

Does desertification diminish biodiversity? Enhancement of ant diversity by shrub invasion in south-western USA

Brandon T. Bestelmeyer

USDA-ARS, Jornada Experimental Range, MSC
3JER, Box 30003, New Mexico State University,
Las Cruces, NM 88003, USA

ABSTRACT

The conversion of desert grasslands to shrublands is a long-standing concern in the south-western United States, but the effects of this change on native animals defy generalization. Here, I consider evidence that shrub invasion and encroachment, particularly that of honey mesquite (*Prosopis glandulosa*), has led to increasing ecological dominance and diversity of ants in general, as well as increases in specific native taxa. The effects of shrub invasion on ants were measured at two scales: (1) between Chihuahuan Desert landscapes that vary slightly in temperature and strongly in the dominance of mesquite, and (2) across variation in mesquite density occurring within a generally mesquite-dominated landscape. Ant richness and numerical dominance was measured at pitfall traps over 2 years and baits were used to assess ecological dominance across different temperatures. The mesquite-dominated Jornada site harboured four times the number of ant foragers found at the relatively 'pristine' Sevilleta site, with several ecologically dominant taxa driving this pattern, especially *Dorymyrmex bicolor*. Species richness and ecological dominance were also greatest at the Jornada. Within the Jornada landscape, turnover in species composition was related to mesquite density, but local richness and abundance was unrelated to mesquite density. Coupled with the results of previous manipulative experiments and comparative studies, there is support for the notion that ant diversity is not negatively affected by shrub invasion but that several taxa prosper from it. The Jornada is uniquely saturated by dominant ant taxa, perhaps as a consequence of an overall high level of shrub availability that provides a reliable source of carbohydrate-rich plant exudates. This raises important questions about the relationship between environmental degradation, ecosystem productivity, and animal diversity.

Keywords

Desert grassland, *Dorymyrmex bicolor*, *Forelius*, Formicidae, functional group, *Prosopis glandulosa*.

Correspondence: Brandon T. Bestelmeyer,
USDA-ARS, Jornada Experimental Range, MSC
3JER, Box 30003, New Mexico State University,
Las Cruces, NM 88003, USA. Tel.: 505-646-5139;
Fax: 505-646-5889; E-mail: bbestelm@nmsu.edu

INTRODUCTION

Semiarid savanna and desert grassland environments worldwide continue to experience shrub and tree invasion and/or encroachment as a consequence of land use and climate change (Archer, 1995; Van Auken, 2000). In the northern Chihuahuan Desert, the local invasion of shrubs into desert grasslands, and their gradual conversion to eroding shrublands with a high cover of bare ground continues unabated, even where grasslands have been protected from grazing (Peters *et al.* in press). These changes are generally regarded as ecosystem degradation because as herbaceous production declines, erosion and nutrient redistribution rates increase, leading to lower or spatially altered ecosystem productivity

and a functional group composition characteristic of deserts (i.e. desertification; Schlesinger *et al.*, 1990; Herrick *et al.*, 2002; Huenneke *et al.*, 2002). This has had clear negative impacts on livestock production (Fredrickson *et al.*, 1998) and there is concern that desertification also contributes to biodiversity loss (Ricketts *et al.*, 1999).

Existing studies of desertification effects on Chihuahuan Desert animal biodiversity, however, do not reveal straightforward patterns. Bird richness may be higher in shrublands than grasslands, although particular species may be uniquely associated with grassland vegetation (Pidgeon *et al.*, 2001). Similarly, small mammal richness may be higher in shrublands than grasslands (Whitford, 1997), but the abundance of the grassland-specialist banner-tailed kangaroo rat

(*Dipodomys spectabilis* Merriam) declines as shrub cover increases (Krogh *et al.*, 2002). Thus, while local vertebrate richness may be favoured by desertification, particular species can decline.

Among invertebrates, ants are abundant and diverse in deserts (Hölldobler & Wilson, 1990; MacKay, 1991) and exhibit strong interactions with many organisms and ecosystem processes (Guo & Brown, 1996; Wagner, 1997). This variety of interactions suggests that important environmental changes in ecosystem structure should be reflected in ant community composition (Andersen, 1997a; Andersen, 2003). Nonetheless, previous studies in the Chihuahuan Desert indicate that ant abundance and/or diversity are not negatively affected by disturbance intensity (Whitford *et al.*, 1999) or grazing history/grass dominance (Bestelmeyer & Wiens, 2001a). In fact, more ant species were strongly associated with Chihuahuan Desert creosotebush (*Larrea tridentata* (DC) Cov.) shrublands than grasslands (Bestelmeyer & Wiens, 2001a). Part of this effect, however, was due to the confounding effects of soil texture variation.

The responses of ant communities to desertification continue to be poorly understood. In this paper, I test the prediction that shrub encroachment, in particular by that of mesquite (*P. glandulosa* Torr.), has led to increases, rather than decreases, in the diversity and ecological dominance of ants (*sensu* Davidson, 1998) in the Chihuahuan Desert. Woody plants provide nesting habitats and food resources, including carbohydrate-rich exudates from hemipteran insects, that support highly active, behaviourally dominant ant taxa (e.g. dominant dolichoderines *sensu* Andersen, 1997b; Davidson, 1998; Nash *et al.*, 2000; Yanoviak & Kaspari, 2000; Davidson *et al.*, 2003). Mesquite appears to be a valuable resource for a wide array of insects (Wisdom, 1991) compared with other shrubs such as creosotebush (Schultz *et al.*, 1977). Mesquite is also the primary species encroaching upon grasslands of sandy soils in the northern Chihuahuan Desert (Gibbens *et al.*, 1992).

The hypothesis was evaluated in two ways. First, I compared ant community structure between two uniquely comparable Chihuahuan Desert landscapes within US Long-Term Ecological Research (LTER) sites located at the northern limit of the biome (Sevilleta LTER) and 257 km further south (Jornada LTER) in New Mexico, USA. Although the soil gradients, mean annual rainfall, mean annual above-ground net primary production, perennial grass composition, and land-use patterns are similar between the sites (Hochstrasser *et al.*, 2002), the Jornada features (1) slightly higher temperatures and (2) a comparatively high abundance of mesquite shrubs, especially in grassland vegetation types (Bestelmeyer & Wiens, 2001a). Thus, I sought to determine whether the ant fauna of the Jornada differed from the Sevilleta in the degree of dominance and diversity, in particular with respect to behaviourally dominant species that may rely on mesquite. Alternatively, if desertification has had a strong negative effect on ants, we would expect the Sevilleta (which is often regarded as 'pristine' desert grassland) to possess a more abundant, richer, and more ecologically dominant ant fauna than the Jornada.

Second, I considered the relationship of ant richness, dominance, and composition to variation in mesquite density within the Jornada site. If the local degree of shrub encroachment has a

negative impact on ants, we should expect negative relationships between mesquite densities and ant abundance, ecological dominance, and richness.

METHODS

Study areas and design

Comparisons of the landscapes were based on observations at transects stratified among the five most dominant habitat/land-use types at each site that occurred within a 100 km² extent. The Sevilleta LTER habitats are located in the Sevilleta National Wildlife Refuge and on adjacent privately owned land in Socorro County, New Mexico, USA. Long-term (80 year) mean annual precipitation (MAP) is 232 ± 79 mm and mean monthly temperature (MMT) ranges from 2.6 to 24.6 °C. This site represents the northern extent of the Chihuahuan Desert. The habitats examined comprise ungrazed (23 year) black grama (*Bouteloua eriopoda* (Torr.) Torr.) grassland, heavily grazed black grama grassland, ungrazed blue grama grassland on mountain footslopes, and two ungrazed creosotebush (*Larrea tridentata*) shrubland types occurring on shallow soils that varied in grass cover. Mesquite was not recorded on the grassland transects and was rare in the creosotebush shrubland. Average above ground net primary production (ANPP) is estimated at 193 g m⁻² in ungrazed black grama grassland. The Jornada 'Basin' LTER habitats are located largely in New Mexico State University's Chihuahuan Desert Rangeland Research Center and Bureau of Land Management land near Las Cruces, Doña Ana County, New Mexico, USA. Long-term MAP is 248 ± 87 mm and MMT ranges from 3.8 to 26.1 °C. Habitats examined included ungrazed black grama grassland (50 year), moderately grazed black grama grassland, two areas that were formerly dominated by grasses but are now dominated by mesquite (one area is forming dunes, the other is not yet forming dunes), and a currently ungrazed creosotebush/mesquite shrubland on shallow soils. Mesquite densities ranged from 2.5 to 8 plants per 100 m². ANPP ranges from 148 ± 33 g m⁻² in ungrazed black grama to 109 ± 65 g m⁻² in grazed black grama grassland.

Within each habitat type at each site, I examined ant activity at four replicate transects/habitat (20 total per site) randomly located along road segments or within grazing exclosures and placed at least 100 m from roads or fencelines. Habitat patches sampled were interspersed as much as was possible (see Bestelmeyer & Wiens, 2001a). Transects consisted of 10 points (10-m spacing). Pitfall trapping was conducted at each point in all replicates to evaluate numerical dominance. At three of the four replicates within four of the five habitat types, ant activity was observed at tuna baits over time as an assay of ecological dominance. At the Sevilleta, the creosotebush shrubland (with high grass) was omitted and at Jornada, the duned mesquite shrubland was omitted.

Pitfall trapping was conducted four times; July/August 1996, April 1997, July/August 1997, and April 1998. The April samples cover cool-season ant activity during times of year when overall foraging is greatly reduced (*c.* 75% at each site) from summer values but during which different ant species may be active. The

1996–97 years sampled featured above average rainfall for Sevilleta (302 and 325 mm) and near average for the Jornada (205 and 269 mm). Temperatures at the sites were similar in July/August but slightly cooler at Sevilleta in April. Pitfall traps were polypropylene sample containers (65 mm diameter, 100 mm deep) filled with 40 mL of a propylene glycol/ethanol mixture. Traps were opened for 72 h. Contents were counted and identified to species.

Tuna baits were used to examine patterns of ‘ecological dominance’ — the degree to which different taxa are able to dominate rich food resources via numbers and individual, aggressive behaviours (Davidson, 1998; cf. the ‘behavioural dominance’ of Andersen, 1997b). In June–August (the period of peak overall ant activity) 1997, baits (1-cm³, c. 3 g) were observed at each transect at three times of day based on temperature periods among which different ant species segregate activity: a moderate period (early morning or late afternoon; 29–34 °C), a hot period (midday, 48–56 °C), and night (> 1 h after dark; 23–28 °C). Baiting periods at each transect were separated by at least 48 h. During each period, baits were observed 5 min after bait placement and every 15 min thereafter until 65 min. At each observation, the ant species (or species group) and abundance per species were tallied according to a 5-point scale: 1, 1 ant; 2, 2–5 ants; 3, 6–20 ants; 4, 21–50 ants; and 5, > 50 ants. Soil-surface temperatures were recorded adjacent to each bait using a thermocouple thermometer (HH-23 Digital Thermometer, type J thermocouple, Omega Engineering, Inc., Stamford, CT, USA) at the beginning and end of each baiting period; these values were averaged for each baiting period.

Grassland habitats sampled within the Jornada possessed considerable mesquite cover. Local mesquite densities within the Jornada were estimated for each transect using average distances of shrubs from each pitfall trap. The area around each trap was divided into four quarters (similar to the point-quarter method; Bonham, 1989) and the distance to the nearest mesquite shrub (> 30 cm tall) within each quarter was recorded. The four values were averaged for each trap and then averaged across the 10 points/transect. Additionally, ground cover and soil texture was measured along each transect as described in Bestelmeyer & Wiens (2001a). Analyses of ant community relationships with distance to mesquite were performed only for grassland transects at the Jornada because other transects had very low mesquite densities.

I also used a unique, sharp ecotone between a sandy mesquite coppice dune field and grassland with medium (‘grass’; *Pleuraphis mutica* Buckl.) to heavy-textured (‘playa grass’; *Sporobolus airoides* (Torr.) Torr.) soils and very few shrubs to examine variation in the dominance of ant taxa in a single locality. Baits were placed every metre for 53 m in September of 2000 during midday when exposed soil surface temperatures exceeded 37 °C. Baits were censused two times while temperatures exceeded 37 °C and twice again once temperatures fell below 37 °C. Bait abundances were scored as above and summed across the two times within each period.

Data analysis

Taxon abundances in pitfall traps were summed for each transect across seasons. Taxa were treated at the species or morphospecies

level for richness and multivariate analysis. For univariate analyses and mixed models (see below), ant species were grouped to genus or treated individually depending upon their functional group designation per Andersen (1997b, 2000) and Brown (2000; Table 1). This permits ecological interpretations of taxon responses.

Nonparametric *t*-tests were used to compare ant species/generic abundances and richness at all transects ($n = 20$) between the sites. Species accumulation curves were used to compare the sites (PCORD 4.0; McCune & Mefford, 1999). Regression and correspondence analysis (PCORD 4.0; McCune & Mefford, 1999) were used to evaluate the relationship between the abundance of ant species/genera and species composition, respectively, with distance to mesquite at grassland transects ($n = 16$) within the Jornada site.

For bait analyses, species were evaluated at the generic or species-group level only, following other comparative studies (Andersen, 1997b). Taxon abundance scores at baits within a period were summed across the five observations and then across the 10 baits. This produces a measure of bait success at each transect that takes into account both the rate and frequency of discovery as well as competitive dominance (Bestelmeyer, 2000). For bait analyses, I used a repeated-measures mixed model (Proc MIXED; SAS, 1996) to examine the relationships between bait scores and sites or distance to mesquite (fixed effects) given variation in scores among temperature periods owing to differences in ant activity (repeated effect, compound symmetry). I also examined the relationship among a taxon’s abundance at the bait and measures of overall ant abundance and richness among sites, with respect to mesquite distance, and among periods.

RESULTS

Contrast between the Jornada and Sevilleta sites

Ant abundance in pitfall transects was c. four times higher at the Jornada (mean \pm SE = 3849 \pm 1106) than at the Sevilleta (952 \pm 94; Wilcoxon’s score = 560; two-tailed $P < 0.0001$). Richness at the transect scale was also higher at the Jornada (23.6 \pm 0.8 vs. 16.5 \pm 0.7; Wilcoxon’s score = 242; two-tailed $P < 0.0001$). The species accumulation curve indicated consistently higher richness at the Jornada (Fig. 1), but total measured and extrapolated species richness values differed little (from 39 to 43 species). In analyses restricted to only the black grama grassland types within each site, the Jornada was also more species rich (Bestelmeyer & Wiens, 2001b).

The primary difference in ant abundance between the sites was because of the Dominant Dolichoderine *D. bicolor* (Fig. 2). This ant was highly abundant in Jornada transects where it occurred (15/20) and exceeded 500 individuals in 9/20 transects and 2000 individuals in 5/20 transects. Additional differences are because of the Dominant Dolichoderine *Forelius*, and Hot Climate Specialists *Myrmecocystus* and *Solenopsis xyloni*. Only two seldom-captured taxa were more abundant at Sevilleta: the Cold-Climature Specialist *Leptothorax* and the Generalized Myrmicine *Crematogaster*.

Table 1 Species commonly observed at baits and pitfall traps at each site, their assignment to species groups used for analysis, and the functional groups to which species groups were associated (Andersen, 2000; Brown, 2000). See Bestelmeyer & Wiens (2001b) for a complete species list

Functional group/Species group	Sevilleta	Jornada
Dominant Dolichoderines		
Notes: High tempo species with large colonies, often successful in interactions at baits.		
<i>Forelius</i>	<i>pruinus</i> (Roger) <i>mccooki</i> McCook	<i>pruinus</i> <i>mccooki</i>
<i>Dorymyrmex bicolor</i> Wheeler	<i>smithi</i> Cole	<i>bicolor</i>
Hot Climate Specialists		
Notes: Geographically associated with warm, open climates, often possess unique adaptations to aridity. <i>Solenopsis</i> may be better characterized as a Generalized Myrmicine.		
<i>Pogonomyrmex</i>	<i>desertorum</i> Wheeler <i>maricopa</i> Wheeler	<i>desertorum</i> <i>maricopa</i>
<i>Solenopsis xyloni</i> McCook	—	<i>xyloni</i> <i>amblychila</i> Wheeler
<i>Myrmecocystus</i>	<i>mimicus</i> Wheeler <i>placodops</i> Forel <i>navajo</i> Wheeler	<i>mimicus</i> <i>depilis</i> Forel <i>mexicanus</i> Wesmael <i>romainei</i> Snelling
Cold Climate Specialists		
Notes: Geographically centred on cooler climates. Locally, some taxa are most active during cool seasons (e.g. <i>L. olbiquicanthus</i>).		
<i>Leptothorax</i>	<i>olbiquicanthus</i> Cole <i>carinatus</i>	<i>carinatus</i> Cole <i>bestelmeyeri</i> MacKay
Cryptic species		
Notes: Minute, sometimes subterranean taxa that interact little with other groups.		
Small myrmicines	<i>Solenopsis</i> (Diplorhoptrum) <i>Monomorium minimum</i> (Buckley)	S. (Diplorhoptrum) <i>Monomorium minimum</i>
Tropical Climate Specialists		
Notes: Geographically centred on tropical climates. <i>Trachymyrmex</i> is a leaf-harvester specializing on mesquite and <i>Acacia</i> leaves at the Jornada.		
<i>Trachymyrmex</i>	—	<i>smithi</i> Buren
Generalized Myrmicines		
Notes: Mass recruiting taxa with lower tempo and are usually subordinate to Dominant Dolichoderines, but achieve dominance where the latter are poorly represented.		
<i>Pheidole</i>	<i>crassicornis</i> Emery <i>longula</i> Emery <i>soritis</i> Wheeler sp. J1 <i>tucsonica</i> <i>xerophila</i> Wheeler	<i>crassicornis</i> <i>hyatti</i> Emery <i>militicida</i> Wheeler <i>tucsonica</i> Wheeler sp. J1 <i>sciophila</i> Wheeler <i>xerophila</i> <i>depilis</i>
<i>Creumatogaster</i>	<i>depilis</i> Wheeler <i>punctulata</i> Emery	<i>depilis</i>
Opportunists		
Notes: Generally submissive taxa that are subordinate to Dominant Dolichoderines and Generalized Myrmicines, but may achieve local dominance where these taxa are poorly represented.		
<i>Dorymyrmex insanus</i> gp	<i>insanus</i> (Buckley)	cf. <i>flavus</i> <i>insanus</i>
<i>Aphaenogaster cockerelli</i> André (both sites)		

The abundance of ants at baits was higher at the Jornada (137 ± 8) than at the Sevilleta (107 ± 9 ; $F = 6.56$; d.f. = 1, 22; $P = 0.02$). Richness at baits was also higher at the Jornada (4.9 ± 0.3 vs. 3.5 ± 0.3 ; $F = 15.0$; d.f. = 1, 22; $P = 0.0008$). Similar to the pitfall trap data, *Forelius* and *D. bicolor* were more common at Jornada baits than at the Sevilleta (Fig. 3). *D. bicolor*,

however, did not dominate baits in proportion to its numerical abundance, reflecting its patchy distribution and limited activity during hot temperature periods (Fig. 4). *Forelius*, on the other hand, was able to exploit baits during hot periods at both sites. Its activity during moderate periods, however, was very limited at the Sevilleta when compared to the Jornada. The submissive

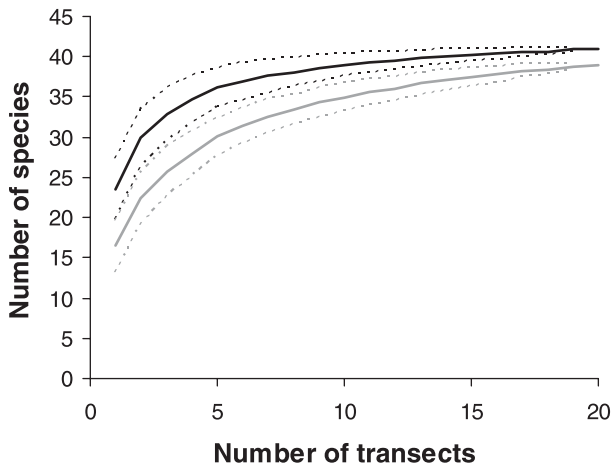


Figure 1 Species-sample curves (solid lines) with an envelope of two standard deviations (dashed lines) based on multiple subsamples of transect richness values. Black = Jornada, grey = Sevilleta.

Dorymyrmex insanus, on the other hand, was able to occupy baits in greater numbers at Sevilleta than at the Jornada.

Effects of variation in mesquite distance within the Jornada

Total ln-transformed ant abundance in pitfall traps was unrelated to mesquite distance (adjusted $R^2 = 0$; $F = 0.13$; d.f. = 1, 14; $P = 0.73$) as was richness (adjusted $R^2 = 0$; $F = 0.11$; d.f. = 1, 14; $P = 0.74$). Correspondence analysis, however, indicated that variation in species composition was related to mesquite distance (Fig. 5). The ordination distances in the first two axes represented 79.8% of the variation in the original chi-square distances. Axis 1 accounted for 62.4% of the original variation. The Axis 1 scores were regressed against a set of potential explanatory

variables including percentage clay, coarse sand, and fine sand, percentage grass cover, percentage bare ground, percentage litter, and distance to mesquite. The best (and only significant) model based on the minimal Mallow’s C(p) included only distance to mesquite (Adjusted $R^2 = 0.34$; $F = 7.34$; d.f. = 1, 14; $P = 0.02$).

The abundances of most functionally distinct taxa were unrelated to mesquite to distance (Fig. 6). Of the 9 taxa examined, only three revealed a significant, negative relationship with mesquite distance, and one of these (*Forelius*) was strong. No taxa exhibited significant negative relationship with mesquite distance. Overall and individual taxon abundances at baits did not reveal an effect of mesquite distance, despite substantial variation in the period of activity for most taxa (Table 2). I also examined the role of percentage grass cover in the models, and in no case did the addition of this term substantially improve the relationships.

The ecotone between the mesquite duneland and the shrub-poor grassland, however, revealed strong differences in ant dominance over time at one site within the Jornada (Fig. 7). During the hot period, *Forelius* attended baits in the mesquite zone but not in the grassland zones. Once temperatures cooled below 37 °C, *D. bicolor* saturated baits within the mesquite zone (but not elsewhere), *Forelius* activity was pushed into the loamy-textured soils of the grass zone, and the Opportunist *Formica perpilosa* Wheeler occupied baits in the fine-textured soils of the playa.

DISCUSSION

Contrast between the Jornada and Sevilleta sites

Patterns revealed in this study indicate that mesquite encroachment has not had an obvious negative impact on ant diversity and numerical dominance at the Jornada. In contrast, there is evidence from the regional scale comparisons that the ant community has either persisted or prospered with increasing mesquite densities. The grassland areas examined at the Jornada LTER are now classified as mesquite-dominated, but were classified

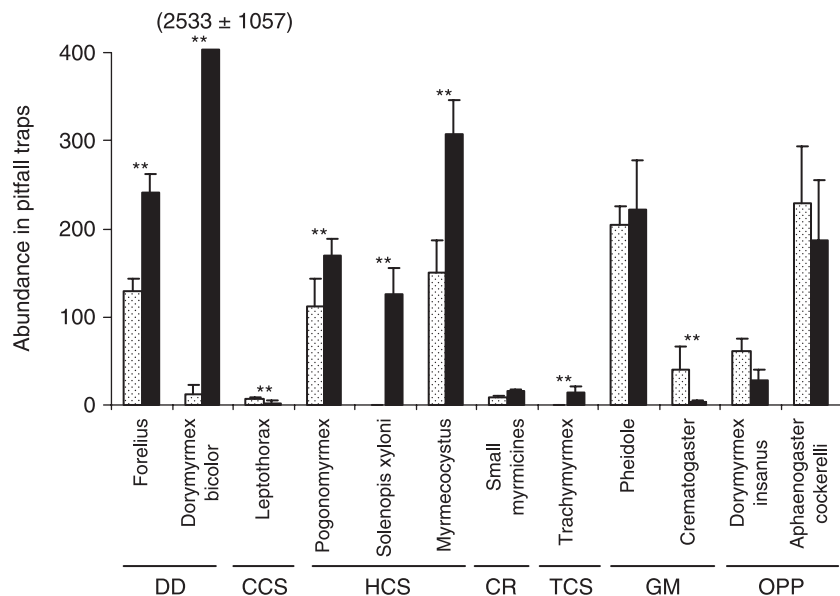


Figure 2 Means (\pm standard errors) of pitfall trap abundances at transects of the Sevilleta (stippled) and Jornada (black). Note that *Dorymyrmex bicolor* bar far exceeds range of the ordinate. A double asterisk indicates that least-squares means differed at $P = 0.05$ level and single asterisk indicates that significance was at the $P > 0.05$ and $= 0.10$ level. DD = Dominant Dolichoderines, HCS = Hot Climate Specialists, CCS = Cold Climate Specialists, CR = Cryptic species, TCS = Tropical Climate Specialists, GM = Generalized Myrmicines, and OPP = Opportunists.

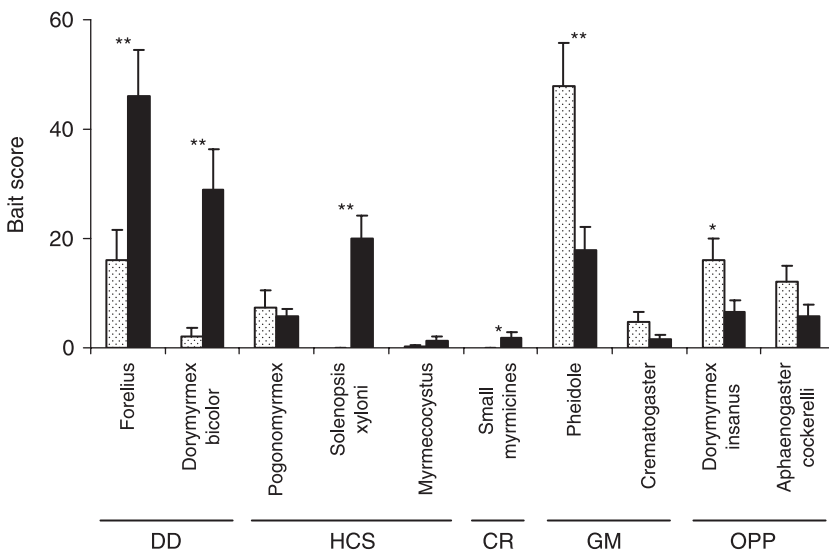


Figure 3 Least-squares means (\pm standard errors) of bait scores at transects of the Sevilleita (stippled) and Jornada (black). Functional group codes and asterisks as in Figure 3.

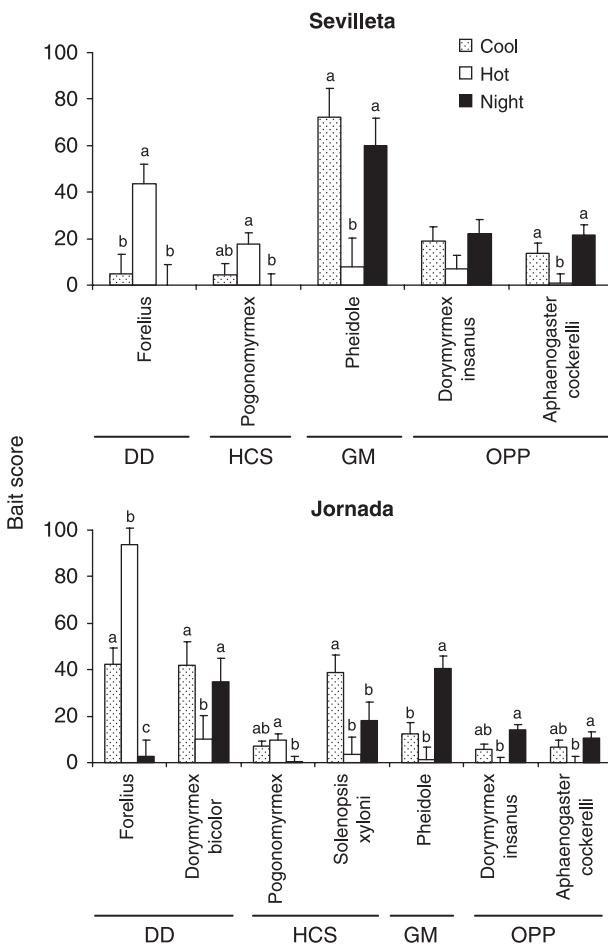


Figure 4 Least-squares means (\pm standard errors) of bait scores at transects within each period at each site. Bars with different letters differed in least-squares contrasts at the $P = 0.05$ level. Functional group codes as in Figure 3.

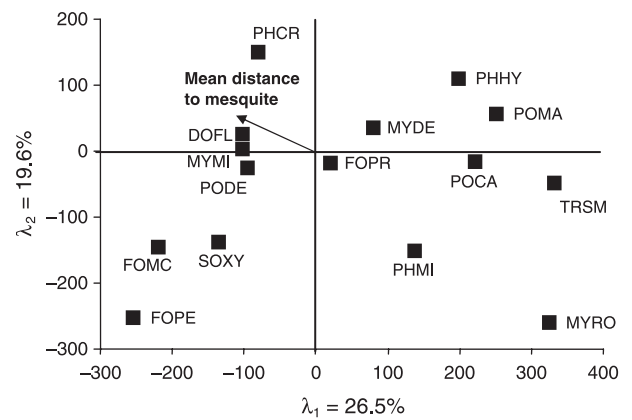


Figure 5 Correspondence analysis ordination of transect pitfall data for 16 grassland transects and 35 species at the Jornada. The axis values indicate the amount of variation in the ordination explained by the axis. Only species whose abundances exhibited a correlation coefficient > 0.30 with axis 1 were plotted for clarity. The arrow direction indicates the direction of maximum change in the environmental variable through unconstrained ordination space. *Formica perpilosa* (FOPE), *Forelius mccooki* (FOMC), *Myrmecocystus mimicus* (MIMI), *Pogonomyrmex desertorum* (PODE), *Solenopsis xyloni* (SOXY), *Dorymyrmex cf. flavus* (DOFL), and *Pheidole crassicornis* (PHCR) occur to the left of the ordination. *Forelius pruinosus* (FOPR), *Myrmecocystus depilis* (MYDE), *Pheidole hyatti* (PHHY), *Myrmecocystus romainei* (MYRO), *Pogonomyrmex californicus* (POCA), *Pogonomyrmex maricopa* (POMA), *Pheidole militica* (PHMI), and *Trachymyrmex smithi* (TRSM) occur to the right.

as grass-dominated within the last 100 years (Gibbens *et al.* in press). Despite this shift, the Jornada exhibited greater overall activity and richness of ants than the mesquite-free Sevilleita under similar climatic conditions, reflected both in the number of foragers present and in their domination of food resources. These differences were driven primarily by behaviourally dominant taxa including *D. bicolor*, *Forelius*, and *Solenopsis xyloni* as

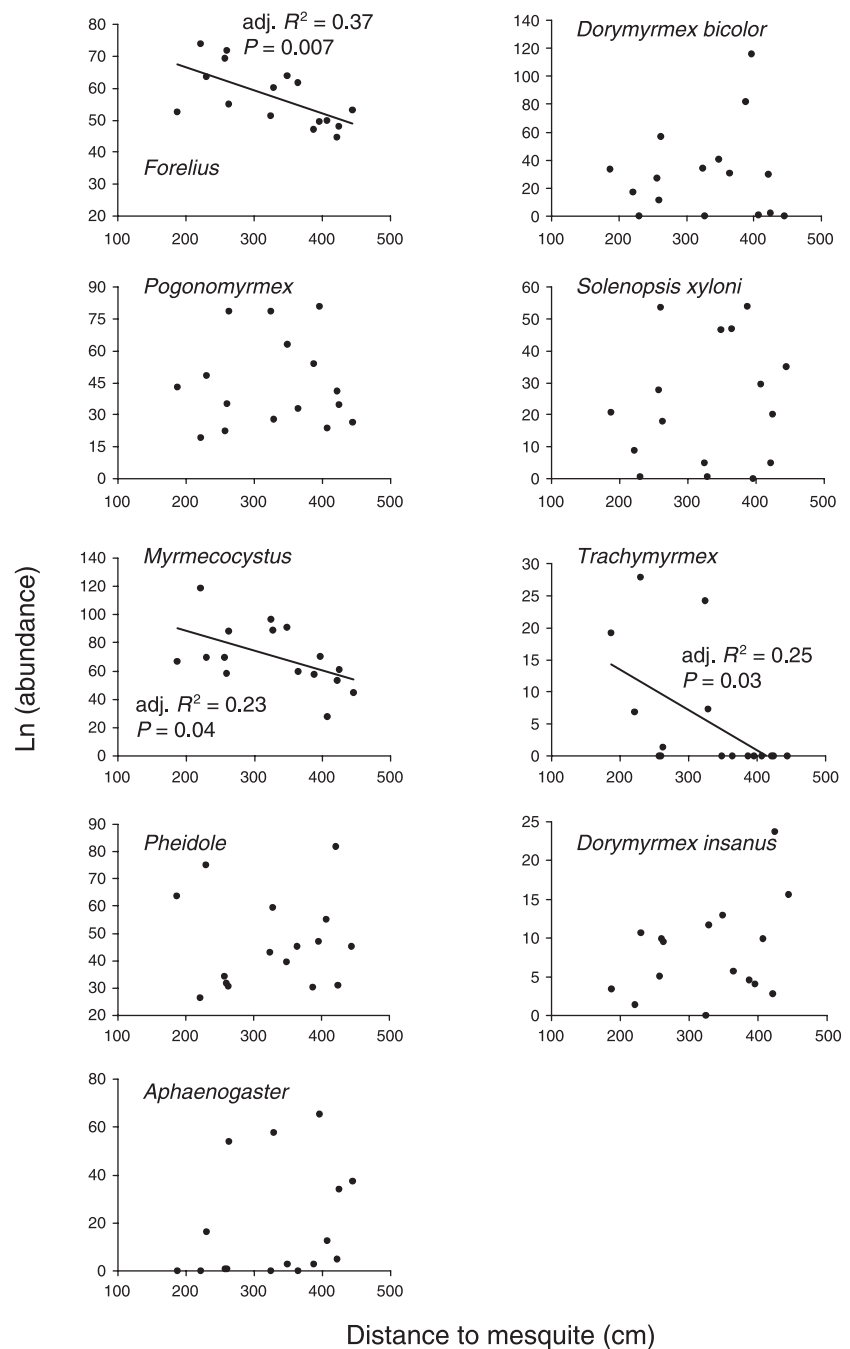


Figure 6 Regressions of the average distance to mesquite shrubs with the abundance of common taxa in the Jornada grasslands. All d.f. = 1, 14. Coefficients are shown only for significant ($P = 0.05$) regressions.

well as more rare taxa such as *Trachymyrmex smithi* and *Myrmecocystus romainei*.

The occupation of baits by different ant functional groups supports the notion that ecological dominance is better developed at the Jornada than at the Sevilleta (cf. Andersen, 1997b). The domination of food resources was higher overall at the Jornada and was driven largely by Dominant Dolichoderines and behaviourally dominant *S. xyloni* within Hot Climate Specialists. *Forelius* was strongly thermophilic and especially dominant at the Jornada (see also Hölldobler, 1982). It saturated baits at hot temperatures to a much greater degree than at Sevilleta. Even at cooler diurnal temperatures, *Forelius* dominated baits to the

same degree as other dominant taxa. In contrast, the Sevilleta's ecological dominance pattern was simpler and dominated by Generalized Myrmicines, particularly small *Pheidole*. Globally, Generalized Myrmicines often dominate in areas that are only moderately productive for ants and where Dominant Dolichoderine abundance is low (Andersen, 2003). Further, Opportunist taxa that indicate lower-quality or disturbed environments for ants (Andersen, 1997b) were more common at baits at the Sevilleta.

It is impossible to attribute these site differences directly to the abundance of mesquite. A number of other factors covary with mesquite density and differ between the landscapes. The Sevilleta experiences cooler winters and it features more reliable spring

Table 2 Results (*F* statistic and *P*-value) of tests of the period (d.f. = 2, 16) and mesquite density (d.f. = 1, 7) terms from mixed models analyses of bait abundance for taxa that were common at baits at the Jornada

Species/genus	Period		Distance to mesquite	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
<i>Forelius</i>	17.0	0.0001	3.5	0.10
<i>Dorymyrmex bicolor</i>	8.0	0.004	0.06	0.81
<i>Pogonomyrmex</i>	3.7	0.05	0.01	0.93
<i>Solenopsis xyloni</i>	5.4	0.02	0.31	0.59
<i>Pheidole</i>	7.5	0.005	0.07	0.80
<i>Dorymyrmex insanus</i>	3.3	0.06	0.56	0.48

rainfall (Hochstrasser *et al.*, 2002). The cooler winters or distinct land-use history may limit mesquite encroachment into grasslands north of the Jornada (Johnson *et al.*, 2000) and either temperature extremes and/or shrub abundance may limit the abundance of dominant ant taxa (Korzukin *et al.*, 2001; Kaspari & Valone, 2002). Nonetheless, it is clear that the presence of mesquite-dominated habitats at the Jornada has not led to reduced diversity relative to the Sevilleta (note the within-site effects of mesquite below).

Instead, it is likely that mesquite shrubs may promote the abundance of some ants and contribute to alpha and gamma diversity at the Jornada. A replicated experiment at the Jornada demonstrated that the abundance of *D. bicolor* was depressed over a series of years where mesquite had been removed (Nash *et al.*, 1998, 2000). Comparative data also support this pattern (Wisdom & Whitford, 1981; Fig. 7). *T. smithi* is a fungus-cultivating species that relies on fallen mesquite leaves and on which to grow fungus (Cole, 1952) and is reliably associated with mesquite dunelands (Bestelmeyer & Wiens, 2001a). This ant also has a restricted distribution in southern New Mexico (MacKay & MacKay, 2002). Another mesquite associate, *Myrmecocystus romainei*, may not rely directly on mesquite but nests in the deep, soft sand (Snelling, 1976) that accumulates around shrubs in desertified environments. *D. bicolor*, *Trachymyrmex*, and *M. romainei* (among others) were not present in the Sevilleta samples.

The presence of a reliable source of carbohydrate-rich plant exudates provided by hemipteran insects on mesquite may be an important cause of the high ecological dominance of ants at the Jornada. A similar explanation exists for intercontinental differences in ant productivity and dominance (Andersen, 2003). This idea originated in tropical forests, where dolichoderine and formicine ants with high foraging tempos (individual activity) and high dynamic densities are believed to be supported by primary consumption of plant resources in the form of exudates (Blüthgen *et al.*, 2000; Davidson *et al.*, 2003). These taxa are able to sequester and expend large amounts of energy and exert both numerical and ecological dominance (Davidson, 1998; Holway, 1999). Hemipteran resources on shrubs would be comparatively reliable when compared to grasses because shrub-based resources are phenologically predictable (Nash *et al.*, 1998) because of the

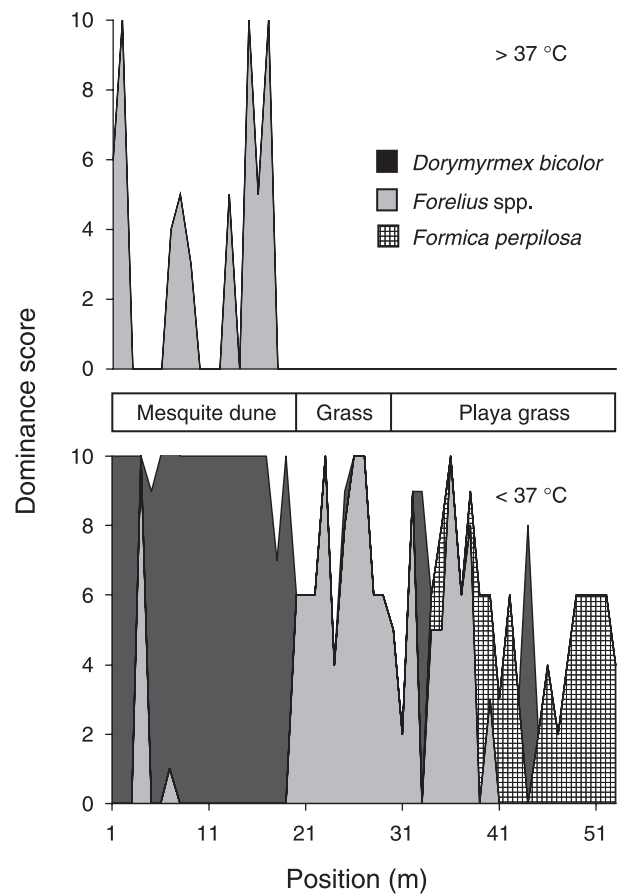


Figure 7 Bait scores for ant taxa observed on a transect bisecting an ecotone between mesquite duneland and grassland types. The location of the boundaries is indicated. The bait scores are the sum of values observed twice each during hot (top) and moderate (bottom) soil-surface temperatures (maximum value of 10 possible/species/bait).

ability of shrubs to track rainfall and use deep soil water through drought (Reynolds *et al.*, 1999). Thus, the use of hemipteran resources by *Forelius*, *D. bicolor*, and *Myrmecocystus* (Van Zee *et al.*, 1997) and their high abundance at the Jornada may be related, but conclusive experiments conducted at appropriate scales have yet to be performed.

Effects of variation in mesquite distance within the Jornada

The patterns observed with respect to mesquite distance within the Jornada provide additional support to the mesquite hypothesis, but also point out inconsistencies. *Forelius*, which was comparatively dominant at the Jornada, was locally most abundant where mesquite densities around transects were high. Another exudate-feeding genus that was dominant at the Jornada, *Myrmecocystus* (Snelling, 1976), also responded positively to shrub proximity. *Dorymyrmex bicolor*, however, was clearly not associated with local mesquite proximity. This may be related to its patchy distribution and because mesquite plants were never

very far away (< 450 cm) in the grassland samples. Only along a very steep gradient of mesquite density associated with soil textural change did *D. bicolor* reveal an association with mesquite (Fig. 7). Other dominant Jornada taxa that were absent at the Sevilleta such as *Solenopsis xyloni*, however, showed no relationship to mesquite. Thus, local responses to mesquite variation (at least over the scales examined) can explain only some of the differences between the sites.

Although local richness and abundance were insensitive to mesquite proximity, the primary axis of community turnover within the Jornada grasslands is best explained by local differences in mesquite density. While some of this turnover was associated with shifts in generic composition, there are also indications of turnover within genera. Thus mesquite density variations appear to contribute to habitat heterogeneity without causing significant changes in richness or in the abundances of most functionally distinct taxa (see Hoffmann & Andersen, 2003). In some cases, a disturbance or stress associated with stable richness and species turnover is a result of exotic invasion or increases in 'weedy' species as native species decrease (McIntyre *et al.*, 2003). In this study, however, none of the species associated with the 'mesquite' side of ordination (Fig. 5) are non-native or can be considered as 'weedy'. In fact, at least one subspecies (*T. smithi neomexicanus*) is rare and a Chihuahuan Desert endemic.

Conclusions and implications

The transition from grasslands to shrublands in the Chihuahuan Desert was believed to have been initiated by historical overgrazing (Paulsen & Ares, 1962) and altered fire regimes (McPherson, 1995) but is now a self-perpetuating phenomenon as a result of positive feedbacks between grass loss and soil erosion (Schlesinger *et al.*, 1990; Herrick *et al.*, 2002). The continued loss of grasslands is of great concern for economic reasons and because of the spectre of species loss. Although undetected, rare ant species may be imperilled by mesquite encroachment, the observations offered here suggest that this change may not impose an obvious negative impact on some native taxa and may even have positive consequences. Belsky (1996) arrived at a comparable conclusion with regard to the encroachment of western juniper (*Juniperus occidentalis* Hook.) expansion, and questioned the indiscriminate removal of this woody species.

The relationships between mesquite and ants observed here are consistent with studies that have been conducted around the world. Particular ant taxa are often associated with woody vegetation and the microenvironments that they create (Punttila *et al.*, 1991; Bestelmeyer & Wiens, 1996; King *et al.*, 1998; Bestelmeyer & Schooley, 1999; Retana & Cerdá, 2000; Farji-Brener *et al.*, 2002; Gomez *et al.*, 2003). The added habitat structure provided by shrubs in otherwise open grasslands can elicit responses at the level of functional groups (Hoffmann & Andersen, 2003) and add functional diversity to grassland environments. By virtue of additional functional groups, ants appear to capture a comparatively high fraction of available productivity in a shrub-dominated environment, even though ecosystem productivity

has reorganized over time (Huenneke *et al.*, 2002). This suggests that blanket statements about the effects of invasions and desertification on 'biodiversity' are sometimes inappropriate — particular processes and taxa should be specified (Lindenmayer *et al.*, 2002). For some taxa, mosaics of 'degraded' shrublands and historic grasslands that feature variation in key structural elements may promote landscape species diversity (Tews *et al.*, 2004).

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