ha/animal since 1961 (see Milchunas et al. 1994). The PNG is administered by the U.S. Forest Service. Grazing intensity across the PNG is also managed at moderate levels based on the protocols used at the CPER (R. Peterson, *personal communication*). Two shrubland types were sampled in the CPER: (1) patches of saltbush (*Atriplex canescens*) that typically occupy low-lying areas (Stapp 1997), and (2) soapweed yucca (*Yucca glauca*)-dominated patches often found on stony hillocks or ridges. These sites were moderately grazed in winter and spring.

SEV was located in the Sevilleta National Wildlife Refuge and on adjacent privately owned land in Socorro County, New Mexico. The area receives ~265 mm precipitation/yr, and represents a transitional zone between shortgrass steppe and Chihuahuan Desert grassland biomes (Gosz 1992). We sampled sites in the MacKenzie Flats area of the refuge that were dominated by black grama grass (*Bouteloua eriopoda*). The refuge has been ungrazed since 1973, although the MacKenzie flats was heavily grazed prior to this time (R. Parmenter, *personal communication*). The grazed transects were located in privately owned land to the north of MacKenzie Flats, where stocking rate information was unavailable. We also sampled in ungrazed blue grama grasslands near the foot of the Los Piños range, creosotebush stands (*Larrea tridentata*), and ecotonal areas between creosotebush and black grama grassland.

JRN was located largely 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) and on Bureau of Land Management (BLM) land near Las Cruces, Doña Ana County, New Mexico. The area receives ~232 mm precipitation/yr. The grassland transects were characterized by black

grama and mesa dropseed (*Sporobolus flexuosus*); shrubs such as honey mesquite (*Prosopis glandulosa*) and *Yucca elata* were often common. Grazing exclosures (1–2 ha) that had been ungrazed since 1946 and moderately grazed grassland were sampled within CDRRC and JER, and historically more heavily grazed areas with a greater cover of honey mesquite were sampled in the BLM land. Moderate grazing in CDRRC employed a stocking rate of 67 ha/animal from 1967, whereas the BLM land was stocked at 42 ha/animal until 1981, when the range was destocked to 72 ha/animal. An extended drought in the 1950s reduced grass cover in both areas (see complete history in Holechek et al. 1994). We also sampled creosotebush shrublands along a gently sloping bajada, as well as honey mesquite-dominated coppice dunes that often represent an irreversible transformation from grassland to shrubland due to a combination of grazing and drought (Hennessy et al. 1983, Schlesinger et al. 1990).

#### *Sampling of environmental variables and ant communities*

Features of ant communities and environmental features were measured at a maximum of 10 stations (sub-samples) along each transect (10-m spacing). We measured environmental variables that are known to influence the distribution and abundance of ants. Soil texture may determine where ants nest (Johnson 1992) and may vary strongly at broad scales. Soil cores were collected at four of the 10 transect stations, so that each sample was separated by 30 m. Soil samples were collected to a depth of 24 cm using a 2.54 cm (1-inch) diameter probe. The samples were homogenized for soil texture analyses and thus represented the average soil properties encountered by ants with nest structures occurring from near the surface to a 24-cm depth. Soil texture was determined following the hydrometer method and calculations presented in Gee and Bauder (1986). For each sample, we calculated the percentage of coarse sand (particles  $>500 \mu\text{m}$ ), fine sand (53–500  $\mu\text{m}$ ), silt, and clay. Values for the four samples were averaged to obtain values for transects.

Basal cover, the vertical complexity of vegetation, and soil strength were recorded around each station of each transect. Cover and vegetative complexity determine the microclimates to which ants are exposed (Perfecto and Vandermeer 1996) as well as nesting sites and food abundance. Soil strength may determine where ants nest. Cover and complexity of vegetation may be altered by grazing (Milchunas and Lauenroth 1989) and soil strength may increase in grazed areas due to soil compaction from livestock trampling (Bryant et al. 1972).

Basal cover at the ground surface and vertical complexity were recorded at five points along each of four 2-m long rays placed at 90° angles around each station. Points on each ray were located at 0.25, 0.5, 1.0, 1.5, and 2.0 m from the station. Cover was classified as

bare ground, grass, shrub, halfshrub, forb, litter, and other. Bare ground was further subdivided into stones/pebbles (2–64 mm) and small particles ( $<2 \text{ mm}$ ). Percent cover was calculated for each station and then averaged across stations to obtain values for transects. Prior to analysis, cover values were arcsine square-root transformed following recommendations in Zar (1997).

Vertical complexity was measured as the number of touches of vegetation to a 1-cm diameter pole held perpendicular to the ground surface at 0–50 and 50–100 cm height intervals. Thus, areas with sparse grass cover and with short-statured grasses tend to have low complexity values, whereas areas with abundant tall-statured grasses and shrubs tend to have higher values, particularly in the 0–50 cm stratum. Vertical complexity values were summed across points within stations and averaged across stations to obtain transect values.

Soil strength was measured as the pressure ( $\text{kg}/\text{cm}^2$ ) required for the end of a soil penetrometer (Pocket Penetrometer, Forestry Suppliers, Incorporated, Jackson, Mississippi, USA) to penetrate the soil to a depth of  $\sim 6.5 \text{ mm}$ . Soil strength was measured at four points located 0.25 cm from the sample point along each ray. Soil strength values were averaged across points within stations and averaged across stations. All soil strength measures were taken when the soil surface was dry.

Ant species composition and abundance were measured using pitfall traps. Pitfall traps were polypropylene sample containers (65 mm diameter, 100 mm deep) filled with 40 mL of a propylene glycol/ethanol mixture. Pitfall traps were buried in the soil with lids on for at least 72 h to allow ants to reestablish foraging trails and become accustomed to the disturbance (Greenslade 1973). Traps within a site were operated simultaneously for 72 h during a trapping session. Trapping sessions occurred in the dry (October/November at SGS, April at SEV and JRN) and wet (June at SGS, July/August at SEV and JRN) seasons of each site over two years (June 1996–June 1998) during periods when temperatures were high enough for ants to be active. This ensured that ants with different seasonal activity would be recorded. 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 University 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, includ-

ing legionary (*Neivamyrmex*), obligate slave-making (*Polyergus*), and subterranean ants (*Hypoponera*), were excluded from analyses. The ln-transformed trap abundance values were summed to obtain transect values. These values represent scaled estimates of ant activity that may provide less biased comparisons between samples than those based on raw abundance values (Andersen 1991b).

Species richness analyses considered the number of species recorded at transects over all sampling periods. For diversity and multivariate analyses (see *Study areas and methods: Data analysis*), the scaled transect abundance values were summed over the four sampling periods. 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). Most colonies of ant species in this study are sessile, but their activity above ground may vary greatly depending upon season or weather events (Whitford 1978). Thus, even when ant species are unrecorded within a seasonal sample, they are likely to be present below ground and thus constitute a component of the community with respect to the characterization of a site's biodiversity (A. N. Andersen, *personal communication*). There was considerable seasonal variation in ant activity (B. Bestelmeyer and J. Wiens, *unpublished manuscript*).

#### Data analysis

We compared overall differences in environmental conditions between habitats using MANOVA (Proc GLM; SAS 1996). All environmental variables, including both the soil and vegetation-related variables, were tested simultaneously. When overall tests were significant, individual variables were evaluated for differences among habitats.

Species diversity (measured as species richness and Fisher's logseries- $\alpha$ ) was compared among habitats within sites at two spatial scales. Values were compared statistically using general linear models at the transect scale ( $n = 4$  replicates per habitat). Habitat-scale values (considering all four transects together) were unreplicated. Additionally, we used species richness extrapolation techniques (EstimateS 5.0.1; R. Colwell)<sup>2</sup> based on trap-level data ( $n = 40$  per habitat) to obtain estimates of true habitat-scale richness given that habitats may have varied in the completeness of the species sampling. Because ant abundances in traps are aggregated due to their colonial structure, only incidence-based estimators were examined (Chao 2, Incidence-based Coverage Estimator [ICE], Jackknife 1 and 2); of these, ICE was used for comparisons because its asymptote appeared most stable (see Colwell and Coddington 1994 for description). Differences among ant

richness and diversity values at the transect scale were analyzed using generalized linear models (GLM; SAS 1996).

We tested for differences in species composition among habitats using the multiresponse permutation procedure (MRPP; McCune and Mefford 1999). MRPP is a nonparametric procedure for testing the hypothesis of no differences in species composition among two or more groups of samples (Zimmerman et al. 1985). The test is based upon a distance measure between samples, and we used Sørensen's distance, calculated as

$$1 - \frac{2w}{A + B}$$

where  $A$  and  $B$  are the number of species in two samples and  $w$  is the number of species shared between the samples. This distance measure performs similarly to the more commonly used Euclidian distance, but has the advantage of de-emphasizing outliers (McCune and Mefford 1999). Tests of significance were based upon an approximated  $P$  value from a Pearson Type III distribution of the test statistic (McCune and Mefford 1999).

Correspondence analysis (CA; CANOCO 4.0; ter Braak and Smilauer 1998) was used to examine variation in community composition among habitats within sites independently of a priori land-type categorizations. CA is an indirect ordination technique that extracts the primary gradients in species composition/abundance patterns, independently of measured environmental variation. Specifically, we sought to assess whether or not gradients in species composition corresponded to land-type categorizations.

We used the canonical form of CA, canonical correspondence analysis (CCA), to examine how the relationships between species and significant environmental variables corresponded to land-type categorizations and to synthetic gradients observed in the species data using CA. By comparing the results of CA with those of CCA, we can evaluate how well that patterns in the species data can be explained by measured environmental variables. Congruent configurations of samples in CA and CCA ordinations increase our confidence that the important environmental variables have been measured (Økland 1996). CCA is a modification of CA in which the ordination axes are constrained to be linear combinations of measured environmental variables (i.e., direct ordination; Jongman et al. 1995). The ordination diagram reflects patterns of species composition with respect to measured environmental gradients. Significant environmental variables were selected through stepwise forward-selection procedures in CANOCO. Variables explaining a significant ( $P < 0.05$ ) amount of variation in Monte Carlo permutation tests (199 random permutations of the samples in the species data) were included in the CCA analyses. Rare species were downweighted in

<sup>2</sup> URL: <http://Viceroy.eeb.uconn.edu/EstimateS>.

TABLE 1. Mean values (1 SE in parentheses) of habitat structural variables measured at transects ( $n = 4$ ) in each habitat of each site (see *Study areas and methods: Sampling*).

Site and habitat	Ground cover (%)					Shrub density	Vertical complexity	
	Total bare	Stones	Grass	Forb/ Subshrub	Litter		0–0.5 m	0.5–1 m
<b>Shortgrass Steppe</b>								
<b>PNG grazed</b>	8.0 (1.7) <sup>b</sup>	0 <sup>b</sup>	46.8 (8.3)	0 <sup>c</sup>	40.8 (7.5)	0 <sup>b</sup>	56.5 (3.2) <sup>c</sup>	...
<b>CPER grazed</b>	3.3 (0.9) <sup>c</sup>	0 <sup>b</sup>	58.9 (0.9)	1.0 (0.4) <sup>ab</sup>	34.1 (0.7)	0 <sup>b</sup>	63.5 (2.3) <sup>bc</sup>	...
<b>Ungrazed</b>	4.6 (1.1) <sup>bc</sup>	0.1 (0.1) <sup>b</sup>	48.4 (11.3)	1.6 (0.6) <sup>a</sup>	41.5 (9.9)	0.19 (0.19) <sup>b</sup>	94.4 (5.1) <sup>a</sup>	...
<i>Atriplex</i> shrub	3.0 (0.5) <sup>c</sup>	0 <sup>b</sup>	37.9 (6.4)	0.4 (0.2) <sup>bc</sup>	55.4 (6.8)	16.2 (4.7) <sup>a</sup>	83.6 (14.5) <sup>ab</sup>	...
<i>Yucca</i>	21.3 (3.3) <sup>a</sup>	1.5 (0.5) <sup>a</sup>	28.8 (1.5)	0.6 (0.5) <sup>abc</sup>	43.6 (4.2)	22.7 (2.2) <sup>a</sup>	57.2 (6.1) <sup>c</sup>	...
<b>Sevilleta</b>								
<b>Grazed</b>	63.3 (5.5) <sup>abc</sup>	0.3 (0.1) <sup>c</sup>	9.1 (1.9) <sup>ab</sup>	0	21.5 (2.2) <sup>c</sup>	0.5 (0.2) <sup>b</sup>	34.3 (2.0) <sup>cd</sup>	...
<b>Ungrazed</b>	53.4 (6.7) <sup>c</sup>	0.7 (0.3) <sup>c</sup>	8.6 (2.8) <sup>ab</sup>	0	36.0 (5.2) <sup>a</sup>	0.9 (0.5) <sup>b</sup>	88.9 (10.6) <sup>a</sup>	...
Blue grama	66.9 (2.2) <sup>ab</sup>	1.0 (0.4) <sup>bc</sup>	10 (1.4) <sup>a</sup>	0.1 (0.1)	21.1 (3.3) <sup>c</sup>	0.6 (0.4) <sup>a</sup>	51.2 (6.5) <sup>bc</sup>	...
<i>Larreal</i> /grass	58.9 (2.6) <sup>bc</sup>	2.1 (0.4) <sup>b</sup>	4.8 (1.2) <sup>b</sup>	0.5 (0.2)	32.9 (2.4) <sup>ab</sup>	11.9 (5.5) <sup>b</sup>	56.5 (5.7) <sup>b</sup>	...
<i>Larrea</i> shrub	72.6 (2.7) <sup>a</sup>	4.2 (0.7) <sup>a</sup>	0.4 (0.2) <sup>c</sup>	0.1 (0.1)	25.0 (2.7) <sup>bc</sup>	38.8 (8.0) <sup>a</sup>	28.1 (3.0) <sup>d</sup>	...
<b>Jornada</b>								
<b>BLM grazed</b>	75.3 (2.5) <sup>a</sup>	0.2 (0.1)	1.3 (0.3) <sup>b</sup>	0.3 (0.1)	21.9 (2.9) <sup>b</sup>	6.1 (1.4) <sup>b</sup>	16.5 (1.9) <sup>b</sup>	4.2 (1.4) <sup>b</sup>
<b>CDRRC grazed</b>	59.1 (5.8) <sup>bc</sup>	0.6 (0.2)	3.9 (2.4) <sup>ab</sup>	0.1 (0.1)	36.3 (5.6) <sup>ab</sup>	2.7 (0.5) <sup>c</sup>	33.1 (8.6) <sup>ab</sup>	3.2 (1.3) <sup>b</sup>
<b>Ungrazed</b>	46 (3.9) <sup>c</sup>	1.7 (0.7)	7.0 (2.1) <sup>a</sup>	0	45.3 (3.0) <sup>a</sup>	2.0 (0.4) <sup>c</sup>	70.6 (14.2) <sup>a</sup>	1.0 (0.8) <sup>b</sup>
Coppice dune	68.0 (7.3) <sup>ab</sup>	0.3 (0.2)	0.5 (0.2) <sup>b</sup>	0.3 (0.1)	29.5 (7.5) <sup>b</sup>	6.0 (1.1) <sup>b</sup>	22.0 (2.7) <sup>b</sup>	8.2 (2.5) <sup>b</sup>
<i>Larrea</i> shrub	70.1 (5.3) <sup>ab</sup>	1.5 (1.3)	2.0 (1.4) <sup>b</sup>	0.1 (0.1)	24.6 (5.0) <sup>b</sup>	16.3 (0.7) <sup>a</sup>	70.9 (29.8) <sup>a</sup>	18.4 (5.7) <sup>a</sup>

Notes: Grazing contrasts are boldface; other habitat types are not. Superscript letters within columns indicate that a variable differed significantly among habitats within a site (ANOVA,  $P < 0.05$ ); values with different letters are significantly different at  $P < 0.05$  (LSD). The units for vertical complexity are number of hits/station (see *Study areas and methods: Study sites*), and shrub density is the number of shrubs within 5 m of a station. Vertical complexity at 0.5–1 m was not analyzed at the Shortgrass Steppe and Sevilleta sites because too few hits were recorded in that stratum. Abbreviations: PNG, Pawnee National Grasslands; CPER, Central Plains Experimental Range; BLM, Bureau of Land Management; CDRRC, Chihuahuan Desert Rangeland Research Center.

CANOCO. Biplot scaling was used and the CCA plots were focused on intersample distances (see ter Braak and Smilauer 1998 for discussion) using sample scores that are linear combinations of the environmental variables (ter Braak 1994). Thus, distances between sample (transect) positions in this CCA indicate chi-square distances in an ordination space defined by the environmental variables (McCune 1997). Only species for which the ordination explained  $\geq 40\%$  of variation in their abundance were plotted on the diagram for clarity.

We measured the degree of association of individual species with particular habitats using indicator species analysis (i.e., the indicator value method [IndVal]; Dufrene and Legendre 1997). Species were assigned indicator values for each habitat that were greatest when (1) all individuals of a species occurred in only one habitat and (2) all samples within one habitat contained an occurrence by that species. Values for each habitat varied from zero (no indication) to 100 (perfect indication). We evaluated the statistical significance of the maximum indicator values for each species using Monte Carlo randomization tests in which species abundance data were randomized among habitats (1000 iterations; McCune and Mefford 1999). Observed indicator values were then directly compared to a distribution of these values generated from randomized communities. The  $P$  value reported is the proportion of randomized trials with values equal to or exceeding the observed values.

## RESULTS

### *Environmental variables*

Together, grazing-induced and natural habitat variation had significant effects on environmental variables at SGS (Wilks'  $\lambda = 0.0005$ ;  $F = 3.84$ ;  $df = 40, 24.6$ ;  $P = 0.0004$ ), SEV (Wilks'  $\lambda = 0.00015$ ;  $F = 5.55$ ;  $df = 40, 24.6$ ;  $P = 0.0001$ ), and JRN (Wilks'  $\lambda = 0.00004$ ;  $F = 6.32$ ;  $df = 44, 21.08$ ;  $P = 0.0001$ ) sites.

The effects of grazing on environmental variables within the dominant grassland types varied among the study areas. At SGS, grazing tended to reduce vertical complexity between the ungrazed and moderately grazed treatments, decrease the cover of nongrass plants (Table 1), and increase soil strength (Table 2), but the cover of grass was unaffected. At SEV, grazing reduced both vertical complexity and litter cover whereas grass cover was unaffected, due largely to the increased dominance of small burrograss (*Scleropogon brevifolius*) plants that were evenly distributed (B. T. Bestelmeyer, *personal observations*). In contrast to SGS, however, soil strength was unaffected by grazing. As at SEV, grazing tended to reduce vertical complexity at JRN and reduced litter cover while increasing the cover of bare ground. In contrast to the other areas, however, the cover of grass decreased with grazing intensity and the density of mesquite shrubs was greater in the BLM land than in either CDRRC-grazed or ungrazed treatments. Again, soil strength did not differ

TABLE 2. Mean values (1 SE in parentheses) of soil variables measured at transects ( $n = 4$ ) in each habitat of each site (see *Study areas and methods: Study sites*).

Site and habitat	Soil texture (%)			Soil strength (kg/cm <sup>2</sup> )
	Coarse sand	Fine sand	Clay	
<b>Shortgrass Steppe</b>				
<b>PNG grazed</b>	6.3 (1.8)	60.2 (4.3)	20.0 (2.5)	3.5 (0.4) <sup>a</sup>
<b>CPER grazed</b>	4.3 (1.0)	63.3 (2.0)	20.3 (1.5)	3.4 (0.1) <sup>a</sup>
<b>Ungrazed</b>	6.6 (1.7)	63.6 (2.1)	18.5 (0.9)	2.2 (0.3) <sup>b</sup>
<i>Atriplex</i> shrub	6.7 (3.0)	57.4 (11.3)	20.0 (7.3)	2.3 (0.4) <sup>b</sup>
<i>Yucca</i>	9.1 (2.7)	62.0 (5.6)	17.6 (2.6)	2.8 (0.1) <sup>ab</sup>
<b>Sevilleta</b>				
<b>Grazed</b>	15.3 (3.2) <sup>b</sup>	49.6 (4.8) <sup>a</sup>	20.6 (2.4) <sup>a</sup>	1.3 (0.3)
<b>Ungrazed</b>	19.3 (3.3) <sup>b</sup>	58.0 (5.4) <sup>a</sup>	13.4 (0.9) <sup>b</sup>	0.8 (0.0)
Blue grama	28.6 (0.9) <sup>a</sup>	31.1 (0.9) <sup>b</sup>	21.7 (2.3) <sup>a</sup>	1.2 (0.1)
<i>Larrea</i> grass	8.1 (1.9) <sup>c</sup>	48.7 (1.1) <sup>a</sup>	22.8 (1.6) <sup>a</sup>	0.7 (0.3)
<i>Larrea</i> shrub	8.3 (1.7) <sup>c</sup>	48.9 (1.6) <sup>a</sup>	21.5 (0.6) <sup>a</sup>	0.5 (0.3)
<b>Jornada</b>				
<b>BLM grazed</b>	5.2 (1.0) <sup>c</sup>	77.3 (2.7) <sup>a</sup>	10.9 (0.9) <sup>b</sup>	0.2 (0.0)
<b>CDRRC grazed</b>	7.8 (1.8) <sup>bc</sup>	73.1 (3.4) <sup>a</sup>	11.8 (1.3) <sup>ab</sup>	0.3 (0.1)
<b>Ungrazed</b>	9.8 (0.8) <sup>b</sup>	69.8 (2.3) <sup>a</sup>	11.7 (1.0) <sup>ab</sup>	0.2 (0.0)
Coppice dune	7.5 (1.0) <sup>bc</sup>	76.9 (2.4) <sup>a</sup>	9.9 (1.6) <sup>b</sup>	0.2 (0.0)
<i>Larrea</i> shrub	25.5 (3.8) <sup>a</sup>	45.2 (1.8) <sup>b</sup>	15.7 (1.2) <sup>a</sup>	0.5 (0.2)

Notes: Grazing contrasts are boldface; other habitat types are not. Superscript letters within columns indicate that a variable differed significantly among habitats within a site (ANOVA,  $P < 0.05$ ); values with different letters are significantly different at  $P < 0.05$  (LSD). Abbreviations are as in Table 1.

among treatments but soil texture did. The percentage of coarse sand was greater in the ungrazed exclosures than in the BLM land. This may reflect a gradient in soil variation between the more southerly exclosures and the BLM transects to the north. Soil texture also differed between grazing treatments at SEV, perhaps due to the location of the fenceline with respect to a natural gradient.

Natural contrasts between dominant grasslands and other habitat types at SGS generally involved large differences in vertical complexity or ground cover, but not soil texture. At SGS, vertical complexity was greater in *Atriplex* shrublands than in grazed grasslands (Table 1), due in part to the taller stature of the grasses present in this shrubland. The *Yucca* sites, in contrast, had low vertical complexity and a greater cover of bare ground and stones. Soil texture did not differ in any systematic way between grassland and shrubland sites, nor between the two shrubland sites (Table 2), although the soil texture of individual transects did vary (see below). The soil strength of the *Atriplex* habitat, however, was similar to that found in ungrazed exclosures and lower than that in other habitats.

Differences between dominant grasslands and shrublands or other grasslands at SEV and JRN were often related to both soil texture and vegetation cover and complexity. The characteristics of *Larrea* shrublands, however, differed between SEV and JRN. At SEV, *Larrea* habitats had a comparatively low proportion of grass and coarse sand, a high cover of stones and bare ground, and low vertical complexity. The *Larrea*/grassland ecotone at SEV also had little coarse sand and

was intermediate in vegetation structure between pure *Larrea* and ungrazed grasslands. At JRN, *Larrea* shrublands had similar grass cover to grazed grassland, and vertical complexity was as great as that in ungrazed exclosures, due in part to large bush muhly plants (*Muhlenbergia porteri*) growing at the bases of *Larrea* shrubs. In a pattern that is reverse to that at SEV, the *Larrea* shrublands at JRN had a higher proportion of coarse sand and less fine sand than the other areas. Blue grama grasslands at SEV also occurred on relatively coarsely textured soils. The soil texture of coppice dune habitats at JRN, however, was indistinguishable from that of the grasslands, perhaps because these sites were formerly grasslands. Overall then, there were important, measurable differences between habitats within a site, but the nature of these differences varied greatly among sites.

#### *Ant communities*

*Ant richness and diversity.*—Over the duration of our sampling, we recorded 35, 39, and 41 ant species in pitfall traps at SGS, SEV, and JRN, respectively. If we restrict attention to the grazing treatments in dominant grassland, grazing had no measurable effect on transect-scale ant richness or logseries- $\alpha$  at any of the sites (Figs. 1 and 2, all  $P > 0.10$ ). Measured habitat-scale richness differed little among grazing treatments at SEV and JRN, but was higher in the ungrazed habitat than the other grasslands at SGS. Estimated richness (ICE), generally followed measured patterns at SGS, was slightly higher in the ungrazed than grazed habitat at SEV, and was similar among grassland habitats at

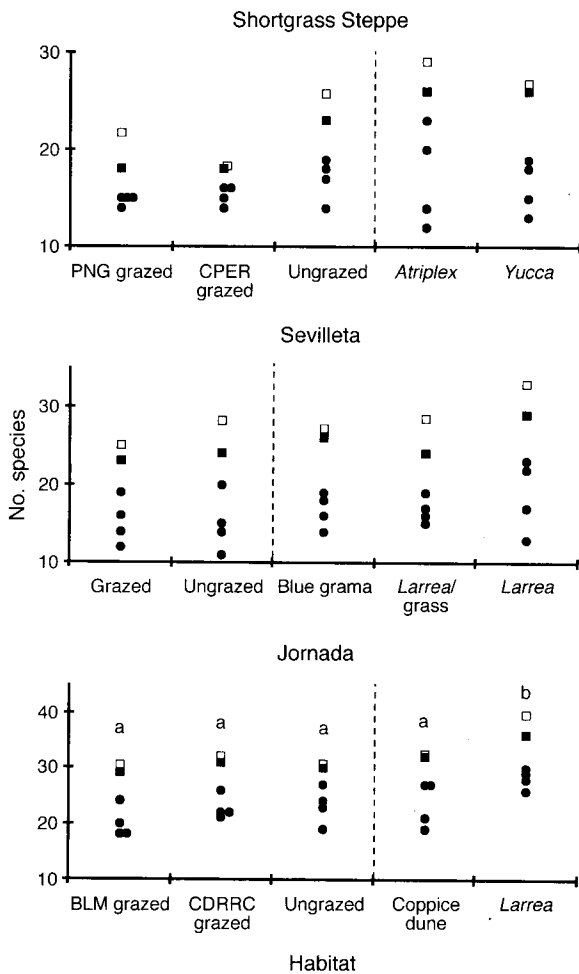


FIG. 1. Species richness patterns at the Shortgrass Steppe (SGS), Sevilleta (SEV), and Jornada (JRN) sites. Grazing contrasts are on the left side of the dashed line. Measured richness values at transects ( $n = 4$ ; solid circles), at the habitat scale (solid square), and a habitat-scale richness estimate (incidence-based estimator [see *Study areas and methods: Data analysis*]; open square) are presented for each habitat at each site. Significant differences were observed only at JRN; habitats sharing letters are not significantly different in post hoc tests of richness at transect-scale (LSD). Abbreviations: PNG, Pawnee National Grasslands; CPER, Central Plains Experimental Range; BLM, Bureau of Land Management; CDRRC, Chihuahuan Desert Rangeland Research Center.

JRN. Habitat-scale logseries- $\alpha$  differed little among the dominant grassland habitats at all three sites.

If we consider both grazing treatments and natural habitats together at each site, transect-scale richness was significantly higher in the *Larrea* habitat at JRN than the others ( $F = 4.05$ ;  $df = 4, 15$ ;  $P = 0.020$ ; Fig. 1). Transect-scale logseries- $\alpha$  was higher in the *Larrea* habitat here than in either of the grazed habitats ( $F = 2.78$ ;  $df = 4, 15$ ;  $P = 0.065$ ; Fig. 2). Transect-scale richness or logseries- $\alpha$  did not differ among habitats at either SGS or SEV (all  $P > 0.10$ ). Both measured and estimated habitat-scale richness and logseries- $\alpha$

were highest in the *Larrea* habitat at both JRN and SEV, but differed little among the other habitats. At SGS, measured and estimated habitat-scale richness and logseries- $\alpha$  were highest in the *Atriplex* and *Yucca* habitats.

At all sites, diversity at the habitat scale tended to be highest in natural habitat variants. At JRN, this tendency was also found at the transect level. Grazing affected diversity measures only at the habitat scale at SGS.

*Ant community composition.*—MRPP analyses revealed significant differences in species composition among habitats at SGS ( $T = -2.06$ ;  $P = 0.028$ ), SEV ( $T = -6.21$ ;  $P = 0.000$ ), and JRN ( $T = -4.27$ ;  $P = 0.000$ ). Subsequent pairwise tests revealed that grazing treatments differed significantly in species composition only at SGS, where the PNG-grazed habitat differed from the ungrazed habitat, but the CPER grazed did not (Table 3). At SGS, the *Yucca* habitat was distinct from all but the CPER-grazed habitat, and the *Larrea*

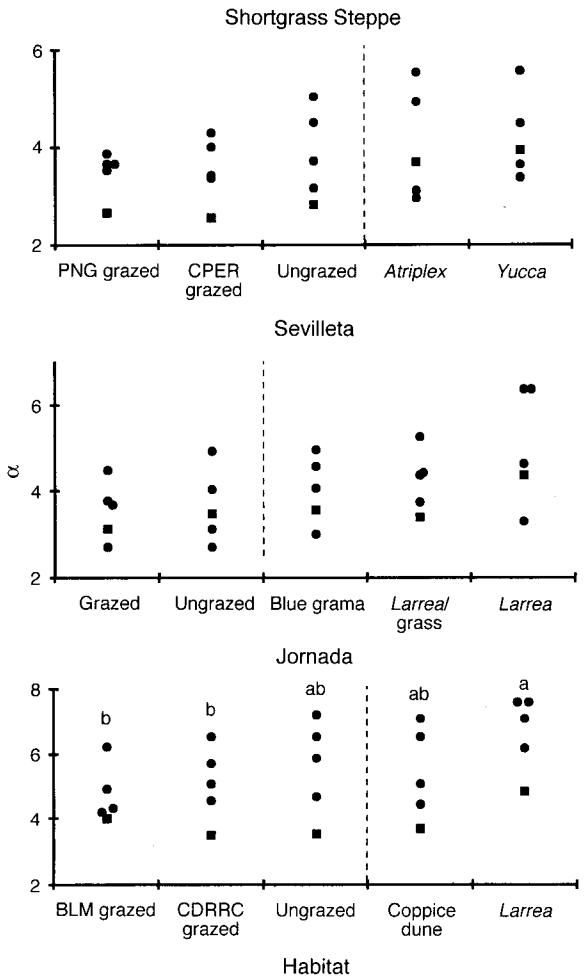


FIG. 2. Logseries- $\alpha$  patterns at the SGS, SEV, and JRN sites (only JRN exhibited significant differences; symbols and abbreviations are as in Fig. 1).



TABLE 3. The results of multiresponse permutation procedure (MRPP) analyses testing the hypothesis that transects grouped by habitat type differed significantly from one another in species composition.

a) Shortgrass steppe habitat	PNG grazed	CPER grazed	Ungrazed	<i>Atriplex</i>
CPER grazed	1.13 (0.905)	...	...	...
Ungrazed	-2.30 ( <b>0.020</b> )	-0.53 (0.272)	...	...
<i>Atriplex</i>	-1.68 ( <i>0.057</i> )	-0.20 (0.394)	1.09 (0.873)	...
<i>Yucca</i>	-2.72 ( <b>0.012</b> )	-0.65 (0.234)	-2.53 ( <b>0.009</b> )	-2.06 ( <b>0.026</b> )
b) Sevilleta habitat	Grazed	Ungrazed	Blue grama	<i>Larreal</i> /grass
Ungrazed	-0.02 (0.422)	...	...	...
Blue grama	-0.59 (0.242)	-1.44 (0.088)	...	...
<i>Larreal</i> /grass	-1.68 ( <i>0.064</i> )	-1.32 (0.099)	-3.67 ( <b>0.006</b> )	...
<i>Larrea</i>	-3.61 ( <b>0.006</b> )	-4.09 ( <b>0.006</b> )	-4.15 ( <b>0.006</b> )	-4.00 ( <b>0.005</b> )
c) Jornada habitat	BLM grazed	CDRRC grazed	Ungrazed	Coppice dune
CDRRC grazed	-1.35 (0.100)	...	...	...
Ungrazed	-1.11 (0.134)	0.31 (0.574)	...	...
Mesquite dune	-2.32 ( <b>0.033</b> )	-0.68 (0.242)	-2.20 ( <b>0.024</b> )	...
<i>Larrea</i>	-2.80 ( <b>0.013</b> )	-1.95 ( <b>0.035</b> )	-3.23 ( <b>0.005</b> )	-3.15 ( <b>0.008</b> )

Notes: Overall tests for between-group heterogeneity were highly significant (see *Results: Ant community composition*). The value reported for each contrast is the *T* statistic (see *Study areas and methods: Data analysis*), and the value in parentheses indicates the probability that the observed segregation of groups based on Sørensen distances could be observed in randomized data. Bold values indicate significance at  $P < 0.05$ ; italic values indicate marginal significance at  $P < 0.07$ .  $N = 4$  for all groups. Abbreviations are as in Table 1.

habitat was distinct from all other habitats at SEV and JRN. At JRN, the coppice dune habitat was distinct from all but the CDRRC-grazed habitat. Overall, differences in species composition among habitats that differed naturally (e.g., grasslands vs. shrubland) were more often significant than among grazing treatments within dominant grassland types.

For all sites, patterns of segregation of the habitat types in the space formed by the first two axes of CA were largely consistent with the results of the MRPP. At SGS, the primary axis of variation in species composition described a gradient from ungrazed and *Atriplex* transects to grazed and then *Yucca* transects (Fig. 3). Axis 2 expressed variation among sites within the shrublands. At SEV, axis 1 revealed a gradient in species composition from *Larrea*, through the *Larreal* grassland ecotone, to black grama grassland, to blue grama grassland (Fig. 4). Axis 2 largely described variation within blue grama grassland transects. At JRN, *Larrea* transects were separated from grassland and coppice dune transects along axis 1, and axis 2 separated the coppice dune transects from most of the grassland transects (Fig. 5). Differences between the coppice dune and BLM-grazed habitats found in MRPP were not reflected in the first two axes of the CA ordination. There was good separation of the coppice dune transects from the BLM-grazed transects along axis 3 (not shown), however.

CCA revealed significant relationships between species composition and two to four environmental variables at each site. In all three cases, both the first canonical axis and the overall relationship between species and environmental variables (all canonical axes)

were significantly different from those derived from randomized data (Table 4).

At SGS, soil strength was negatively correlated ( $-0.79$ ) with CCA axis 1 (i.e., the "inter-set" correlation; ter Braak 1994), and increasing percentage clay and a decrease in the percentage fine sand were correlated with variation in species abundance along axis 2 (0.82 and  $-0.65$ , respectively; Fig. 6). The ordination shows that the relatively low values of soil strength (cf. Table 2) at two *Atriplex* transects and three ungrazed transects were related to their distinct ant species composition. Variation along axis 2 mainly separated an *Atriplex* transect with relatively high clay content from sandier *Yucca* and *Atriplex* transects. Additionally, increasing surface stone cover, poorly correlated with either axis, was related to the separation of the *Yucca* transects and a CPER-grazed transect along a diagonal (cf. Table 3a). Variation at SEV along axis 1 was best correlated with increasing shrub density (0.92) and decreasing percentage of coarse sand (0.72; Fig. 7). Variation at JRN on axis 1 was best correlated with decreasing percentage fine sand (0.94) and increasing shrub density (0.77; Fig. 8). Shrub density was also positively correlated with axis 2 (0.46), reflecting the influence of some shrubbier BLM-grazed and coppice dune sites on species composition. Overall, environmental variables related to natural habitat variation were significant descriptors of variation in ant species composition at all three sites, and one variable, soil hardness, was related to both grazing-induced and natural habitat differences at SGS.

The percentage of variation in species composition explained by the first two axes of the CA and CCA

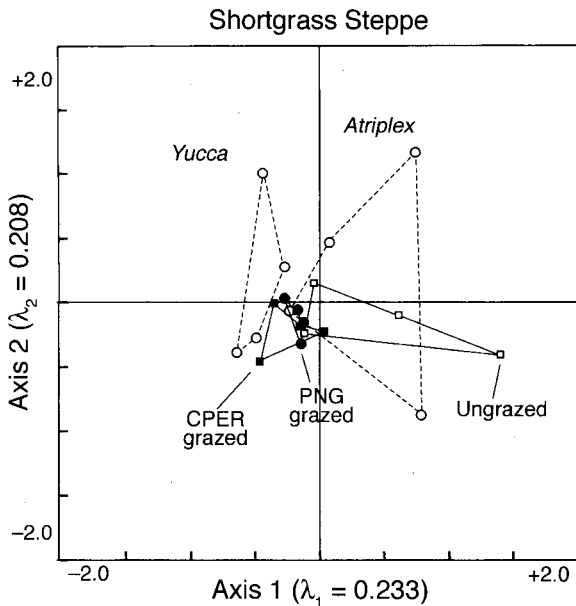


FIG. 3. Correspondence analysis ordination of transects at the SGS site. Site scores of transects belonging to the same habitat are joined by lines; solid lines indicate grazing treatments within the dominant grassland type, and dashed lines indicate natural habitat types. Adjacent to each axis, eigenvalues are reported. Abbreviations are as in Fig. 1.

ordinations was identical at SGS, but the percentage explained by the CCAs at the SEV and JRN was lower (14–16%) than in the CAs (Table 4). Within each site, the ordinations of transects derived from CA and CCA analyses were similar along axis 1, reinforcing our confidence that the environmental variables identified in

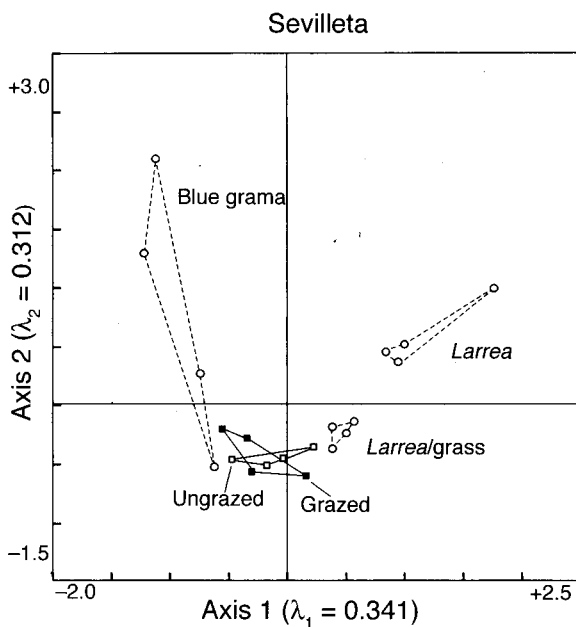


FIG. 4. Correspondence analysis ordination of transects at the Sevilleta site; interpretation follows Fig. 3.

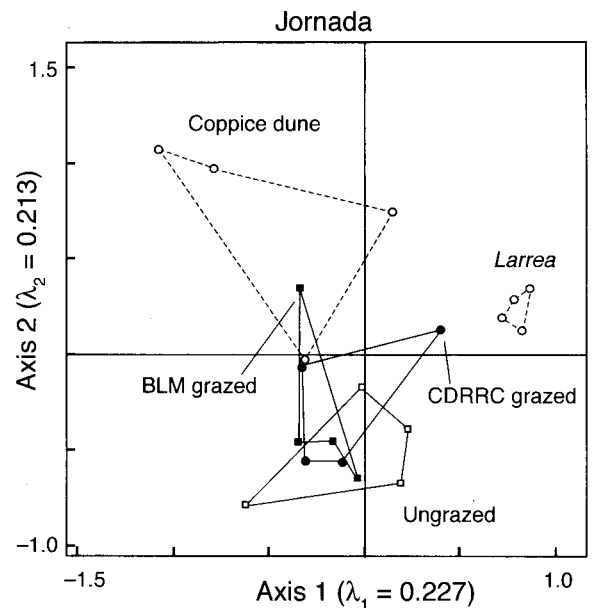


FIG. 5. Correspondence analysis ordination of transects at the Jornada site; interpretation follows Fig. 3. Abbreviations are as in Fig. 1.

the forward selection were related to the primary axis of variation in the species data. The results for axis 2 were less satisfactory. We did not identify an environmental variable that could explain the distinct species composition of one distant *Yucca* transect at SGS detected by CA (Fig. 3), nor for two blue grama transects at SEV (Fig. 4) and three coppice dune transects at JRN (Fig. 5).

Tests of association between individual species and habitats using the IndVal method revealed that grazing treatments, and dominant grasslands in general, possessed relatively few strongly associated ant taxa, whereas other habitats, in particular shrublands, had many strong associations (Table 5). Associations of species with habitats at SGS were generally weak. *Formica densiventris* was associated with the *Atriplex* habitat and two other species with grasslands in general.

TABLE 4. The percentage of variation in the species abundance data explained by the first two ordination axes in correspondence analysis (CA) and canonical correspondence analysis (CCA), and *F* statistics for significance tests of the first canonical axis and all canonical axes.

Site	Percentage of species variation explained in CA	Percentage of species variation explained in CCA	<i>F</i> of CCA axis 1 test	<i>F</i> of CCA all axes test
SGS	30.1	30.4	3.121	2.847
SEV	52.4	36.4	5.925	4.870
JRN	41.2	27.2	3.822	3.169

Notes: All tests were significant at the  $P = 0.005$  level (Monte Carlo permutation tests). Abbreviations: SGS, shortgrass steppe; SEV, Sevilleta; JRN, Jornada.

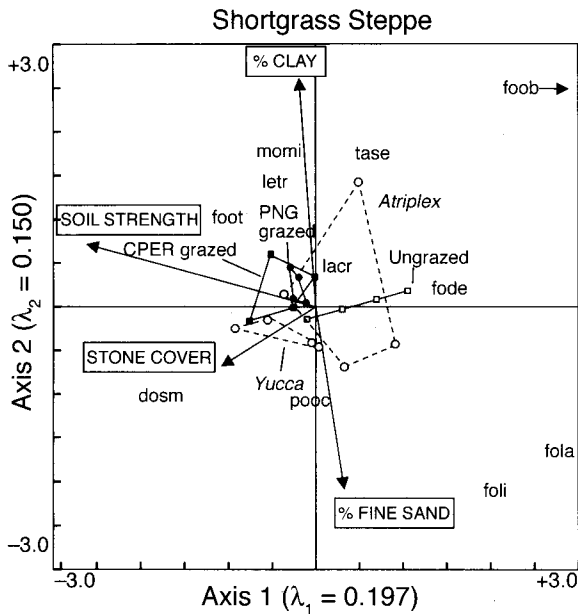


FIG. 6. Canonical correspondence analysis ordination of transects at the SGS site. Site scores of transects belonging to the same habitat are joined by lines; solid lines indicate grazing treatments within the dominant grassland type, and dashed lines indicate natural habitat types. Species scores are indicated by lowercase codes; only species for which the ordination explained >40% of variation in their abundance are shown for clarity. Abbreviations: dosm = *Dorymyrmex smithi*, fode = *Formica densiventris*, foia = *F. lasiodes*, foli = *F. limata*, foob = *F. obscuripes*, foot = *F. obtusopilosa*, lacr = *Lasius crypticus*, letr = *Leptothorax tricarlinatus*, momi = *Monomorium minimum*, pocc = *Pogonomyrmex occidentalis*, and tase = *Tapinoma sessile*. The interpretation of environmental arrows in the CCA diagram, following ter Braak and Verdonschot (1995), is that the direction of the arrow represents the vector of maximum change in the values of the environmental variable, whereas the length of the arrow indicates the rate of change in the variable. The rank of the transects with respect to an environmental variable is approximated by projecting the transect point in the diagram perpendicularly onto the environmental arrow. The origin (0,0) is the mean for each environmental variable, so that transects projecting onto the axis of, but on the side opposite of, the arrow are inferred to exhibit a lower than average value of the variable. Species scores that occur close to a transect point are inferred to have a relatively high abundance at that transect. Adjacent to each axis, eigenvalues are reported. Abbreviations are as in Fig. 1.

No species was significantly associated with the grazing types. Because the MRPP revealed an effect of grazing but CCA revealed that some ungrazed transects were similar to *Atriplex* transects at SGS, we performed ANOVAs to test whether the abundance of any species was affected by grazing; only *Formica lasiodes* was significantly affected by grazing, ( $F = 8.04$ ;  $df = 2, 9$ ;  $P = 0.02$ ) being more abundant in the ungrazed habitat than the other habitats.

In contrast to the situation at SGS, many species at SEV and JRN were strongly associated with particular habitats. At SEV, two species were associated with the

dominant grassland, eight species with the blue grama grassland, and eight species with the shrublands. Most of the shrubland species exhibited their greatest indicator values when the combined *Larrea* and *Larrea*/grass ecotone habitats were compared with the grassland habitats, but two species were most strongly associated with pure *Larrea* stands. Patterns at JRN were similar to those observed at SEV. In the grassland/shrubland contrast, three species were associated with grassland and nine species with shrublands. Within shrublands, four species were associated with coppice dunes and ten species with *Larrea* shrublands. Within the dominant grassland type, however, few species were associated with particular grazing treatments at either SEV or JRN. At SEV, one species was associated with the grazed, and one species with the ungrazed habitat. At JRN, one species was associated with the ungrazed habitat but none with the other grazing treatments.

A comparison of the results from the gradient-based analysis techniques (CA, CCA) with techniques based upon the a priori designation of habitat types (MRPP and IndVal) illustrates that the environmental variation to which ant composition responded did not always differ systematically among habitats. For example, at SGS, relatively high abundances of species such as *Formica obscuripes*, *F. limata*, and *F. lasiodes* were related to low soil strength values (Fig. 6), but transects with low soil strength were present in both ungrazed and *Atriplex* habitats. Further, another *Atriplex* transect exhibiting high clay content had high abundances of species such as *Monomorium minimum* and *Tapinoma sessile*.

In contrast, environmental variables important to ants differed with habitat type at both SEV and JRN. At SEV only one of the eight species displayed in the CCA did not associate with an a priori habitat. At JRN, one species of seven did not associate with a habitat. In contrast, only three of 11 species displayed at SGS revealed habitat associations using IndVal.

DISCUSSION

*The effects of grazing*

The consequences of grazing on the dominant grassland environments examined here were great, and correspond well with results found in previous studies at JRN (Holechek et al. 1994) and SGS (Milchunas and Lauenroth 1989, Milchunas et al. 1989). In general, grazing resulted in a simplified vegetation structure; at all three sites foliage complexity was significantly and substantially reduced by grazing. There were important differences, however, in other impacts of grazing among the sites. The maximum impact of grazing on vertical complexity increased along the aridity gradient, from a 40% reduction at SGS to 62% at SEV to 77% at JRN (Table 1). This reduction was accompanied by a reduction in grass cover at JRN but not at SEV

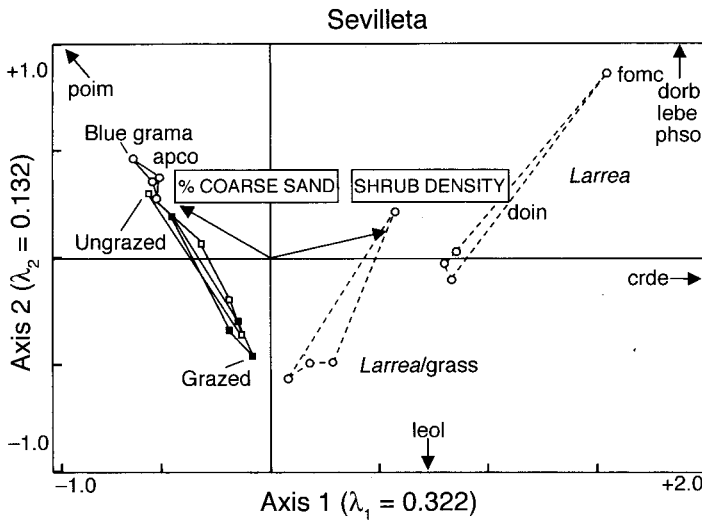


FIG. 7. CCA of the SEV site. Interpretation is as in Fig. 6. Abbreviations: apco = *Aphaenogaster cockerelli*, crde = *Crematogaster depilis*, dorb = *Dorymyrmex* sp. B, doin = *Dorymyrmex insanus*, fomc = *Forelius mccoeki*, lebe = *Leptothorax* sp. J1, leol = *Leptothorax obliquicanthus*, phso = *Pheidole soritis*, poim = *Pogonomyrmex imberbiculus*.

or SGS. Grazing appeared to result in soil compaction at SGS, but not at the more southerly sites. At JRN, heavier grazing resulted in increased shrub densities but this effect was not observed at SEV and might even have been reversed at SGS, where woody halfshrubs increased in ungrazed exclosures (Milchunas et al. 1989; Table 1).

Despite the strong effects of grazing on soil properties and/or vegetation, an effect of grazing on ant diversity was observed only at SGS, where habitat-scale richness was higher in the ungrazed habitat (Figs. 1 and 2). There were no detectable effects on richness or logseries- $\alpha$  at any site at transect scales. The results at SEV and JRN are consistent with those found in

other studies that have considered grazing impacts on ants in semiarid zones. Negligible or even positive effects of grazing on overall ant richness have been documented in Argentine Chaco woodlands (Bestelmeyer and Wiens 1996), western Australian woodlands (Abensperg-Traun et al. 1996, Majer and Beeston 1996), and central and south Australian shrublands (Landsberg et al. 1997). All of these studies, however, detected important changes in species composition with differences in grazing intensity. In this study, changes in species composition were detected only at SGS (Table 3). Nonetheless, the variable composition of the ungrazed treatments apparent in CA and CCA (Figs. 3 and 6) indicate that the effects of grazing exclosures were not consistent. Of 35 species, only *Formica lasiodes* exhibited a significant response to grazing. Additionally, the large, conspicuous nests of the thatching ant, *F. obscuripes*, occurred only in three of the ungrazed exclosures in the grassland (one nest per exclosure). We never observed these nests in grazed grasslands at the site.

The mechanisms by which *F. lasiodes* and *F. obscuripes* responded to grazing at SGS differed. It is unclear why *F. lasiodes* was more abundant in ungrazed sites, although its response may be related to a preference for nesting in less compact soils (Fig. 3). Our observations of *F. obscuripes* suggest that its local distribution may be limited by the availability of woody plant material with which to build its large nests. The presence of this species in only the *Atriplex*, *Yucca*, and ungrazed habitat is consistent with this suggestion. In the ungrazed habitat, the woody parts of halfshrubs and forbs that were favored there, such as *Artemisia frigida*, were used as building materials (B. T. Bestelmeyer, personal observations).

Why were there no observable responses to grazing at either SEV or JRN, despite the profound changes in vegetation cover (see also Whitford et al. 1999)? Two

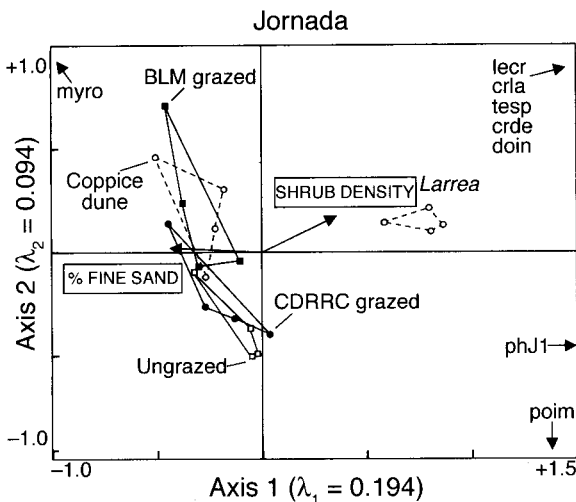


FIG. 8. CCA of the JRN site. Interpretation is as in Fig. 6. Abbreviations: crde = *Crematogaster depilis*, crla = *C. larreae*, doin = *Dorymyrmex insanus*, lecr = *Leptothorax carinatus*, myro = *Myrmecocystus romainei*, phJ1 = *Pheidole* sp. J1, poim = *Pogonomyrmex imberbiculus*, tesp = *Tetramorium spinosum*. Abbreviations are as in Fig. 1.

TABLE 5. Indicator species (see *Study area and methods: data analysis*) of habitat types for which indicator values (IndVal) were significantly different from that expected from randomized data, organized by site.

Site	Habitat type	Indicator species	Relative abundance	Relative frequency	Maximum IndVal	P		
Shortgrass steppe	Grassland	<i>Lasius crypticus</i>	72	100	72.2	0.004		
		<i>Tapinoma sessile</i>	71	100	70.7	0.021		
		<i>Formica densiventris</i>	83	75	62.3	0.031		
Sevilleta	Grassland	<i>Pheidole longula</i>	55	100	55.3	0.022		
		<b><i>Pogonomyrmex maricopa</i></b>	90	88	79.1	0.000		
		<i>Pogonomyrmex maricopa</i>	45	100	45.1	0.040		
	Grazed	<i>Myrmecocystus navajo</i>	42	100	42.0	0.019		
		<i>Brachymyrmex minutus</i>	100	50	50	0.026		
	Ungrazed	<i>Crematogaster punctulata</i>	98	75	73.3	0.009		
		<i>Crematogaster navajoa</i>	100	50	50	0.037		
	Blue grama	<i>Dorymyrmex smithi</i>	100	50	50	0.027		
		<i>Pheidole cerebrostor</i>	73	75	55.1	0.040		
	Shrubland	<i>Pheidole</i> sp. J1	95	75	70.9	0.008		
		<i>Pogonomyrmex imberbiculus</i>	75	100	74.6	0.005		
		<i>Pogonomyrmex apache</i>	100	50	50	0.033		
		<b><i>Crematogaster depilis</i></b>	100	88	87.5	0.001		
		<b><i>Dorymyrmex insanus</i></b>	59	100	59.3	0.006		
		<b><i>Dorymyrmex</i> sp. S1</b>	100	63	62.5	0.031		
		<b><i>Forelius mccooki</i></b>	77	100	77.1	0.000		
		<b><i>Leptothorax olbiquicanthus</i></b>	77	100	77.3	0.000		
		<i>Leptothorax</i> sp. J1	95	50	47.3	0.050		
		<i>Myrmecocystus placodops</i>	79	100	79	0.002		
		<i>Pheidole soritis</i>	81	100	70.9	0.008		
		Larrea/grass	<i>Leptothorax obliquicanthus</i>	58	100	58.1	0.001	
			<i>Crematogaster depilis</i>	60	100	60.4	0.015	
		Larrea	<i>Dorymyrmex insanus</i>	47	100	46.5	0.000	
			<i>Dorymyrmex</i> sp. S1	79	75	58.9	0.046	
			<b><i>Forelius mccooki</i></b>	52	100	52.4	0.005	
			<b><i>Leptothorax</i> sp. J1</b>	95	100	94.7	0.000	
			<b><i>Pheidole soritis</i></b>	73	100	72.6	0.000	
			<i>Pheidole tepicana?</i>	77	75	57.9	0.027	
			Jornada	Grassland	<i>Myrmecocystus mimicus</i>	72	100	72.1
		<i>Pogonomyrmex desertorum</i>			72	100	71.8	0.003
		<i>Solenopsis krockowi</i>			80	100	80.3	0.002
		Ungrazed		<i>Monomorium minimum</i>	48	100	48.3	0.016
	<i>Crematogaster depilis</i>			94	50	46.9	0.041	
Shrubland	<i>Crematogaster larreae</i>	100		50	50	0.013		
	<i>Dorymyrmex insanus</i>	84		75	63.1	0.031		
	<b><i>Myrmecocystus depilis</i></b>	66		100	66	0.033		
	<i>Pheidole sciophila</i>	98		75	73.5	0.002		
	<i>Pheidole tusconica</i>	100		38	37.5	0.047		
	<b><i>Pogonomyrmex californicus</i></b>	84		100	84.2	0.002		
	<i>Tetramorium spinosum</i>	100		50	50	0.013		
	<i>Trachymyrmex smithi</i>	89		63	55.3	0.025		
	Coppice dunes	<i>Myrmecocystus romainei</i>		74	100	73.8	0.004	
		<i>Pogonomyrmex californicus</i>		43	100	42.7	0.039	
		<i>Pogonomyrmex maricopa</i>		68	100	67.6	0.022	
	Larrea	<b><i>Trachymyrmex smithi</i></b>		83	100	82.9	0.002	
		<i>Crematogaster depilis</i>		91	100	91.0	0.000	
<b><i>Crematogaster larreae</i></b>		100		100	100	0.000		
<b><i>Dorymyrmex insanus</i></b>		72		100	72.0	0.000		
<i>Pogonomyrmex imberbiculus</i>		43		100	43.3	0.009		
<i>Leptothorax carinatus</i>		86		75	64.8	0.028		
<i>Myrmecocystus depilis</i>		35		100	34.8	0.039		
<i>Pheidole</i> sp. J1		60		100	60	0.012		
<b><i>Pheidole sciophila</i></b>		89		100	89.2	0.005		
<b><i>Pheidole tusconica</i></b>		100		75	75	0.018		
<b><i>Tetramorium spinosum</i></b>	100	100		100	0.000			

Notes: Values reported are those for the habitat type where maximum indicator values were attained. Two sets of analyses were performed: first grouping transects of related habitat types into broader categories (usually grassland vs. shrubland) and then analyzing them grouped by their narrower habitat type (e.g., grazed, ungrazed). When a species exhibited significant indicator properties in both analyses, the species name appears in bold next to the grouping in which its maximum IndVal was attained. Relative abundance = the average abundance of a species in the habitat type divided by the average abundance of that species in all habitat types; relative frequency = the percentage of transects in the habitat type in which a species was present (both relative abundance and relative frequency are expressed as percentages). The P value denotes the proportion of randomized data sets that had a greater maximum indicator value. Abbreviations are as in Table 4.

potential explanations come to mind, based upon hypothesized mechanisms that may mediate the effects of grazing on ant populations. First, the changes in vegetative cover or stature may not significantly alter the microclimates to which foraging ants are exposed. Thus, even though grazing at JRN dramatically increased the cover of bare ground, bare ground was still the dominant cover type in ungrazed grassland (Table 1). Diurnally foraging ants will likely be exposed to unshaded, dangerously hot microclimates (e.g., Marsh 1985) while foraging in desert grassland environments, irrespective of differences in grass cover. Second, ant species nesting in vegetation may be flexible with respect to the type of vegetation in which they feed or nest. Workers of *Forelius pruinosus* at JRN, for example, nested most frequently at the bases of grasses in the ungrazed habitat but nested more often under mesquite shrubs and snakeweed (*Xanthocephalum* spp.) in the BLM-grazed area (Bestelmeyer 2000).

The desert grassland ant fauna has been exposed to large temporal variations in environmental conditions throughout the Holocene (Van Devender 1995). Gibbens and Beck (1988) report that the worst drought at JRN in 350 years occurred in the 1950s, leading to great reductions in the basal cover of black grama grass. Thus, the ant species persisting at JRN have probably been exposed to and tolerate relatively desertified conditions. In general, drought events have a greater impact on patterns of grass cover than does grazing (Herbel et al. 1972, Gibbens and Beck 1988) and may also have acted as a climatic extinction filter (sensu Balmford 1996) that eliminated those species that would be most sensitive to contemporary grazing impacts. Janzen (1967) first recognized that organismal adaptation to spatial heterogeneity may be closely linked to adaptations to temporal variation in environmental conditions (see also Mönkkönen and Welsh 1994). Understanding and predicting the consequences of anthropogenic impacts on biodiversity requires a knowledge of the range of environmental conditions to which species are and have been exposed in both space and time.

#### *The role of natural landscape heterogeneity*

Natural environmental features, in particular soil texture and associated changes in vegetation cover, were often better correlates of variation in ant richness and composition than was grazing-induced variation. This was clearly true at SEV and JRN. At both sites, habitat-scale species richness was greatest in the *Larrea* habitat, as was transect-scale richness at JRN. This pattern was paralleled by relatively large shifts in species composition between the *Larrea* sites and the others. Indicator species analysis revealed that many more species were strongly associated with particular natural habitat variants, especially *Larrea* shrublands, than with grazing-treatment variants.

At SGS, both grazing and natural environmental var-

iation were important. The *Atriplex* and *Yucca* habitats were the most species rich at the habitat scale and the *Yucca* habitat differed from most other habitats in species abundances (Table 3). Variation in soil texture was related to patterns of species abundance. The most important component of environmental variation affecting species composition (i.e., soil strength), however, may have resulted from both grazing-induced and natural processes. Two of the low-soil-strength *Atriplex* transects had relatively high values of percentage fine sand (Fig. 3); thus, both the resistance of sandier soils to compaction and a lack of grazing may affect species composition in similar ways.

The processes affecting ant diversity at the coppice dunes at JRN may also be interpreted as a combination of anthropogenic (grazing) and natural (drought) effects (Buffington and Herbel 1965, Hennessy et al. 1983). We failed to measure an environmental variable that could be related to the differences in species composition observed between the coppice dune and the BLM-grazed and ungrazed habitats. It is possible that soil characteristics below 24 cm, differing patterns of surface-water runoff, or differences in vegetation patch size (Schlesinger et al. 1990, Ludwig et al. 1994) may affect ant nest-site characteristics. For example, Snelling (1976) noted that *Myrmecocystus romainei*, an indicator species of the coppice dunes (Table 5), exhibited a peculiar nest structure relative to other members of the genus. This is presumably an adaptation to nesting in deep, soft sand. The association of *Trachymyrmex smithi* with coppice dunes, on the other hand, is clearly related to the presence of large mesquite patches that provide both shade and abundant litter for fungus cultivation (Schumaker and Whitford 1974).

#### *Environmental variation and habitat typology*

The environmental variables emerging from the CCA were often able to explain the differences in ant composition between habitats that were detected by MRPP and IndVal; the exception was the coppice dune habitat at JRN discussed above. The most important variation in species-environment relationships often corresponded well to the a priori typology of natural habitats based upon vegetation characteristics (i.e., grassland/shrubland types) at the SEV and JRN, but this matching was less apparent at the SGS site. The *Atriplex* transects, for example, varied widely in their characteristics, ranging from moderate to high soil strength and from relatively clay soils to sandy soils. In addition, one *Yucca* transect located in a "blowout" harbored a high abundance of two species (*Lasius neoniger* and *Formica bradleyi*) not recorded elsewhere at the SGS site. As with the coppice dune habitat, the depth and looseness of the sand is an important feature for ants such as *F. bradleyi* (Halverson et al. 1976), but these features were not quantified in this study. The small number of species exhibiting significant habitat associations with IndVal at SGS is another indication of the lack of con-

gruence between what ants recognize as important environmental variation and a vegetation-based habitat typology.

The observation that plant and animal communities may not be tightly associated (Elton 1927, Wiens and Rotenberry 1981) is not new. Nonetheless, this observation has critical importance for modern efforts to conserve biodiversity. Landscape pattern inferred from remote sensing of vegetation formations (e.g., from LANDSAT imagery; Scott et al. 1993) may not adequately reflect the variation that is important to some animal taxa (Short and Hestbeck 1995). Such a lack of congruence can occur in animals that are directly affected by features such as soil texture and that respond to variation in soil texture differently than do plant communities. In addition, for small animals such as ants, important environmental variation occurring below the resolution of vegetation maps may be ignored (Edwards et al. 1996). Recognizing the relative uniqueness of small patches of sandy-blowout habitat at SGS, for example, might be precluded by both of the problems.

In other cases, however, the distribution of plant communities may covary with animal distributions. This may occur when there are parallel responses to variation in soil properties or when the distribution of animal species is directly linked to that of particular plants. Part of the strong relationship between plant-defined and ant communities at SGS and JRN, for example, is due to ants such as *Crematogaster larreae* (Table 5) that nest exclusively at the base of creosotebush shrubs (so far as is known; Buren 1968). Other species, such as *C. depilis*, are more catholic with respect to shrub species.

Even when plant and animal distributions are concordant within one landscape, this association may break down across a broader region. Indicator species analysis results for *Pogonomyrmex imberbiculus* and *Pheidole* sp. J1 revealed that these ants were associated with creosotebush at JRN and blue grama at SEV (Table 5). These habitats both occurred on soils with a high percentage of coarse sand (Table 2). At SEV, however, creosotebush shrublands occurred on soils with a low percentage of coarse sand. Thus, it appears that the abundances of *P. imberbiculus* and *Ph.* sp. J1 are favored by coarse sand (Figs. 7 and 8), but varying plant-soil relationships between SEV and JRN led to differing plant community-ant associations between these sites. It is clear that animal species differ in the nature of their responses to landscape heterogeneity, and a broadscale understanding of species distribution and natural history will be necessary to adequately assess biodiversity-habitat relationships (Ingham and Samways 1996).

#### *Implications for ant biodiversity conservation and bioindication*

Cooperrider (1991) stated that the "available evidence indicates that livestock grazing has profound

ecological costs," among them, "reductions in species richness, and changing community organization." This statement was not supported in this study. At most, grazing affected the abundances of some taxa, but did not result in a great degree of species turnover or loss. Previous studies at the LTER sites have demonstrated that different taxonomic groups vary in their sensitivity to grazing (Whitford 1997, Milchunas et al. 1998).

The small response by ants to grazing-induced changes in vegetation led Whitford et al. (1999) to conclude that ants were not useful indicators of faunal diversity patterns in rangeland ecosystems. We have demonstrated that ants do, however, respond to gradients in soil texture and vegetation that might be important to other taxa. Variation in soil texture has been shown to affect other arthropod groups in steppe and desert grasslands (Crawford 1988, Stapp 1997). The value of shrubs for maintaining both arthropod (Stapp 1997, Bestelmeyer and Schooley 1999) and vertebrate (Stapp and Van Horne 1997, Whitford 1997) biodiversity has also been recognized. A full evaluation of the utility of ants as bioindicators in rangelands awaits parallel studies of the responses of ants and other taxa to different soil texture and vegetation gradients.

These considerations suggest that both the recognition of degradation and the evaluation of habitat heterogeneity should be defined with respect to varying organismal perspectives (Levins 1968, Kolasa and Rollo 1991). Our results suggest that for most ants we observed, the "environmental changes" to vegetation due to cattle grazing within the LTER sites may fall within a range of variability to which the ants are adapted. From this perspective, "human transformations of nature merge with natural processes: there are no absolute standards to distinguish between human-induced and natural change" (Haila and Margules 1996). A focus on the correlations between the composition of different taxa and carefully selected environmental variables at broad scales can aid our understanding of the relationships between human-induced and natural variation. The ants of the shortgrass steppe and desert grassland sites we examined revealed that variation in soil properties, whether of human or natural origin, is of paramount importance.

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