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Influence of small-scale disturbances by kangaroo rats on Chihuahuan Desert ants

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Abstract Banner-tailed kangaroo rats (*Dipodomys spectabilis*) are prominent ecosystem engineers that build large mounds that influence the spatial structuring of fungi, plants, and some ground-dwelling animals. Ants are diverse and functionally important components of arid ecosystems; some species are also ecosystem engineers. We investigated the effects of patch disturbances created by *D. spectabilis* mounds on ant assemblages in a Chihuahuan Desert grassland in southern New Mexico by using pitfall traps in a paired design (mound vs. matrix). Although the disturbances did not alter species richness or harbor unique ant communities relative to the matrix, they did alter species composition; the abundances of 6 of 26 species were affected. The disturbances might also act to disrupt spatial patterning of ants caused by other environmental gradients. In contrast to previous investigations of larger-scale disturbances, we detected no effects of the disturbances on ants at the functional-group level. Whether ant communities respond to disturbance at a functional-group or within-functional-group level may depend on the size and intensity of the disturbance. Useful functional-group schemes also may be scale-dependent, however, or species may respond idiosyncratically. Interactions between disturbance-generating mammals and ants may produce a nested spatial structure of patches.

Key words Ecosystem engineers · Disturbances · Formicidae · Heteromyidae · Spatial scale

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Introduction

Natural disturbances create environmental patchiness that can strongly influence organisms and ecological processes (Watt 1947; Wiens 1976; Pickett and White 1985; Turner 1987). In particular, patch disturbances can affect patterns of species richness and community structure by increasing habitat heterogeneity and permitting the coexistence of species with differing competitive and colonization abilities (Horn and MacArthur 1972; Denslow 1985; Huston 1994). In terrestrial systems, the disturbances created by the activities of burrowing mammals are important generators of spatial heterogeneity (Huntley and Inouye 1988; Whicker and Detling 1988; Hansell 1993). These effects are especially evident in arid and semi-arid environments (Wiens 1985; Whitford and Kay 1999). Burrowing mammals may be ecosystem engineers (sensu Jones et al. 1994; Lawton 1994) because they directly modify habitats and change the abundance and dispersion of resources used by other species.

Banner-tailed kangaroo rats (*Dipodomys spectabilis*) are conspicuous ecosystem engineers in deserts of southwestern United States and northern Mexico. These large (ca. 120 g) heteromyid rodents build mounds that influence the spatial heterogeneity of soil nutrients, soil texture, and soil moisture in the Chihuahuan Desert (Mun and Whitford 1990; Whitford and Kay 1999). Changes in the soil characteristics of mounds, together with soil disturbances, selective granivory (Brown and Heske 1990; Heske et al. 1993), and graminivory (Kerley et al. 1997) in nearby foraging areas, can create pronounced changes in the composition of plant communities on and near *D. spectabilis* mounds (Moroka et al. 1982; Moorhead et al. 1988; Mun and Whitford 1990; Heske et al. 1993; Fields et al. 1999). Guo (1996) concluded that patches disturbed by *D. spectabilis* supported unique plant communities and that species richness was higher in the area adjacent to mounds than in either the matrix or the mounds. These observations are consistent with the intermediate disturbance hypothesis (Grime 1973; Horn 1975; Connell 1978).

Burrows of *D. spectabilis* also alter the abundance and distribution of soil fungi (Hawkins 1996) and some ground-dwelling animals in Chihuahuan Desert grasslands (Hawkins and Nicoletto 1992). Compared with the intervening habitat, mound disturbances had a greater abundance of two species of lizards and several groups of insects (darkling beetles, desert cockroaches, and camel crickets).

Despite considerable research on patch disturbances of *D. spectabilis*, the interactions of these granivorous desert rodents with ants (Hymenoptera: Formicidae) have received only limited attention. Previous investigations examined the potential for exploitative competition between heteromyid rodents and granivorous ants (Brown and Davidson 1977; Davidson et al. 1985; Samson et al. 1992; Valone et al. 1994). Specialized granivorous ants, however, generally constitute a minority of the species in the Sonoran and Chihuahuan deserts (Whitford 1978; Bestelmeyer and Schooley 1999) (Appendix); many ant species are omnivorous scavengers and predators. More generally, little is known about the response of ants to mammal-caused disturbances in any environment.

Why investigate whether the spatial structuring of ants is influenced by *D. spectabilis* disturbances? First, ants are diverse, abundant, and functionally important in arid and semi-arid environments (Majer 1983; Andersen 1990; MacKay 1991; Folgarait 1998). Second, ants are sensitive to habitat change and disturbance at numerous spatial scales (Wisdom and Whitford 1981; Bestelmeyer and Wiens 1996; Andersen 1997a; Peck et al. 1998). Third, because their activities influence soil properties and redistribute resources used by other organisms, some ants are also ecosystem engineers (Jones et al. 1994; Folgarait 1998). Linkages between ecosystem-engineer species should be important regulators of ecosystem processes. Finally, Andersen (1991a) presented a strong case for the existence of many parallels between ants and plants: modularity, fixed positions, common resource requirements, competitively structured communities, and similar functional groups. Given the documented responses of plant communities to activities of banner-tailed kangaroo rats, similarly strong effects might be expected for ant communities.

We evaluated the responses of ants to landscape disturbances created by *D. spectabilis* in a Chihuahuan Desert grassland habitat. Our focus was on the entire ant community and not just on specialized granivores. We used a hierarchical approach, examining effects at the community, functional group, and individual species levels.

Materials and methods

Study site and disturbance regime

We conducted the study in a 15-ha area at the Jornada long-term ecological research (LTER) site, 37 km north of Las Cruces, New Mexico. The vegetation at the site is typical of the northern Chihuahuan Desert and includes either grasslands or shrublands (*Larrea tridentata*, *Prosopis glandulosa*, *Flourensia cernua*), depending on geomorphic processes, soils (Wondzell et al. 1996), and interactions between climate and land use (Schlesinger et al. 1990). Our plot was in grassland dominated by black grama (*Bouteloua eriopoda*) with scattered yucca (*Yucca elata*) and few shrubs. Several other grasses were present, including *Aristida* spp. and *Sporobolus* spp.. Common forbs included *Croton pottsii*, *Eriogonum abertianum*, *Zinnia grandiflora*, and *Euphorbia* spp.; sub-shrubs were primarily snakeweed (*Xanthocephalum sarothrae*). Moderate grazing by cattle occurred on the site. Precipitation at the Jornada LTER is extremely variable among years, but averages 230 mm annually, with >50% generally occurring in convective thunderstorms from July to September (Gibbens and Beck 1988).

Typically, only one adult *D. spectabilis* occupies each mound, which is used for shelter, reproduction, and seed caching. Their impressive mounds are approximately circular, average 31 cm in height, and have 3–12 burrow openings (Best 1988). At our site, the mounds had an average area of 20 m^2. Mound densities at the Jornada LTER site vary among habitats, from 2.5 ha^{-1} in *Prosopis* grasslands to 9.4 ha^{-1} in black grama grasslands (Moroka et al. 1982) such as our site. Mound development takes 23–30 months and abandoned mounds deteriorate markedly in 1 year (Best 1972). Mounds are often inherited by subsequent generations of *D. spectabilis*, however, and thus may persist for ≥50 years (Parmenter and Van Devender 1995).

Sampling design and data analysis

We sampled ants and vegetation in late July-early August 1996, following heavy rains in July that ended a 2-year drought in the area. There can be considerable seasonal variation in the activity of ants in arid systems (Whitford 1978), so we sampled during the warm-wet season to reveal patterns for the greatest number of species (e.g., Bestelmeyer and Wiens 1996).

Using a paired sampling design, we chose ten mounds of banner-tailed kangaroo rats (assumed to be active based on animal sign; Schroder and Geluso 1975; Jones 1984), and matched them with ten locations in the matrix. Grids of six pitfall traps (Andersen 1991b; Bestelmeyer and Schooley 1999) were established 1 m (mound) and 17 m (matrix) from active mounds in a random direction. We did not place traps directly on mounds because preliminary tests indicated that the kangaroo rats would not tolerate them. Thus, we sampled ants in the area adjacent to the mound where disturbance is intermediate and species richness of plants is highest (Guo 1996). The distance between mound and matrix samples was dictated by typical inter-mound distances and our desire to keep the distance similar to that used in a previous investigation (see Hawkins and Nicoletto 1992). All matrix locations were ≥24 m from unsampled kangaroo rat mounds. Each sampling grid included two rows (1 m apart) of three traps (separated by 1.5 m). Individual traps were treated as subsamples; we pooled data for all six traps and used the grids as replicate samples (10 mound and 10 matrix samples, 120 total traps).

The traps were polypropylene sample cups (65 mm diameter, 100 mm deep) filled with 40 ml of a propylene-glycol and ethanol mixture. We placed traps in the ground with the upper lip even with the soil surface and allowed them to settle for 48 h before initiating sampling. Traps were opened for ca. 72 h during sampling (Bestelmeyer and Schooley 1999). Most voucher specimens are housed in the C. P. Gillete Museum at Colorado State University.

At each grid location, we measured the cover by grasses, forbs, sub-shrubs, and bare ground using point-intercept sampling. Points were spaced every 10 cm (starting at 10 cm) along three 3-m transects; each transect was centered on two traps (one from each row). We did not sample points at actual trap stations, and thus there was a total of 84 intercepts $location^{-1}$. We compared vegetation cover between mound and matrix habitats with Wilcoxon signed rank tests (a nonparametric paired analysis).

All ant abundances were ln-transformed prior to analyses. We compared species richness and evenness between habitats with Wilcoxon signed rank tests. Evenness was calculated using Pielou's (1969) measure [Shannon diversity index÷ln(richness)]. To test for differences in species composition between mound and matrix samples, we used blocked multi-response permutation procedures (MRBP), which is an extension of multi-response permutation procedures to randomized block or paired designs (Mielke and Berry 1982). MRBP is a nonparametric procedure and thus does not require assumptions associated with alternative paramet-

ric tests (multivariate normality and homogeneity of variances; Zimmerman et al. 1985). In our analysis, we used Euclidian distance, within-block median alignment, and an approximated *P*-value from a Pearson type III distribution of the test statistic.

To explore possible gradients in species composition, we ordinated all samples using detrended correspondence analysis (DCA; Jongman et al. 1995). DCA is an eigenanalysis ordination technique based on reciprocal averaging that ordinates species and samples simultaneously. We report coefficients of determination (r^2) using Euclidian distances in ordination space and in original space; this allowed us to evaluate how the variance explained was partitioned among the DCA axes (McCune and Mefford 1999). We then compared ordination scores on axis 1 and axis 2 between mound and matrix samples with Wilcoxon signed rank tests. This approach allowed us to use DCA to reduce the species composition data while maintaining the power of our paired design.

We assigned ants to functional groups (Appendix), which allowed us to evaluate their responses to environmental heterogeneity using broad ecological traits. For our primary functional group, we used designations similar to those previously used for ants (Andersen 1990, 1997a; Bestelmeyer and Wiens 1996; Bestelmeyer and Schooley 1999). Groups were divided initially based on diet and foraging mode and then omnivores were further grouped according to activity patterns and dominance (Bestelmeyer and Wiens 1996). Granivores are specialists that rely largely on seeds. Generalized myrmicines include widespread genera that have aggressive workers that mass-recruit to food sources. We divided this group further based on body-size traits of workers and recruitment behavior. Large generalized myrmicines are relatively large, dimorphic or polymorphic species that recruit rapidly. Small generalized myrmicines are smaller, monomorphic species that recruit relatively slowly. Nocturnal scavengers include two species of honey ants (*Myrmecocystus*) that prey on small insects, gather floral nectar, and collect honeydew from aphids. Diurnal scavengers include two, day-active, species of honey ants. Opportunists include unspecialized, behaviorally submissive species. Thermophiles are primarily diurnal and are most active when soil-surface temperatures are hot enough to limit the activity of many other ant species.

We constructed two alternate functional-group designations based on foraging mode (granivores, granivore-scavengers, scavengers) and on activity patterns (heat-tolerant species, heat-intolerant species, nocturnal species). These simplified schemes were devised to decouple aspects of diet and thermal preferences of ants, which might allow for a better understanding of mechanisms underlying any observed responses by groups. We compared the abundances of functional groups between mound and matrix habitats with Wilcoxon signed rank tests.

We measured the degree of association of individual species with either the disturbed mound habitat or the intervening matrix using indicator-species analysis (Dufrêne and Legendre 1997). Indicator values, which were calculated for each species for both habitats, combine information on relative abundance and relative frequency of occurrence. Perfect indication of a habitat (indicator value=100) occurs when all individuals of a species occur in one of the habitats, and all samples from that habitat contain an occurrence by that species. We tested for statistical significance of maximum indicator values (i.e., highest of the two habitats) with Monte Carlo randomization tests (1000 iterations), in which species abundance data were randomized among the two habitats. We omitted from this analysis four species that occurred in only one sample; thus, we considered 26 species.

The MRBP test, DCA ordination, and indicator-species analysis were conducted using PC-ORD (McCune and Mefford 1999). Other statistical analyses were conducted using SAS (SAS Institute 1989).

Results

Disturbances by banner-tailed kangaroo rats influenced vegetation coverage within our grassland site (Fig. 1). The main effect was an increase in forb cover (T=23.5, P=0.0137) and a decrease in grass cover (T=22.5, P=0.0195) relative to the matrix habitat. Bare ground (T=4, P=0.6680) and sub-shrub (T=10, P=0.3281) cover did not differ between the two habitats.

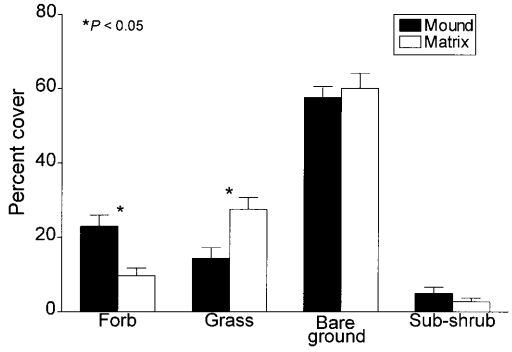

Fig. 1 Influence of mound disturbances of banner-tailed kangaroo rats (*Dipodomys spectabilis*) on vegetation coverage at a Chihuahuan Desert grassland site. Ground cover was measured 1 m from the mounds (*mound*) and 17 m from the mounds (*matrix*). Each *bar* represents a mean (+1 SE) for ten paired mound-matrix samples. Significant differences are based on Wilcoxon signed rank tests for each cover category

We captured 8728 individuals that represented 30 species of ants from 12 genera (Appendix), including 26 species from the mound habitat and 28 species from the matrix habitat. The most species-rich genera were *Pheidole* (eight species), *Pogonomyrmex* (six species), *Myrmecocystus* (four species), and *Solenopsis* (three species). In both mound and matrix habitats, the three most abundant species were *Forelius pruinosus*, *Myrmecocystus mimicus*, and *Aphaenogaster cockerelli*.

Species richness did not differ (T=2, P=0.856) between mound ($\bar{x}$=15.6, SE=0.65, n=10) and matrix habitats ($\bar{x}$=15.8, SE=0.87, n=10). Although evenness differed (T=18.5, P=0.065) between mound samples ($\bar{x}$=0.863, SE=0.009, n=10) and matrix samples ($\bar{x}$=0.893, SE=0.014, n=10), the average difference in the evenness index between pairs was small (0.03), and we doubt that it represented a biologically meaningful contrast. Rank-abundance curves for the two habitats supported this conclusion.

The MRBP test revealed that species composition of ants differed between the mound and matrix samples (T=–1.437, P=0.088, n=10 pairs). Indicator-species analysis (see below) identified the particular species whose abundance patterns were the primary factors creating this contrast in species composition.

Mound and matrix samples did not separate (T=2.5, P=0.846) along axis 1 (eigenvalue=0.208, r^2=0.50, gradient length=1.93) of the DCA ordination (Fig. 2). Instead, axis 2 (eigenvalue=0.100, r^2=0.13, gradient length=1.67) corresponded with the disturbance gradient (Fig. 2). Most matrix samples (eight out of ten) had higher scores than their paired mound samples on axis 2 (T=19.5, P=0.049). We conducted some additional correlative analyses to aid in our interpretation of the primary gradient represented by axis 1. Scores on axis 1 were not correlated with the coverage of forbs (r_s=0.067, P=0.779), grasses (r_s=0.089, P=0.710), or bare ground (r_s=-0.191, P=0.421), but they were correlated with the

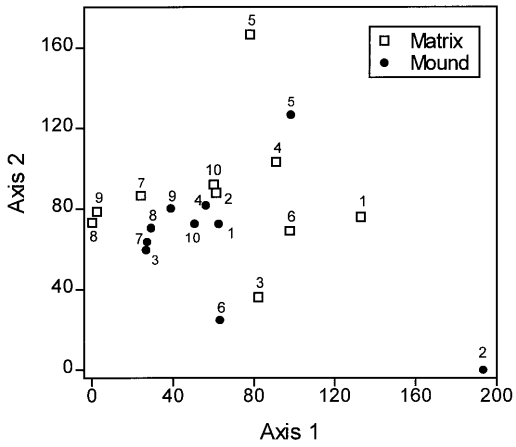

Fig. 2 Detrended correspondence analysis (*DCA*) ordination of samples based on composition and abundance of ant species. Samples were from locations near mounds of *Dipodomys spectabilis* and from those in the intervening grassland matrix. We used a paired design with the *numbers next to symbols* indicating the mound-matrix pairs. Pairs are numbered in ascending order to indicate their spatial locations from south to north (i.e., pair 1–10). Axes are based on the average SD of species turnover (×100) and are shifted so that all scores are positive (McCune and Mefford 1999)

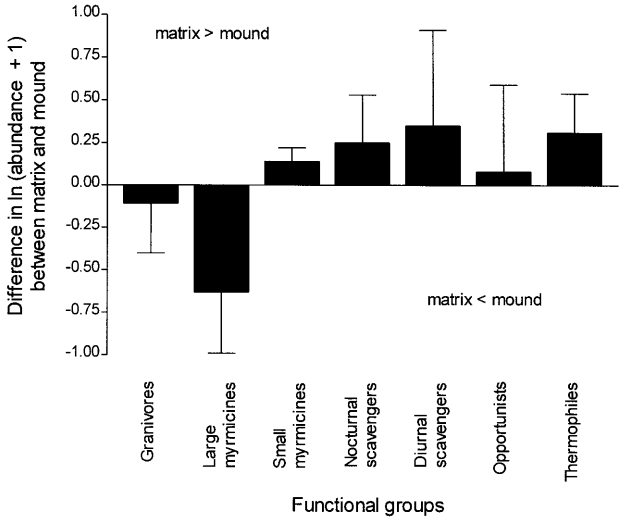

Fig. 3 Responses of functional groups of ants to disturbances created by banner-tailed kangaroo rats (*Dipodomys spectabilis*). Each *bar* represents the mean difference (+1 SE) between ten paired samples collected 17 m from mounds (*matrix*) and 1 m from mounds (*mound*). Functional-group designations for individual ant species are given in the Appendix

south-north spatial location of the samples (r_s=–0.580, P=0.007). Higher axis 1 scores were associated with samples that were farthest south along the 500-m extent of our sampling. However, closer inspection revealed that matrix samples were correlated with the south-north spatial location (r_s=–0.709, P=0.022), but mound samples were not (r_s=–0.382, P=0.276). Therefore, the ants in the matrix responded strongly to some unmeasured spatial gradient, but the ant assemblages near to the disturbances were unaffected by this environmental variation. Consequently, the mound samples were limited to a relatively small domain on axis 1 (eight out of ten mound samples were within 37 SD units, whereas eight out of ten matrix samples were within 90 SD units).

Table 1 Results of Wilcoxon signed rank tests that examined the responses of functional groups of ants to disturbances of *Dipodomys spectabilis*. Functional-group designations for individual ant species are given in the Appendix

Functional group	*T*	*P*
Granivores	4.5	0.695
Large myrmicines	16.5	0.106
Small myrmicines	16.5	0.106
Nocturnal scavengers	0.5	0.977
Diurnal scavengers	2.5	0.846
Opportunists	1.5	0.922
Thermophiles	12.5	0.232

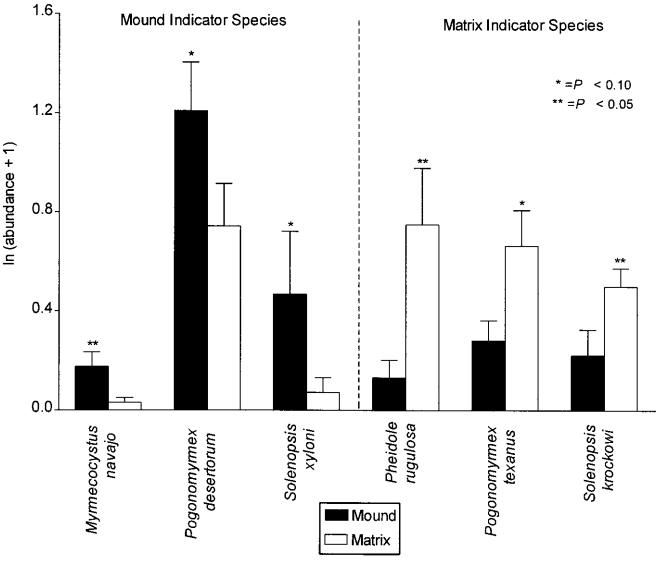

Fig. 4 Mean abundances (+1 SE) for six species of ants that were associated with either the mounds of banner-tailed kangaroo rats (*Dipodomys spectabilis*) or the intervening matrix in a Chihuahuan desert grassland. Associations are based on indicator-species analysis (Dufrêne and Legendre 1997)

None of the functional groups of ants from our primary scheme differed in abundances between the mound and matrix habitats (Fig. 3; Table 1). Alternate group designations, based on either foraging mode or activity, also provided no evidence of responses by ants to the disturbances at the functional-group level (all $Ps \geq 0.49$).

Indicator-species analysis identified six species of ants that were associated with either the mound or the matrix habitat (Fig. 4). The mound indicators were *Myrmecocystus navajo* [indicator value (IV)=60, P=0.031], *Pogonomyrmex desertorum* (IV=62, P=0.090), and *Solenopsis xyloni* (IV=52, P=0.094); whereas the matrix indicators were *Pheidole rugulosa* (IV=60, P=0.033), *Pogonomyrmex texanus* (IV=63, P=0.067), and *Solenopsis krockowi* (IV=69, P=0.023). Finally, this analysis supported our interpretations of axes in the DCA ordination. The abundances of five of the six (83%) indicator species were more strongly correlated with axis 2 than with axis 1; mound indicators had negative associations and matrix indicators had positive associ-

ations. In contrast, only 5 of the remaining 14 (35%) most abundant species had their highest correlation with axis 2.

Discussion

Chihuahuan Desert ants respond to patch disturbances created by *D. spectabilis*, but only at certain levels of organization. We detected no effects of the disturbances on species richness and no indication that the mounds supported unique ant communities. Likewise, ants did not differ between the mounds and matrix at the functional-group level. Community composition differed between these two habitats, however, primarily due to the abundance patterns of six species.

The DCA ordination suggested that the disturbances also can create small-scale patchiness of ants along other environmental gradients. That is, disturbances might disrupt spatial gradients in a way analogous to how they disrupt temporal gradients (i.e., succession; Pickett and White 1985). Axis 2 of the DCA ordination represented the main disturbance gradient, but it explained a small amount of variation (13%). Axis 1 explained 50% of the variation, but it represented an unmeasured gradient that was orientated in a south-north direction, perhaps corresponding to variation in soil texture or microtopography. Samples near the mounds did not correspond to this gradient and occupied a relatively constrained range on axis 1 (Fig. 2); patch disturbances thus led to moderate homogeneity of ant species composition. These results suggest a hypothesis that could be explicitly tested by establishing a transect along a known environmental gradient, such as soil texture, and then comparing the response in species composition between mound and matrix areas.

Many of the documented responses of ant communities to disturbance have occurred across much larger spatial scales than the size of *D. spectabilis* mounds (but see Kaspari 1996). At the scales of mining activities (Majer 1983; Andersen 1997a), fires (Andersen 1991c), and grazing regimes (Bestelmeyer and Wiens 1996), for example, strong responses often are evident at the functional-group level, with opportunists and thermophiles increasing with disturbance (Andersen 1991c; Bestelmeyer and Wiens 1996). The submissive, ruderal-like opportunists respond because disturbance causes mortality of colonies of dominant ant species, whereas thermophiles respond to disturbance because reduced vegetative cover leads to increased soil-surface temperatures. There are several possible reasons for why we did not detect similar patterns in our study (Fig. 3). First, broad-scale disturbances may be most likely to manifest strong responses at the functional-group level, but small-scale disturbances may be more likely to alter the spatial distribution of species within functional groups. Species that partition space at small scales in response to relatively subtle environmental variation may be ecologically similar species that are likely to belong to the same functional group. For instance, within the large generalized myrmicines that we recorded, *Solenopsis xyloni* was an indicator species for mounds, whereas *Pheidole rugulosa* was an indicator species for matrix habitat (Fig. 4). Likewise, within the granivore functional group, *Pogonomyrmex desertorum* was a mound indicator but *P. texanus* was a matrix indicator (Fig. 4). The notion that the expected level of response (among or within functional groups) differs with the scale of disturbance, however, will depend greatly on whether species within functional groups are indeed those most likely to interact for resources at small scales, and on the degree of generalization or specialization within groups.

Second, Andersen (1997b) asserted that functional-group schemes are scale-dependent; functional groups recognized at a global scale may be inappropriate at regional or local scales. Our results extend this caution in that existing functional-group schemes may not apply to small-scale patches within a local area. Groups such as opportunists and thermophiles might respond to disturbances at larger spatial scales within Chihuahuan Desert, such as between grasslands not disturbed by *D. spectabilis* and those with a high density of mounds, instead of at the scale of mounds versus matrix within a grassland. It might be feasible to develop additional functional-group schemes useful for examining and predicting the response of ants to small-scale heterogeneity. This would not be a trivial task because small-scale heterogeneity should be relevant to ants; colonies primarily interact with other colonies in their immediate neighborhood (e.g., Gordon and Kulig 1996). The best approach probably would be to couple research to identify additional species that respond to small patch disturbances with investigations of their natural histories to develop functional groups “from the ground up”, instead of trying to refine existing schemes created for larger scales.

Finally, an alternative explanation for our results is that species respond to fine-scale disturbances individualistically, without regard to current functional-group schemes or any that could be developed. Guo (1996) suggested that much of the response of plants to disturbances by *D. spectabilis* seemed to be individualistic. In our study, one species might have preferred forb-dominated areas for foraging, whereas another might have scavenged preferentially on dead insects within the *D. spectabilis* burrow, and another might have selected thick grass for nesting. For instance, *Pheidole rugulosa* was associated with the matrix habitat (Fig. 4) with a greater coverage of grasses (Fig. 1). Likewise, in long-term experiments on interactions among granivores in the Chihuahuan Desert (Davidson et al. 1985; Samson et al. 1992), the main effect of rodent removals on ants was an increase in colony densities of *P. rugulosa* due to their positive correlation with grass cover (Valone et al. 1994). This consistent association of *P. rugulosa* with areas of high grass cover may be related to nest-site preferences. If so, it would be difficult to develop a functional-group scheme that reflected this response, together with other individualistic responses, given that the goal of the approach is to use broad ecological traits to gain a predictive understanding of how ants respond to disturbance (Andersen 1997a).

Because banner-tailed kangaroo rats and ants both may be ecosystem engineers (Jones et al. 1994), the response of ants to the patch disturbances of *D. spectabilis* might generate a nested spatial hierarchy of animal-created disturbances. The abundance and spatial distribution of *D. spectabilis* mounds could influence resource distributions for other organisms not only directly, but also indirectly by altering the spatial patterns of the smaller ant mounds. For instance, mounds of *D. spectabilis* (Whitford and Kay 1999) and ants (Folgarait 1998) both alter the physical and chemical properties of soil and create patches where plant composition differs from the surrounding matrix. Such nested spatial structuring should be important to a foraging herbivore. Whether this scenario applies to our study area depends, in part, on whether the ecosystem engineering effects differ between those ant species associated with the mounds (*Myrmecocystus navajo*, *Pogonomyrmex desertorum*, *Solenopsis xyloni*) and those with the matrix (*Pheidole rugulosa*, *Pogonomyrmex texanus*, *Solenopsis krockowi*). Do these species have unique roles or is there redundancy among species? Our ability to evaluate these ideas is constrained by the scarcity of autecological data for most ant species, but our work has identified species that would be logical choices for mechanistic studies of their response to disturbance and their functional roles in the Chihuahuan Desert.

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Appendix

Ant species captured at a Chihuahuan Desert grassland at Jornada long-term ecological research site, New Mexico, 30 July–4 August 1996. The primary functional group scheme is based on ones used by Andersen (1990, 1997a), Bestelmeyer and Wiens (1996), and Bestelmeyer and Schooley (1999). The rank abundances of ants are from means of ten samples from areas adjacent to mound disturbances (*mound*) of banner-tailed kangaroo rats (*Dipodomys spectabilis*) and from the intervening grassland (*matrix*). *Dashes* indicate there was insufficient information to assign three uncommon species to functional groups. *G* Granivores, *LM* large generalized myrmicines, *SM* small generalized myrmicines, *NS* nocturnal scavengers, *DS* diurnal scavengers, *O* opportunists, *T* thermophiles, *GS* granivore-scavengers, *S* scavengers, *HT* heat-tolerant species, *HI* heat-intolerant species, *N* nocturnal species

Subfamily (Species)	Functional groups			Rank abundance	
	Primary	Foraging	Activity	Matrix	Mound
Myrmicinae					
Aphaenogaster cockerelli André	O	GS	HI	3	3
Crematogaster punctulata Emery	–	–	–	20	
Monomorium minimum (Buckley)	SM	S	HI	25	18
Pheidole cerebrosior Wheeler	LM	GS	HI	10	6
Pheidole crassicornis Emery	LM	GS	HI	7	9
Pheidole hyatti Emery	LM	GS	HI	17	23.5
Pheidole militicida Wheeler	LM	GS	HI	6	4
Pheidole rugulosa Gregg	LM	GS	HI	8	20
Pheidole sciophila Wheeler	LM	GS	HI	27	23.5
Pheidole xerophila Wheeler	LM	GS	HI	16	12
Pheidole sp. A	LM	GS	HI	13	8
Pogonomyrmex californicus (Buckley)	G	G	HT		16
Pogonomyrmex desertorum Wheeler	G	G	HT	9	5
Pogonomyrmex imberbiculus Wheeler	G	G	HI	15	13
Pogonomyrmex maricopa Wheeler	G	G	HT	19	
Pogonomyrmex rugosus Emery	G	G	HT		25.5
Pogonomyrmex texanus Francke and Merickel	G	G	HT	11	14
Solenopsis krockowi Wheeler	SM	GS	HI	14	15
Solenopsis salina Wheeler	SM	GS	HI	28	22
Solenopsis xyloni McCook	LM	GS	HI	21	11
Tetramorium spinosum (Pergande)	–	–	–	21	
Dolichoderinae					
Dorymyrmex insanus (Buckley)	O	S	HI	23	25.5
Dorymyrmex cf. *flavus* McCook	O	S	N	5	7
Forelius pruinosus (Roger)	T	S	HT	1	1
Forelius mccooki McCook	T	S	HT	18	21
Formicinae					
Myrmecocystus depilis Forel	DS	S	HT	4	10
Myrmecocystus mexicanus Wesmael	NS	S	N	12	19
Myrmecocystus mimicus Wheeler	DS	S	HT	2	2
Myrmecocystus navajo Wheeler	NS	S	N	26	17
Paratrechina terricola (Buckley)	–	–	–	24	

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