

# Animal disturbances promote shrub maintenance in a desertified grassland

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## Summary

**1.** Soil disturbance by animals affects the availability of water, nutrients, sediment and seeds, which are critical for the maintenance of functional ecosystems. We examined long-lived faunal structures across six vegetation communities in the northern Chihuahuan desert of New Mexico, USA, testing the proposition that disturbances in undesertified grassland differ in magnitude and effect from those in desertified grassland.

**2.** Vertebrate and invertebrate disturbances totalled 18.9 structures ha<sup>-1</sup> across 18 sites. The most common were pits and mounds of American badgers (*Taxidea taxus*, 32%), nests of the ant *Aphaenogaster cockerelli* (18.8%) and mounds of kangaroo rats (*Dipodomys spectabilis*, 31%).

**3.** Desertification was associated with a doubling of the density of structures, but no effects on cover or volume. The greatest density was in desertified mesquite and creosote bush shrublands, and the lowest density in undesertified grass swales. Badger and wood rat (*Neotoma* sp.) mounds were significant indicators of desertified communities.

**4.** Desertification did not affect the density of kangaroo rat mounds (6.7 ha<sup>-1</sup> in black grama grasslands and creosote bush shrublands). However, mounds in creosote bush shrubland were smaller and had more and larger shrubs than adjacent inter-mound hummocks. Desertification was associated with increases in the density of *Aphaenogaster cockerelli* and *Trachymyrmex smithii* nests, and declines in *Pogonomyrmex rugosus* nests. Substantial increases in soil nitrate and electrical conductivity on *Myrmecocystus* nests were associated with desertification.

**5. Synthesis.** Desertification shaped this desert environment in two main ways. First, while kangaroo rat mound density changed little with desertification, mounds in shrubland continued to enhance shrub persistence long after abandonment, reinforcing desertification processes. Second, marked changes in the density of nests of the key ant species altered the spatial distribution of soil nitrate and electrical conductivity, likely affecting soil fertility and the distribution of desert plants. Our results highlight the importance of animal activity in shaping desert plant communities, and in maintaining or reinforcing desertification processes.

**Key-words:** animal activity, biopedturbation, Chihuahuan desert, desertification, disturbance, ecosystem engineering, pedogenesis

## Introduction

In many desert systems, the physical activity of animals dramatically alters soil ecological processes at a range of spatial scales (Huntley & Inouye 1988). This disturbance by animals (biopedturbation) is a potential driver of ecosystem processes in deserts and may be equally important as abiotic processes (Lavelle 1997; Whitford 2002). Soil disturbance results when

animals 'engineer' the soil surface while foraging or constructing burrows, nests or resting sites. Although there are many studies of the small-scale effects of ephemeral structures such as foraging pits and seed caches on ecosystem processes (e.g. Dean & Milton 1991; Longland 1995; James, Eldridge & Hill 2009), few studies have addressed the functional role of disturbances across broad scales such as communities or landscapes.

Animal structures that are relatively large in relation to the engineer who created them and persistent over decadal time scales, have a marked influence on plant and soil processes

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operating at landscape scales. For example, decomposing seed and organic matter within the larder hoards of banner-tailed kangaroo rat (*Dipodomys spectabilis*) mounds (Mun & Whitford 1990) form patches of higher soil nitrogen, which are preferred sites for desert annuals (Krogh *et al.* 2002). Their tunnels are also sites of greater breakdown of faeces and urine, support diverse desert fungi and bacteria (Hawkins 1996; Whitford & Kay 1999) and develop into nutrient-rich patches. Conversely, while the ejecta mounds (mounds formed from excavated soil material) of American badgers (*Taxidea taxus*) are nutrient-poor, the soil surrounding the mounds has greater moisture due to enhanced run-off from the mounds (Eldridge 2009), supporting a diverse plant community (Platt 1975).

In the Chihuahuan desert of north-western Mexico and south-western United States, substantial increases in the extent of woody plants such as mesquite (*Prosopis glandulosa*) and creosote bush (*Larrea tridentata*) have largely been responsible for the 'desertification' of extensive areas of former black grama (*Bouteloua eriopoda*) grasslands into dense shrublands (Buffington & Herbel 1965; Gibbens *et al.* 2005). Apart from widespread soil loss, desertification is accompanied by altered soil chemistry, particularly changes in the spatial distribution of nutrients resulting from the replacement of resource-rich closely spaced grass tussocks with resource-rich, widely spaced shrub islands (Schlesinger *et al.* 1996). Although some communities such as mesquite coppice dunes are severely degraded, others such as tobosa grass (*Pleuraphis mutica*) playas remain virtually unchanged.

Desertification affects animal populations by changing habitat characteristics and/or resource availability. Examples include increased foraging efficiency of *Myrmecocystus* ants that forage on homopteran-produced honeydew in mesquite-dominated shrublands (Forbes *et al.* 2005), or the loss of banner-tailed kangaroo rats from eroded creosote bush shrubland due to extensive erosion and loss of grasses (Kerley, Whitford & Kay 1997; Schooley, Bestelmeyer & Kelly 2000). Desertification-induced changes in animal populations can even induce feedback processes that tend to maintain or reinforce the desertified state. Such situations occur when rodents preferentially remove grass tillers from desertified grasslands, preventing a return to an intact grassland (e.g. Kerley, Whitford & Kay 1997; Bestelmeyer, Khalil & Peters 2007). Changes in animal populations will invariably result in changes in the density or size of their structures, affecting soil physical and chemical properties and processes, and altering plant community structure by changing annual plant communities on and off their structures (Mun & Whitford 1990). Changes in the density of animal-produced structures may be more influential and persistent than changes in the number of animals, given the greater relative importance of engineering effects over trophic-level effects such as herbivory in resource-limited environments (Wilby & Shachak 2004).

Given the likely effects of such widespread changes in plant community structure associated with desertification, we would expect desertified grasslands to be characterized by a markedly different community of soil-disturbing animals, and therefore a different spectrum of soil disturbances, compared with intact,

undesertified grassland. We would also expect that the impacts of desertification on soil-disturbing animals would have flow-on effects on desert plant communities. Further, the loss of functional desert grasslands may be partly attributable to reductions in, or loss of, ecosystem services provided by these animals (Whitford 2002).

Our study predicts therefore that a change from intact grasslands to shrub-dominated ecosystems (desertification) will be associated with a change in composition and a reduction in diversity and abundance of structures used by successive generations of soil-disturbing animals. While it is generally acknowledged that animal activity is critical for the functioning of arid ecosystems (e.g. Jones, Lawton & Shachak 1997), we are unaware of any empirically based studies that have sought to test this general proposition among a range of communities, organisms and trophic groups. Our discussion here focuses on longer-lived disturbances across six vegetation communities in two desertification states (desertified, undesertified). Specifically, we examine (i) changes in the spectrum of animal structures in relation to desertification state, (ii) the effects of mounds of banner-tailed kangaroo rats on creosote bush shrubs in former black grama grassland, and (iii) effects of a range of ant species on soil chemistry and the ensuing effects on plant communities. We contend that changes in the populations of soil-disturbing animals alter the degree and nature of their disturbances, and thus have dramatic effects on desert plant communities. Using these examples we argue that the loss of desert animals and their attendant functions are key mechanisms for reinforcing the maintenance of desertified grasslands.

## Materials and methods

### SITE DESCRIPTION

The data were collected from two adjacent research stations, which are both part of the Jornada LTER network: the USDA-ARS Jornada Experimental Range (JER) and the New Mexico State University Chihuahuan Desert Rangeland Research Centre, both located about 40 km north of Las Cruces, New Mexico, USA.

The landscape ranges in elevation from 1300 m in the basin to 2000 m a.s.l. on the montane slopes. The 100-year average annual rainfall is 211 mm ( $\pm 77$  mm SD; Houghton 1972). More than half of the rain falls between July and early October during intense convective storms (Whitford & DiMarco 1995). Summer temperatures often reach 40 °C and winter minima range from 0 °C to -10 °C (Whitford & DiMarco 1995). The geomorphology and soils of these stations have been described (Gile, Hawley & Grossman 1981; see Appendices S1 and S2 in Supporting Information). The vegetation is a mixture of C<sub>4</sub> grasses and C<sub>3</sub> shrubs (Havstad, Huenneke & Schlesinger 2006).

Some piedmont areas that had black grama grasslands about a century ago are now dominated by creosote bush, and no black grama grasslands remain on the eroded piedmont slopes. The only remaining grassland sites in both stations are on sandy loam soils in the low-elevation, gently undulating plains. On the low slopes (< 2% slope) of the watersheds of the Dona Ana Mountains, the functional ecosystem is a banded vegetation community comprising unvegetated bands of soil separating bands of tarbush-tobosa grass-burro grass

(*Flourensia cernua*–*Pleuraphis mutica*–*Scleropogon brevifolia*) vegetation. The undesertified banded community is characterized by fine-textured silty clay or clay–loam soils. Sites in the banded community serve as undesertified reference sites for tarbush sites in local basins that historically were banded or burro grass–tobosa grass flats (Buffington & Herbel 1965). Low-elevation swales with silty clay soils are dominated by tobosa grass and serve as reference sites for tarbush-dominated areas on silty clay soils. In the JER, however, tobosa grass has not been invaded by tarbush because extensive grass cover has been maintained by low stocking rates.

Our study focused on six vegetation communities or habitat types (Appendix S3); (i) black grama grasslands, (ii) creosote bush shrubland, (iii) mesquite coppice dunefields, (iv) banded burro grass swales, (v) tobosa grass swales and (vi) tarbush shrubland. Based on their historical support of particular grasses, the degraded landscapes are paired with comparable undesertified landscapes. Black grama grassland is compared with two degraded analogues (mesquite and creosote bush), while the two undesertified two-phase mosaic communities (burro grass swales, tobosa grass swales) are compared with a degraded tarbush shrubland.

#### DENSITY, COVER AND VOLUME OF DISPLACED SOIL

We established three replicate 1-ha sites (100 × 100 m) in each of the six vegetation communities. Data were collected in summer 1999, and in summer, fall, winter and spring 2000 and 2001. Large, persistent animal structures (banner-tailed kangaroo rat mounds, badger pits and mounds, wood rat (*Neotoma* spp.) mounds, harvester ant (*Pogonomyrmex rugosus*) pavements, nests of the ants *Aphaenogaster albisetosus*, *Aphaenogaster cockerelli*, *Myrmecocystus depilis*, *Myrmecocystus mexicanus*, *Trachymyrmex smithii* and *Pogonomyrmex maricopa*) were counted and measured within the entire 1-ha plots. Within each plot, we recorded the animal species responsible for the disturbance, one dimension through the centre, a second dimension perpendicular to the first measurement through the centre, pit depth and mound height of each disturbance. From these measurements, we derived two measures: (i) the area (using the formula for a circle) and (ii) the volume (using the formula for volume of a half prolate spheroid) of each disturbance.

#### SHRUB GROWTH ON BANNER-TAILED KANGAROO RAT MOUNDS

We established four 15 × 10 m plots in a desertified creosote bush-dominated upper piedmont area that was grassland more than half a century ago. The presence of tall *Yucca elata*, a grassland perennial, is evidence of the past grassland community. Shrubs in this eroded upper piedmont occur on abandoned banner-tailed kangaroo rat mounds, and shrubs in the areas between rat mounds retain low hummocks of soil. We measured the length and width of 20 rat mounds and paired these with 20 adjacent shrubs or shrub complexes. We used allometric relationships in Ludwig, Reynolds & Whitson (1975), which relate shrub size to biomass, to determine the contribution of abandoned rat mounds to site-level shrub biomass.

#### SOIL BIOGEOCHEMISTRY OF LONG-LIVED ANT NESTS

The literature on the effects of ant nests on soils is dominated by seed harvesters such as *Pogonomyrmex* spp. (e.g. Wagner & Jones 2006), with few studies of other species or multi-species effects at any one location (Whitford & DiMarco 1995). We examined therefore the soil chemistry of nests of a range of species that occurred in different

communities. A sample of the top 5 cm of the soil was collected from seven nests each of *Myrmecocystus depilis*, *Myrmecocystus mexicanus*, *Aphaenogaster cockerelli*, *Pogonomyrmex rugosus* and *Trachymyrmex smithii*, and from an adjacent non-nest reference surface on all but the tarbush communities. Not all nests of species found in the larger (1-ha sites) study were sampled for soil chemistry as they were either poorly developed or at such low densities to be considered ecologically unimportant. Similarly, nests of some species not recorded in the larger study were sampled (e.g. *Trachymyrmex smithii* in black grama grassland), because the soil chemistry study was not restricted to the three 1-ha sites in each community. Further, as only one of the three larger tarbush sites supported any long-lived ant nests, and those nests were relatively low in density, their soil chemistry was not assessed. Soils were assayed for electrical conductivity (EC) and pH on 1:5 water:soil extract, NO<sub>3</sub>-N (Keeney & Nelson 1982), organic matter (loss on ignition at 550 °C), inorganic P (at pH 8.5) and exchangeable (available) Ca and K (Olsen & Sommers 1982). These chemical attributes were assayed because we expected nest soils to contain higher concentrations of these nutrients compared with non-nest soils (*sensu* Lei 2000; Snyder, Crist & Friese 2002; James *et al.* 2008).

#### STATISTICAL ANALYSES

Differences in density and cover, and the volume of either excavated (pits) or accumulated (mounds) soil were examined in relation to vegetation community with a completely random design ANOVA model or, where variances could not be stabilized, by the nonparametric Kruskal–Wallis test (Payne *et al.* 1993). Prior to ANOVA, we used Levene's test to check for stability of residuals and therefore the need for transformation. Tukey's least significant difference testing was used to separate mean values after a significant *F*-statistic was reported. Bonferroni corrections were made when comparing means among a large number ( $n = 15$ ) of multiple comparisons. Differences in shrub height, density and biomass between rat and non-rat mounds and hummocks were tested using one-way ANOVA after testing for normality and homogeneity of residuals with Levene's test (Minitab 2007). Relationships between hummock area, and shrub height and number were examined using linear regression (Minitab 2007). Paired Student's *t*-tests were used to test for differences in biogeochemistry of soils from long-lived ant nests with adjacent non-nest (reference) areas. We used permutational multi-variate analysis of variance (PERMANOVA, Anderson, Gorley & Clarke 2008) with the Bray–Curtis similarity coefficients to test whether the composition of animal disturbances varied among the six vegetation communities, and displayed the relative positions of the 18 sites with a canonical analysis of principal coordinates biplot (Anderson, Gorley & Clarke 2008). The degree of association of different animal disturbances with vegetation community was assessed with indicator species analysis using PC-ORD (McCune & Mefford 1999). Indicator values (IV) are maximal (100%) when all individuals of a given disturbance type are restricted, for example, to a particular vegetation community, or all samples from that community contain that disturbance type.

## Results

#### DENSITY, COVER AND VOLUME OF ANIMAL DISTURBANCES

We recorded  $18.9 \pm 2.7$  (mean  $\pm$  SE) persistent structures per hectare across all vegetation communities ( $n = 18$ ). Badger

mounds were the most common (31.7% by density) followed by *Aphaenogaster cockerelli* nests (18.8%), kangaroo rat mounds (13.2%), *Pogonomyrmex rugosus* nests (11.7%) and wood rat mounds (9.1%).

The three desertified (shrubland) communities had more than twice the average density of structures ( $26.0 \pm 3.5 \text{ ha}^{-1}$ ) than the three undesertified (grassland) communities ( $11.9 \pm 2.7 \text{ ha}^{-1}$ ;  $F_{1,16} = 10.32$ ,  $P = 0.005$ ;  $n = 18$ , Table 1, Fig. 1). Badger mounds were more abundant in shrubland ( $10.3 \pm 1.8 \text{ mounds ha}^{-1}$ ) than in grassland ( $1.7 \pm 0.9 \text{ mounds ha}^{-1}$ ;  $F_{1,16} = 19.3$ ,  $P = 0.001$ ) communities, with the density of ejecta mounds greatest in the tarbush shrubland, intermediate in the creosote bush and mesquite shrublands and grasslands, and absent in the banded burro grass and tobosa grass playa ( $F_{5,12} = 19.9$ ,  $P < 0.001$  on  $\log_{10}(x + 0.1)$ -transformed data; Table 1). Wood rat mounds were twice as abundant in shrublands (Kruskal–Wallis  $H = 8.17$ , d.f. = 1,  $P = 0.004$ ; Table 1). Specifically, mounds were more abundant in the creosote bush shrublands than in any other communities ( $F_{5,12} = 10.4$ ,  $P < 0.001$ ; Table 1).

The density of structures created by other taxa did not vary significantly in relation to desertification ( $P > 0.05$ ). Total density of structures was greater in the creosote bush shrubland ( $37.7 \pm 1.4 \text{ structures ha}^{-1}$ ,  $n = 3$ ) than in the other communities ( $F_{5,12} = 5.88$ ,  $P = 0.006$ ), and the lowest density occurred in the banded burro grass swale ( $7.7 \pm 2.2 \text{ ha}^{-1}$ ,  $n = 3$ ).

Averaged over all sites, there was no difference in either cover or volume of excavated soil between shrublands and

grasslands ( $P > 0.09$ ; Tables 1 and 2; Fig. 1). Cover was greatest in the black grama grasslands and least in the burro grass swales (Fig. 1). Soil volume was greatest in black grama grasslands and creosote bush shrublands, but least in tobosa and banded burro grass sites ( $F_{5,12} = 25.3$ ,  $P < 0.001$  on  $\log_{10}$ -transformed data, Fig. 1, Table 2).

There were up to five times more kangaroo rat mounds in the black grama grasslands and creosote bush shrubland than in the other communities ( $F_{5,12} = 16.4$ ,  $P < 0.001$  on  $\sqrt{}$ -transformed data, Table 1). However, while desertification had little effect on the overall density of kangaroo rat mounds, mounds in black grama grasslands were larger ( $83.6 \pm 25.5 \text{ m}^2 \text{ ha}^{-1}$  cover,  $18.5 \pm 5.5 \text{ m}^3 \text{ ha}^{-1}$ ,  $n = 3$ ) than those in other communities (cover range:  $1\text{--}22 \text{ m}^2 \text{ ha}^{-1}$ , volume range:  $0.1\text{--}3.7 \text{ m}^3 \text{ ha}^{-1}$ ;  $F_{5,12} = 16.6$ ,  $P < 0.001$  on  $\sqrt{}$ -transformed data). While mounds in grassland were large ( $1.6\text{--}4.6 \text{ m}^3$ ), those in creosote bush shrubland were small and ill-defined (range:  $0.2\text{--}0.7 \text{ m}^3$ ).

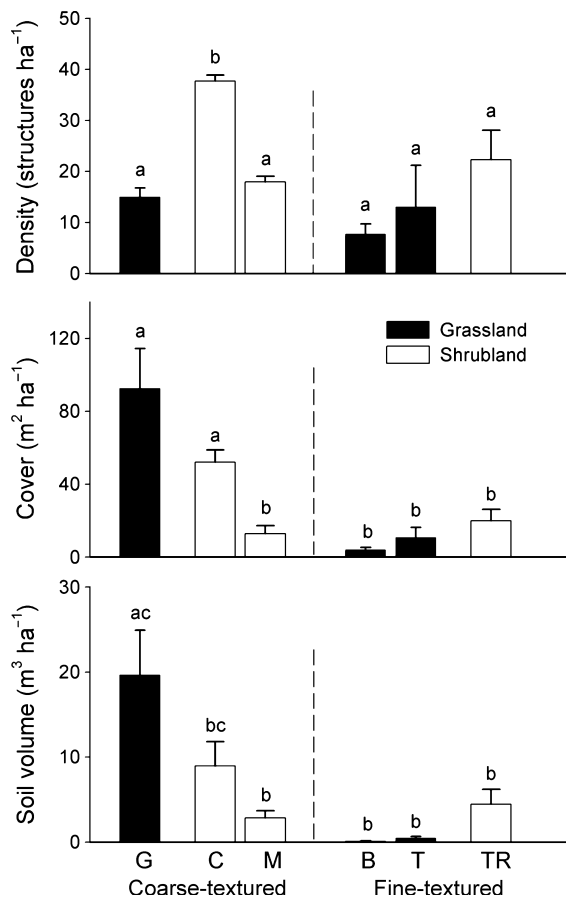
Density and cover of *Aphaenogaster cockerelli* nests were greater in the creosote bush shrublands ( $F_{5,12} = 3.38$ ,  $P = 0.039$ ), and no nests were found in the black grama grasslands. *Pogonomyrmex rugosus* nest density was greater in the banded burro grass than the tarbush shrubland (Table 1). The greatest overall density of *Pogonomyrmex rugosus* nests was in the tobosa grass swales. *Trachymyrmex smithii* nests were found only in mesquite dunefields, while very few nests of *Aphaenogaster albisetosus*, *Myrmecocystus mexicanus* or *Pogonomyrmex maricopa* were found in the study area overall (Table 1).

**Table 1.** Mean ( $\pm$  SE) density (structures  $\text{ha}^{-1}$ ) and cover ( $\text{m}^2 \text{ ha}^{-1}$ ) of structures by species and vegetation community

Species	Black grama grassland	Creosote bush shrubland	Mesquite dunefield	Banded burro grass swale	Tobosa grass playa	Tarbush shrubland
	Undesertified	Desertified	Desertified	Undesertified	Undesertified	Desertified
<b>Density</b>						
<i>Aphaenogaster albisetosus</i>	0 (0)	0 (0)	0.7 (0.7)	0 (0)	0 (0)	0.7 (0.7)
<i>Aphaenogaster cockerelli</i>	0 (0)	14.0 (2.1)	0 (0)	4.0 (1.2)	0 (0)	3.3 (1.7)
<i>Myrmecocystus depilis</i>	1.3 (0.9)	3.0 (0.6)	1.3 (0.3)	1.0 (0.6)	2.3 (2.3)	1.0 (0)
<i>Myrmecocystus mexicanus</i>	0 (0)	1.0 (0)	0 (0)	0 (0)	0.7 (0.7)	0 (0)
<i>Trachymyrmex smithii</i>	0 (0)	0 (0)	3.7 (0.9)	0 (0)	0 (0)	0 (0)
<i>Pogonomyrmex maricopa</i>	0.7 (0.7)	0 (0)	0.3 (0.3)	0 (0)	0 (0)	0 (0)
<i>Pogonomyrmex rugosus</i>	0 (0)	0.3 (0.3)	0.3 (0.3)	2.7 (2.2)	9.3 (5.8)	0.7 (0.7)
<i>Neotoma</i> spp.*	1.3 (0.3)	4.7 (0.9)	1.3 (0.3)	0 (0)	0.7 (0.7)	2.3 (0.3)
<i>Dipodomys spectabilis</i>	6.7 (1.2)	6.7 (1.8)	1.3 (0.9)	0 (0)	0 (0)	0.3 (0.3)
<i>Taxidea taxus</i> *	5.0 (1.2)	8.0 (1.6)	9.0 (1.0)	0 (0)	0 (0)	14.0 (5.0)
<b>Cover</b>						
<i>Aphaenogaster albisetosus</i>	0 (0)	0 (0)	0.64 (0.64)	0 (0)	0 (0)	0.23 (0.23)
<i>Aphaenogaster cockerelli</i>	0 (0)	10.83 (1.06)	0 (0)	2.03 (1.22)	0 (0)	1.61 (0.56)
<i>Myrmecocystus depilis</i>	0.02 (0.02)	0.11 (0.05)	0.08 (0.05)	0.06 (0.05)	0.02 (0.02)	0.07 (0.01)
<i>Myrmecocystus mexicanus</i>	0 (0)	0.03 (0.01)	0 (0)	0 (0)	0.03 (0.03)	0 (0)
<i>Trachymyrmex smithii</i>	0 (0)	0 (0)	0.14 (0.02)	0 (0)	0 (0)	0 (0)
<i>Pogonomyrmex maricopa</i>	0.03 (0.03)	0 (0)	0.01 (0.01)	0 (0)	0 (0)	0 (0)
<i>Pogonomyrmex rugosus</i>	0 (0)	0.04 (0.04)	0.24 (0.24)	1.87 (1.47)	9.28 (6.51)	0.09 (0.09)
<i>Neotoma</i> spp.*	2.96 (1.29)	8.38 (1.45)	0.16 (0.12)	0 (0)	1.42 (1.42)	8.28 (2.72)
<i>Dipodomys spectabilis</i>	83.60 (25.50)	22.37 (6.14)	8.78 (4.87)	0 (0)	0 (0)	1.80 (1.80)
<i>Taxidea taxus</i> *	2.56 (0.42)	7.08 (1.48)	3.48 (0.33)	0 (0)	0 (0)	7.31 (3.00)

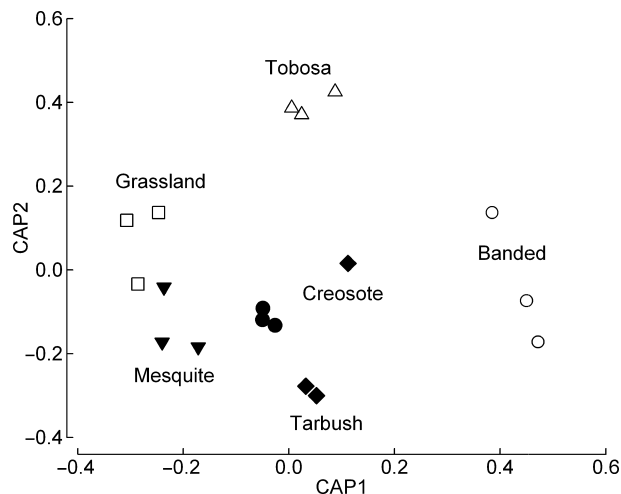
\*includes mounds and pits.





**Fig. 1.** Mean ( $\pm$ SE) density of all structures (structures  $\text{ha}^{-1}$ ), cover ( $\text{m}^2 \text{ha}^{-1}$ ) and volume of displaced soil ( $\text{m}^3 \text{ha}^{-1}$ ) for coarse- and fine-textured soils in the six communities. G, black grama grassland; C, creosote bush shrubland; M, mesquite coppice dunefield; B, banded burro grass playa; T, tobosa grass playa; TR, tarbush shrubland. Different superscripts indicate significant differences among the six communities at  $P < 0.01$ .

PERMANOVA indicated a significant difference in the spectrum of disturbance types in relation to desertification (Pseudo  $F_{1,16} = 2.99$ ,  $P$  (perm) = 0.022). Both wood rat (IV = 80.6,



**Fig. 2.** Canonical analysis of principle coordinates biplot of the 18 sites in relation to their density of disturbances for all fauna i.e. kangaroo rat and wood rat mounds, badger pits and mounds, and nests of all ant species.

$P = 0.004$ ) and badger (IV = 86.1,  $P < 0.001$ ) mounds were significant indicators of shrublands. Composition was similar between black grama grassland and mesquite dunefields ( $P > 0.05$ ) but differed markedly among the other communities ( $P < 0.05$ ; Fig. 2).

#### SHRUB GROWTH ON BANNER-TAILED KANGAROO RAT MOUNDS

Individual creosote bush shrubs on abandoned kangaroo rat mounds were taller ( $151.0 \pm 3.7$  cm,  $n = 20$ ,  $F_{1,38} = 73.99$ ,  $P < 0.001$ ) and had greater biomass ( $3.87 \pm 0.32$  kg  $\text{m}^{-2}$ ,  $n = 20$ ,  $F_{1,38} = 32.7$ ,  $P < 0.001$  on  $\log_{10}$ -transformed data) than shrubs in the inter-mound areas ( $87.0 \pm 6.5$  cm tall;  $1.89 \pm 0.14$  kg  $\text{m}^{-2}$ ,  $n = 20$ ). Scaled up to the landscape level by accounting for the relative proportion of rat mounds and inter-mounds, abandoned rat mounds supported 28% more shrubs ( $2781 \pm 463$  shrubs  $\text{ha}^{-1}$ ,  $n = 20$ ) than inter-mound

**Table 2.** Mean ( $\pm$ SE) volume of displaced soil ( $\text{m}^3 \text{ha}^{-1}$ ) by species and vegetation community

Species	Black grama grassland	Creosote bush shrubland	Mesquite dunefield	Banded burro grass swale	Tobosa grass playa	Tarbush shrubland
	Undesertified	Desertified	Desertified	Undesertified	Undesertified	Desertified
<i>Aphaenogaster albisetosus</i>	0 (0)	0 (0)	0.045 (0.045)	0 (0)	0 (0)	0.006 (0.006)
<i>Aphaenogaster cockerelli</i>	0 (0)	0.868	0 (0)	0.060 (0.011)	0 (0)	0.093 (0.046)
<i>Myrmecocystus depilis</i>	0.001 (0)	0.013	0.002 (0.001)	0.004 (0.003)	0.001 (0.001)	0.002 (0.001)
<i>Myrmecocystus mexicanus</i>	0 (0)	0.009	0 (0)	0 (0)	0.002 (0.002)	0 (0)
<i>Trachymyrmex smithii</i>	0 (0)	0 (0)	0.004 (0.001)	0 (0)	0 (0)	0 (0)
<i>Pogonomyrmex maricopa</i>	0.001 (0.001)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Pogonomyrmex rugosus</i>	0 (0)	0.001 (0.001)	0.061 (0.061)	0.076 (0.050)	0.376 (0.256)	0.010 (0.010)
<i>Neotoma</i> spp. (mound)	0.704 (0.270)	1.709 (0.300)	0.027 (0.027)	0 (0)	0.081 (0.081)	0.884 (0.164)
<i>Dipodomys spectabilis</i>	17.959 (5.540)	3.710 (1.560)	1.219 (0.767)	0 (0)	0 (0)	0.096 (0.096)
<i>Taxidea taxus</i> (mound)	1.002 (0.032)	2.708 (1.310)	1.505 (0.103)	0 (0)	0 (0)	3.664 (1.810)
<i>Taxidea taxus</i> (pit)	0.281 (0.198)	0.269 (0.093)	0.083 (0.024)	0 (0)	0 (0)	0.478 (0.132)

areas ( $2175 \pm 123$  shrubs  $\text{ha}^{-1}$ ,  $n=20$ ). Larger mounds supported more creosote bush shrubs, irrespective of whether they were abandoned rat mounds ( $F_{1,18}=26.9$ ,  $P<0.001$ ,  $R^2=0.58$ ) or mounds resulting from accumulating wind and/or water deposited material ( $F_{1,18}=73.8$ ,  $P<0.001$ ,  $R^2=0.79$ ).

#### SOIL BIOGEOCHEMISTRY OF LONG-LIVED ANT NESTS

Soil from *Trachymyrmex smithii* nests in black grama grassland had three times the concentration of nitrate, five times the concentration of inorganic P, eight times the concentrations of exchangeable Ca and almost 20-times more exchangeable K than non-nest control soils ( $t=5.6$ – $6.3$ ,  $P<0.001$ ). Trends were similar in mesquite shrubland (Table 3). There were few effects of *Myrmecocystus depilis* nests, except for two- to three-fold reductions in EC ( $t=2.76$ ,  $P<0.03$ ) and exchangeable Ca ( $t=2.84$ ,  $P<0.025$ ) in creosote bush shrubland, small reductions in exchangeable K in mesquite shrublands ( $t=2.43$ ,  $P=0.045$ ) and small increases in organic matter in tobosa grass playa ( $t=2.33$ ,  $P=0.042$ ). In banded burro grass playa, soils from *Aphaenogaster cockerelli* nests contained higher concentrations of inorganic P ( $29.6 \pm 5.8$   $\text{mg kg}^{-1}$  soil,  $n=7$ ) compared with reference soils ( $6.3 \pm 0.9$   $\text{mg kg}^{-1}$  soil,  $n=7$ ,  $t=7.4$ ,  $P<0.005$ ). Despite some site-level differences, we detected no significant differences in relation to desertification ( $P > 0.05$ ).

## Discussion

### LOSS OF KANGAROO RATS REINFORCES A SHRUB-INVADDED STATE

We recorded 6.6 kangaroo rat mounds per hectare in both intact grasslands and shrublands even though mounds in former grassland had been abandoned almost a century ago following encroachment by creosote bush (Whitford 1997). However, mounds in shrublands were considerably smaller ( $<4$   $\text{m}^3$   $\text{ha}^{-1}$ ) than those in grassland ( $34$   $\text{m}^3$   $\text{ha}^{-1}$ ), probably due to prolonged wind and water erosion coupled with the cessation of burrow maintenance by rats. Mounds persist over decadal time scales, and our finding that abandoned mounds supported taller shrubs with twice the biomass as inter-mound areas (Chew & Whitford 1992) indicates that even abandoned mounds continue to affect shrublands long after extirpation of the resident rats.

During burrow excavation, kangaroo rats penetrate the caliche layer close to the surface (Gile, Hawley & Grossman 1981), allowing creosote bush roots to access water and nutrients below the otherwise impenetrable hardpan as well as P- and N-rich faecal microsites within the mounds. Shrub facilitation by rats also likely results from increased deposition of  $\text{CaCO}_3$ , N and P through the weathering of caliche transported to the surface by the rats (Eghbal & Southard 1993), similar to processes observed in the plains viscacha (*Lagostomus maximus*; Villarreal *et al.* 2008). Greater access to soil N

**Table 3.** Mean ( $\pm$ SE) values of selected soil chemical properties for ant nest soils and control (adjacent to ant nest) within five vegetation communities. Ca and K concentrations ( $\text{meq } 100$   $\text{g}^{-1}$  soil),  $\text{NO}_3$ -N and inorganic P concentrations ( $\text{mg kg}^{-1}$ ), electrical conductivity (EC,  $\text{dS m}^{-1}$ ), organic matter (OM, %). Within a site and chemical property, a different letter indicates a difference between ant nest and control soils at  $P < 0.05$ . n.d. no data available;  $n = 7$  replicates

Vegetation community and ant species	Soil chemical properties					
	$\text{NO}_3$ -N	P	K	EC	Ca	OM
<b>Black grama grassland</b>						
Control	4.9a (1.3)	4.3a (0.8)	27.2a (4.2)	0.3a (0.1)	2.5a (0.7)	0.2 (0.1)
<i>Trachymyrmex smithii</i>	17.7b (4.4)	20.7b (7.8)	264.3b (176.5)	2.6b (1.1)	19.9b (5.0)	1.5 (1.2)
<i>Myrmecocystus depilis</i>	5.6a (2.8)	5.9a (0.6)	24.3a (6.4)	0.5a (0.1)	4.0a (0.9)	0.3 (0.2)
<b>Creosote bush shrubland</b>						
Control	12.5 (4.4)	14.1 (3.7)	26.6 (3.5)	1.1a (0.2)	13.9a (3.1)	0.9 (0.1)
<i>Aphaenogaster cockerelli</i>	20.9 (9.2)	17.2 (3.8)	37.5 (7.7)	0.9a (0.3)	9.9a (3.9)	0.6 (0.1)
<i>Myrmecocystus depilis</i>	3.9 (0.4)	11.7 (0.7)	23.0 (0.4)	0.5b (0.1)	3.7b (0.8)	0.7 (0.0)
<i>Myrmecocystus mexicanus</i>	1.7 (1.2)	2.1 (1.0)	1.7 (1.1)	1.4a (1.3)	2.1b (1.0)	1.4 (1.3)
<i>Pogonomyrmex rugosus</i>	n.d.	17.7 (0.5)	n.d.	0.8a (0.01)	n.d.	0.4 (0.01)
<b>Mesquite dunefield</b>						
Control	3.2 (0.4)	4.1a (0.8)	33.8a (4.8)	0.4a (0.1)	3.4a (1.5)	0.4a (0.1)
<i>Trachymyrmex smithii</i>	62.0 (30.5)	25.1b (4.9)	249.7b (77.6)	4.2b (1.6)	25.6b (7.5)	1.7b (0.4)
<i>Myrmecocystus depilis</i>	2.5 (0.6)	5.4a (0.3)	22.0c (2.1)	0.3a (0.1)	2.1a (0.7)	0.4a (0.1)
<b>Banded burro grass swale</b>						
Control	3.6 (1.2)	6.3a (0.5)	38.0 (2.1)	0.4 (0.1)	2.9 (0.5)	0.5 (0.0)
<i>Aphaenogaster cockerelli</i>	207.7 (182.3)	29.6b (2.9)	69.8 (26.6)	5.8 (4.7)	36.9 (27.8)	1.0 (0.2)
<i>Pogonomyrmex rugosus</i>	n.d.	15.4 (0.4)	n.d.	0.13 (0.01)	n.d.	0.9 (0.01)
<b>Tobosa grass playa</b>						
Control	8.1 (2.8)	8.1 (1.2)	42.3 (11.6)	0.7 (0.2)	6.9 (2.7)	0.9a (0.1)
<i>Myrmecocystus depilis</i>	4.7 (0.9)	10.7 (2.3)	33.8 (0.9)	0.5 (0.0)	4.3 (0.2)	1.1b (0.1)
<i>Myrmecocystus mexicanus</i>	5.8 (2.4)	9.6 (1.2)	37.5 (13.9)	0.5 (0.1)	4.8 (0.8)	1.4b (0.2)

would be reflected in enhanced creosote bush growth and biomass, and higher concentrations of foliar N (Hamerlynck *et al.* 2004; Villarreal *et al.* 2008).

The foraging mounds of badgers also persist for many years after their construction, but unlike kangaroo rat mounds, represent nutrient-poor microsites with sparse vascular plant cover (Eldridge 2004). However, mounds shed water and nutrients to the surrounding annular zone (Eldridge 2009). The likely long-term effect of badger mounds on fine-textured tarbush soils therefore is to create a mosaic of nutrient-poor mounds and their resource-rich annual plant-dominated halos (Eldridge & Whitford 2008). A loss of badgers and their mounds represents therefore a loss of ecosystem function and a change in the distribution of annual plant mosaics (Platt 1975).

Kangaroo rats also have dramatic and long-lived effects on plant processes by caching seeds and excavating pits that act as finer-scale fertile patches and are preferred sites for seed germination (Whitford 2002). The loss of viable mounds and their resident rat populations in shrubland will influence both the diversity and biomass of mound- and pit-dependent annual plants (Moorehead, Fisher & Whitford 1988) and other biota that depend on a functional burrow system (Kay & Whitford 1978; Schooley, Bestelmeyer & Kelly 2000). Loss of rat populations could also lead to reductions in populations of desert fungi (Hawkins 1996), which could be critical for mutualistic associations with plants.

The reduction in black grama grass cover, particularly green grass, leads to repressed reproductive activity and lactation in kangaroo rats (Kerley & Whitford 1994) and abandonment of mounds, reinforcing increases in shrub size and biomass on abandoned mounds. A combination of biotic cycling under shrubs and abiotic capture of wind- and water-transported sediments by the shrubs themselves reinforce the 'fertile island' effect, increasing the resistance of shrublands to change (Schlesinger *et al.* 1996), even if rat populations could persist in shrublands. Surface erosion and exposure of caliche layers may reduce the soil depth to a level that restricts rats from constructing a viable mound (Whitford 1997). The loss of kangaroo rats therefore has had substantial effects on ecosystem functions. Absence of rats from sites where shrub cover exceeds 20% could therefore be considered one of the impediments to reversing desertification in the northern Chihuahuan desert (Krogh *et al.* 2002).

#### MYRMECOCYSTUS AND TRACHYMYRMEX NEST CHEMISTRY AND NUTRIENT LOSS

*Myrmecocystus* spp. forage in grasslands and in the canopies of creosote bush and mesquite (Shaefer & Whitford 1981; Schowalter, Lightfoot & Whitford 1999), and we attribute differences in their densities to differences in the relative abundances of these shrubs. The spread of mesquite into grasslands facilitated the expansion of *Trachymyrmex smithii* into formerly unsuitable grassland habitat, with a threefold increase in soil nitrate and a doubling of EC of surface nest. *Trachymyrmex*, which was found only in mesquite dunefields, increased in density with desertification because the ants have greater

access to mesquite leaves as a substrate for tending subterranean fungi. Deeper soil profiles and greater cover of mesquite coppice dunes would also reduce suitable microsites for *Trachymyrmex* nests due to deeper sand cover.

While desertification did not alter *Trachymyrmex* nest chemistry, it did affect nest chemistry of *Myrmecocystus depilis*, with lower values of EC and Ca on nests in creosote bush shrubland but no nest effect in intact grassland. Similarly, there was no consistent ant species effect on soil chemistry, even within the same community. Thus while P concentrations increased in *Trachymyrmex* nest soil in black grama grasslands relative to the reference site, the trend was not apparent for *Myrmecocystus* nests, even in the same grassland.

Similar to kangaroo rats, *Trachymyrmex* can penetrate caliche layers to 1.5 m below the surface, and the P- and Ca-rich fine material transported to the surface is incorporated in nest ejecta or used to cement nest caps (Whitford 2003). Unlike biologically derived C and N, there are no sources of P, Ca and K extrinsic to the soil. Phosphorus is involved in complex immobilization reactions with CaCO<sub>3</sub> (Kuo & Lotse 1972), and in the calcareous soils at our study sites, fixation rates are low and P is known to be readily lost from the system (Lajtha & Schlesinger 1988). In functional grasslands, highly erodible ant ejecta would likely be captured in grass tussocks and recycled within the grassland (Schlesinger, Ward & Anderson 2000). In shrubland, however, the highly erodible P- and Ca-laden nest ejecta is likely to be lost through wind erosion (Li *et al.* 2000; Whitford 2003) so that the transport of P-bound subsoil to the surface by ants would lead to gradual P depletion.

Reductions in plant-available P are likely to have substantial consequences for desert plant communities (Lajtha & Schlesinger 1988). A loss of plant-available P from Chihuahuan desert soils would likely favour (i) plant growth forms with a greater ability to resorb P from senescing leaves (Drenovsky & Richards 2006), (ii) species that form mycorrhizal associations in order to enhance P uptake (Cellier, Yarnes & Herman 2003) or (iii) growth forms characterized by finely-branched root systems that have a competitive advantage for P absorption over larger diameter, less-branched root systems (Moody & Bollard 2001). Ant activity therefore has potentially large, but relatively unknown, effects on desert vegetation.

#### POGONOMYRMEX NESTS AS HOT-SPOTS FOR DESERT ANNUALS

Desertification was also associated with an eightfold reduction in the densities of *Pogonomyrmex* nests in grasslands (Wisdom & Whitford 1981). Although we failed to detect a significant desertification effect on soil nutrients for *Pogonomyrmex* nests, they have been shown elsewhere to substantially affect soil moisture, N and therefore annual plant communities (MacMahon, Mull & Crist 2000; James *et al.* 2008). Enhanced biomass and cover of annual forbs (e.g. *Erodium texanum*) and grasses (e.g. *Bouteloua aristoides*, *Bouteloua barbata*) around *Pogonomyrmex* nests in the Chihuahuan desert (Whitford 1978) has been attributed to greater soil moisture and available N (Gutierrez & Whitford 1987). Greater biomass of grasses

(Rogers & Lavigne 1974) and shrubs (Wight & Nichols 1966) around functionally similar nests of *Pogonomyrmex occidentalis* (in Colorado shortgrass prairie) and *Pogonomyrmex owyheeii* (in Wyoming saltbush steppe) are attributed to enhanced soil moisture and nutrients, suggesting a general effect of long-lived nests on vegetation. Similar effects on density, richness and cover of annuals are associated with the nests of *Aphaenogaster cockerelli* (Whitford, Barnes & Steinberger 2008) and nests of *Messor capensis* in Israel (Wilby & Shachak 2004) and South Africa (Dean & Yeaton 1993).

Desertification-induced reductions in *Pogonomyrmex* nest density are therefore likely to have substantial moderating effects on plant community structure, though increases in *Aphaenogaster cockerelli* nest density could partly offset these effects. An indirect mechanism for the annual plant effect is through nest construction and maintenance, and the disposal of viable seed and plant, insect and animal detritus in refuse dumps around the nest, which contribute to soil nutrient build-up and therefore abundant annual plant growth. *Pogonomyrmex* nests are strongly water repellent due to the thick lag of surface gravel, and the annular zone around the nests has up to four times greater ponded infiltration, due to ant-produced macropores (James *et al.* 2008), but also greater surface runoff. As ant colonies age they increase the number of tunnels and storage galleries in their nests (W.G. Whitford & Y. Steinberger, unpublished data), and the effect of these nests on organic matter storage and soil moisture increases (Wagner, Jones & Gordon 2004). As *Pogonomyrmex* and *Aphaenogaster* nests are both occupied continuously for up to 35 years (Chew 1995), their effects on annual plant communities will also be long-lived.

In conclusion, this study demonstrates that a range of Chihuahuan desert fauna affect key ecosystem processes through their soil disturbing activities. Our study is one of few that consider the effects of more than one species, from different trophic groups, on ecosystem processes. However, we considered relatively few taxa, and a wider examination of other animal disturbances with shorter half-lives is requisite to an improved understanding of state change in deserts. The more ephemeral structures such as ejecta surrounding beetle and spider burrows and the foraging pits of heteromyid rodents may well show contrasting responses to desertification in some communities.

Our work highlights the fact that states adjusting to the loss of key ecosystem engineers have a persistent abiotic legacy (*sensu* D'Antonio & Meyerson 2002). Thus animals are important not only maintaining key ecosystem processes such as seed dispersal and nutrient transport in intact grasslands, but also for exerting strong pressures that reinforce the maintenance of a stable, yet desertified state. Their disturbance thus provides a mechanism for maintaining intact grasslands and also reinforcing the shrub-encroached state where processes have been severely compromised by persistent overgrazing. Consistent with ecosystem engineering theory (Byers *et al.* 2006), considerable energy inputs are likely required to shift these stable altered systems back to their original grassland states.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Vegetation community soil and vegetation descriptions.

**Appendix S2.** Soil and landscape attributes for the communities.

**Appendix S3.** Images of the six vegetation communities.

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