

Disturbances by desert rodents are more strongly associated with spatial changes in soil texture than woody encroachment

David J. Eldridge · Walter G. Whitford

Received: 18 January 2014 / Accepted: 6 May 2014
© Springer International Publishing Switzerland 2014

Abstract

Background and Aims Soil texture is an important determinant of ecosystem structure and productivity in drylands, and may influence animal foraging and, indirectly, plant community composition.

Methods We measured the density and composition of surface disturbances (foraging pits) of small, soil-foraging desert vertebrates in shrubland and grasslands, both with coarse- and fine-textured soils. We predicted that the density and functional significance of disturbances would be related more to differences in texture than shrub encroachment.

Results Soil texture had a stronger influence on animal foraging sites than shrub encroachment. There were

more disturbances, greater richness and abundance of trapped seed, and greater richness of germinating plants on coarse- than fine-textured soils. Pits in coarse soils trapped 50 % more litter than those in finer soils. Apart from slightly more soil removal and greater litter capture in shrubland pits, there were no effects of encroachment. **Conclusions** Although the process of woody encroachment has been shown to have marked effects on some ecosystem properties, it is likely to have a more subordinate effect on surface disturbances and therefore their effects on desert plant communities than soil texture. Our results highlight the importance of animal activity in shaping desert plant communities, and potentially, in maintaining or reinforcing shrub dominant processes.

Responsible Editor: Jeffrey Walck .

Electronic supplementary material The online version of this article (doi:10.1007/s11104-014-2142-5) contains supplementary material, which is available to authorized users.

D. J. Eldridge (✉)

Centre for Ecosystem Science, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia
e-mail: d.eldridge@unsw.edu.au

W. G. Whitford

USDA-ARS Jornada Experimental Range, MSC 3JER, New Mexico State University,
PO Box 3003, Las Cruces, NM 88003, USA

Present Address:

D. J. Eldridge
School of BEES, University of NSW,
High Street, Kensington, NSW 2052, Australia

Keywords Bioturbation · Drylands · Seed capture · Litter · Foraging pits · Encroachment · Soils · Shrubs

Introduction

Soil texture is an important driver of plant productivity and diversity in resource-limited environments such as drylands (Bucini and Hanan 2007; Lane et al. 2009). Texture is a property of soil that describes the arrangement of primary particles, sand, silt and clay and relates, therefore, to the ability of the soil to retain moisture. Texture influences net primary productivity by affecting soil hydraulic behaviour and soil water holding capacity (Noy-Meir 1979; Dodd et al. 2002), and has been shown to influence faunal communities through its effect on vegetation composition and distribution (Woinarski

et al. 1999). Changes in vegetation structure also have direct and indirect effects on the distribution of faunal assemblages and hence the processes that they influence (Rosenzweig and Winakur 1969). For example, changes in habitat structure can alter interaction networks, through losses or increases in habitat heterogeneity, or through changes in immigration and emigration rates. Spatial changes in soil texture, vegetation cover and configuration are known to be strong predictors of the distribution of desert rodents (Whitford and Kay 1999).

Soil texture determines the energy costs of digging, i.e. the force that animals such as rodents must apply with their forelimbs to penetrate the soil surface (Price and Podolsky 1989). Similarly, texture is an important consideration in nest site selection by ants such as *Pogonomyrmex* and *Messor* species (Johnson 1992), which have been shown to have profound landscape-level effects on infiltration and erosion processes (James and Eldridge 2007). Changes in vegetation structure such as the encroachment of woody plants into open grassland (Eldridge et al. 2011) are also thought to influence the distribution of rodent communities, either directly, by altering seed rain (Muñoz et al. 2009), or indirectly, by reducing grass cover, which regulates lactation and therefore fecundity of rodents such as kangaroo rats (*Dipodomys spectabilis*, Kerley et al. 1997). Woody encroachment, a widespread form of vegetation change in arid and semi-arid areas (Eldridge et al. 2011) is also accompanied by changes in the composition of shrubland- and grassland-dependent fauna (Kerley et al. 1997; Schooley et al. 2000; Roth et al. 2007). Shifts in the relative composition of animal disturbances, such as increases in the densities of large mounds constructed by badgers (*Taxidea taxus*) and wood rats (*Neotoma* spp.), have been shown to have marked effects on a range of ecosystem processes (Eldridge et al. 2009).

These and other examples suggest that spatial changes in both soil texture and vegetation structure are likely to have measurable effects on fauna and thus on ecosystem processes they control through their surface foraging activities. In this study we examined changes in the density and distribution of surface disturbances created by soil-disturbing fauna while foraging or creating habitat, across communities differing in structure (i.e. relic grasslands cf. encroached shrublands), on both coarse- and fine-textured soils. This allowed us to test the relative importance of both structural changes in vegetation i.e. encroachment by shrubs, spatial changes in

soil texture, and their interaction, on the magnitude and consequences of disturbances for dryland plant communities. The relative effects of these on foraging, and indirectly on plant community composition, are largely unknown. Although a number of separate studies has identified the singular effects of spatial changes in either soil texture or vegetation structure on desert fauna, we are unaware of studies that have explicitly examined the dual and interactive effects of changes in these two attributes on the activity of soil-disturbing animals and hence the processes that they moderate.

Our study was conducted in the northern Chihuahuan Desert grasslands, which has been severely degraded for more than a century since the introduction of livestock grazing (Havstad et al. 2006), and substantial encroachment of shrubs such as mesquite (*Prosopis glandulosa*), creosotebush (*Larrea tridentata*) and tar bush (*Flourensia cernua*) have largely been responsible for the conversion of extensive black grama (*Bouteloua eriopoda*) grasslands into shrublands (Gibbens et al. 2005). Shrub encroachment occurs on both fine- and coarse-textured soils, and therefore has the potential to alter populations of small mammals such as jackrabbits (*Lepus californicus*), ground squirrels (*Spermophilus spilosoma*), pocket mice (*Perognathus* spp.), and pocket gophers (*Thomomys bottae* and *Geomys bursarius*) that create small-scale disturbances in the Chihuahuan Desert. This is likely to have flow-on effects to desert plant communities (Eldridge and Whitford 2009).

The focus of our work is the ephemeral structures created by small desert mammals. We restricted our study to foraging pits and cache pits created by these mammals because we expected them to exhibit the strongest contrasting responses to spatial changes in texture and encroachment. Our predictions were that (1) coarse-textured soils would support more foraging pits because of both the lower energy costs of digging in sandy soils (Price and Podolsky 1989) and the greater efficiency of seed recovery from sands (Price and Reichman 1987; Krasnov et al. 2000); (2) shrublands would support a greater density of rodent foraging pits than grasslands because of the greater seed rain resulting from a higher shrub density (Reichman 1979) and potentially, reduced risk of predation (Sivy et al. 2011); (3) the functional significance of foraging pits would differ in relation to soil texture. Specifically, we expected that litter and seed capture would be greater in foraging pits in coarse-textured soils due to the general instability of the surrounding surface and thus the greater likelihood

of erosion that would cover pit–resident material (James et al. 2009), and, (4) germination of pit–resident seeds would also be greater in coarse–textured soils because of their greater capacity to respond to small falls of rainfall (sensu Inverse Texture Hypothesis Noy-Meir 1979).

Methods

Site description

Our study was conducted on two adjacent research stations; the USDA-ARS Jornada Experimental Range, and the New Mexico State University Chihuahuan Desert Rangeland Research Centre, about 40 km north of Las Cruces, New Mexico, USA. The research stations include two mountain ranges, with drainage lines that terminate in a closed basin. A broad alluvial plain of the San Andres Mountain that extends to the escarpment of the Rio Grande occupies the northern half of both research stations.

Animal disturbances were studied in six vegetation communities (see Appendix S1 in Supporting Information). Three of the communities were characterised by coarse-textured soils and three by fine-textured soils (Table 1). Each of the three communities; the black grama (*Bouteloua eriopoda*) grassland, mesquite (*Prosopis glandulosa*) coppice dunes and the tobosa grass (*Pleuraphis mutica*)–alkali sacaton (*Sporobolus airoides*) swales occurred in the basin plain. Extensive overgrazing of the black grama grassland prior to 1900 resulted in the encroachment by mesquite and other shrubs into large areas of black grama, drop-seed (*Sporobolus* spp.) and three awn (*Aristida* spp.) grasslands in the southern basin (Eldridge et al. 2009). The northern basin plain is dominated by a mesquite coppice dunefield, varying in height from 30 cm to >3 m and separated by sparsely vegetated inter-dunal swales.

The other three vegetation communities were on a watershed of the Dona Ana mountains that range in elevation from 1,200 to 2,000 m. The upper and middle elevation slopes (1 to 5 % slope) are characterized by a piedmont of coarse-textured gravelly soils or lag-pavement stony soils dominated by creosotebush (*Larrea tridentata*). The shrub interspaces are generally devoid of plant cover. Lower elevation slopes of <1 % are characterized as a two-phase mosaic. This landscape unit on fine-textured clay-loam soils is composed of

Table 1 Dominant plant species, slope and soil classification and textural class for the six communities studied

Community	Dominant plant species	Slope (%)	US Soil Classification and soil texture
Black grama grassland (coarse grassland)	<i>Bouteloua eriopoda</i> <i>Pleuraphis mutica</i>	1–3	Thermic Calciargid; coarse sandy clay loam
Creosotebush shrubland (coarse shrubland)	<i>Larrea tridentata</i>	3–5	Thermic Ustic Haplargid; coarse loamy sand
Mesquite dunefield (coarse shrubland)	<i>Prosopis glandulosa</i>	0–3	Thermic Ustic Haplargid to Ustic Calcicid; coarse loamy sand
Banded burro grass swale (fine grassland)	<i>Scleropogon brevifolia</i> <i>Pleuraphis mutica</i> <i>Flourensia cernua</i>	0–2	Thermic Ustic Calciargid; fine loam to clay loam
Tobosa grass swale (fine grassland)	<i>Pleuraphis mutica</i>	0–1	Thermic Ustic Haplocalcid; fine loam to clay loam
Tarbush shrubland (fine shrubland)	<i>Flourensia cernua</i>	0–2	Thermic Ustic Calciargid fine loam to clay loam

vegetation bands with a mixture of burro-grass (*Scleropogon brevifolia*), tobosa grass, tarbush (*Flourensia cernua*) and mesquite separated by unvegetated runoff zones. The two-phase mosaic merges into tarbush-dominated shrubland on level soils.

The three coarse–textured communities (black grama, mesquite, creosotebush) had predominantly sandy surface textures with an average of 74.0 ± 9.3 % (mean \pm SE) sand in the surface horizons. Soils in the tarbush, tobosa grass and banded communities had an average of about 36.7 ± 3.9 % sand in the surface (Appendix S2). The coarse–textured communities also had surfaces that were relatively water stable, with higher infiltration rates ($16\text{--}27$ mm h^{-1}) than the finer soils ($3.2\text{--}4.0$ mm h^{-1}), caliche layers close to the surface (<0.2 m cf. $0.75\text{--} >1.5$ m deep) and a relatively weak or absent argilic layers compared to strong layers in the finer–textured sites (Jornada LTER unpublished data, Eldridge et al. 2009).

Assessing the density, surface area and volume of animal disturbances

Data were collected from three replicate 1 ha (100×100 m) plots in each vegetation community over seven time intervals between 1999 and 2000. These intervals represent different climatic periods experienced in the Chihuahuan Desert and comprise cool (COOL; November to April), warm dry (WD, May to June) and warm wet (WW; July to October) periods. In our study we assessed rodent disturbances in the warm dry period in 1999, 2000 and 2001, and during the cool and warm wet periods in both 2000 and 2001. This resulted in data for seven time intervals between 1999 and 2001. In 1999 and 2000 we collected data from within a 10×10 m quadrat located at each corner of each 1 ha plot. In 2001 the sampling was changed to a 10 m radius circular quadrat located at three of the corners of each 1 ha plot in order to sample a larger area of each community.

Small disturbances such as foraging pits, mounds and burrows of heteromyid rodents, skunks and pocket gophers were counted and measured within each square (10×10 m) or circular (10 m radius) quadrat. We recorded the type of disturbance (e.g. pit, mound, burrow) and animal species that created the disturbance. For each disturbance we measured its depth (for pits) or height (for mounds). For pits and mounds we measured the longest diameter through the centre and a second diameter perpendicular to this. These field-based measurements we determined the area of each disturbance (assuming a circle) and the volume of the disturbance (using the formula for a prolate sphere). Soil mass was calculated using a conservative estimate of 0.8 Mg m^{-3} soil.

Rodent foraging pits as traps for litter and seed, and sites for germination

We measured the surface openings of all foraging pits ($n=81$) excavated over a 2-day period in May 2000 in one 10 by 10 m quadrat in the centre of one of the 1 ha replicate plots in each of the six vegetation communities. Pits were tagged and their contents collected a month after tagging. The contents were sorted, seeds of each plant species counted, and the mass of various litter components measured. For the germination study we positioned three 2.5 m wide transects of variable length (up to 25 m long) in one of the replicate 1 ha plots in each of vegetation communities in May 2001.

Along each transect we tagged the first 10 rodent foraging pits encountered and marked out an equivalent paired non-pit area. We recorded the number of germinants, by species, emerging from the pit and non-pit surfaces over a 10-month period.

Statistical analyses

For small disturbances, data for each of the 3 years were pooled into three seasons corresponding to periods of high or low animal activity identified in previous studies (e.g. Eldridge et al. 2011) i.e. cool season (November to April), warm-dry season (May to June), and warm-wet season (July to October). This had the effect of collapsing our data into seven, year-season combinations i.e. warm-dry season (1999, 2000, 2001), cool season (2000, 2001), and warm-wet season (2000, 2001). For assessing differences among times, textures and communities we used a mixed-models ANOVA approach (Payne et al. 2008). First, a three strata model was used on site-level data pooled into two soil texture groups (coarse, fine). The first stratum considered texture effects, the second year-season effects and its interaction with texture, and the third assessed differences among the three replicate plots within each vegetation community. For the second analysis we considered community-level effects. The main plots considered communities, and the sub-plots the 7 year-season effects and their interactions with community. Data were transformed, where necessary, prior to ANOVA, after examination of diagnostic plots. Where some communities had no data for that variable (e.g. where relatively few structures were found in that community), the number of communities was reduced in the analyses. Least Significant Difference testing was used to examine differences among mean values. Bonferroni corrections were made when comparing means among a large number of multiple comparisons arising from the six vegetation communities or 7 year-seasons.

We used separate one-way ANOVAs to test for differences in mass of captured litter (adjusted for differences in pit aperture) and diversity of seeds between coarse- and fine-textured soils and among the six vegetation communities. Permutational multi-variate analysis of variance (PERMANOVA, Anderson et al. 2008) was used, with the Bray-Curtis similarity coefficients, to examine patterns in seed composition between coarse- and fine-textured sites, and among the six vegetation communities. The relative positions of the communities

were displayed with a Canonical Analysis of Principal Coordinates (CAP) biplot (Anderson et al. 2008).

Germination data were averaged over each transect, giving us, for each plot, three average values for pits and three for non-pits. The Diverse routine of PERMANOVA was used to calculate seedling diversity (average number of species per pit or surface per month) and abundance (average number of plants germinating per m² of pit or surface per month). Separate General Linear Models were used to test for the effects of encroachment (or soil texture) and microsite (pit, surface), and their interaction, on seedling diversity and abundance. In the first analysis the main plot considered texture (coarse, fine), and the sub-plot microsite and its interactions with texture. In a second analysis the main plot was vegetation community and sub-plot microsite and its interaction with community. Homogeneity of residuals using Levene's test using the Genstat statistical package (Payne et al. 1993) confirmed that data transformation was unnecessary. Patterns in the composition of emerging germinants from pits and non-pit surfaces were examined using PERMANOVA as described above.

Results

Effects of soil texture and encroachment

We recorded five-times more rodent pits on coarse- (2,406±207 pits ha⁻¹; mean ± SE) than fine-textured (449±65 pits ha⁻¹) soils (Table 2, Appendix S3). In general, variance among the four replicate quadrats for each of community was very low, with coefficients of variation ranging from 0.262 to 0.591 pits per 100 m². This is also reflected in the low SEM values shown in Fig. 1. The volume of soil excavated on coarse soils was four-times greater (5.67±1.3 m³ ha⁻¹) than that on fine soils (1.73±0.7 m³ ha⁻¹), and pits covered about five-times the area on coarse (74.0±15.3 m² ha⁻¹) than fine soils (14.9±3.2 m² ha⁻¹). Density (1,141–1,654 pits ha⁻¹, $P=0.70$) and surface area (30.0–53.8 m² ha⁻¹, $P=0.10$) of rodent pits were similar in grassland and shrubland, but slightly more soil was removed from pits in shrublands (3.9±1.1 m³ ha⁻¹) than grassland (3.6±1.0 m³ ha⁻¹). Significant texture by encroachment interactions for both pit volume ($F_{1,12}=7.70$, $P=0.017$) and surface area ($F_{1,12}=6.86$, $P=0.022$) of rodent pits on

coarse soils indicated that most of the effects were from the creosotebush community (Appendix S3).

There were strong and significant differences in all attributes over time ($P<0.001$; Appendix S3) and some ill-defined trends in relation to season (Fig. 1). Rodent pits were denser in all three periods in 2000 (range: 2,163–2,318 pits ha⁻¹) than any other time period (range: 495–1,206 pits ha⁻¹, $F_{6,72}=25.61$, $P<0.001$ on $\sqrt{(x+0.5)}$ -transformed data; Fig. 1). The surface area of rodent pits was significantly greater during the warm-dry periods in both 1999 (86 m² ha⁻¹) and 2000 (63.7 m² ha⁻¹) compared with other times (18.3–44.7 m² ha⁻¹; $F_{6,72}=4.12$, $P<0.001$), and total volume of pit soil was greater in the warm-dry 1999 period (10.3 m³ ha⁻¹) compared with other periods (0.68–3.60 m³ ha⁻¹; $F_{6,72}=5.03$, $P<0.001$ on $\log_e(x+1)$ data).

Seed and litter capture in rodent pits

Across all vegetation communities, rodent pits trapped mainly grass (42 %) and leaves (23 %), with smaller amounts of seed (13 %), woody material (13 %) and faeces (9 %). Twice as much litter was recorded from pits in shrubland (418.7 g m⁻²) than grassland (215.5 g m⁻², $F_{1,75}=8.41$, $P=0.005$) and from coarse- (351 g m⁻²) than fine-textured soils (213 g m⁻², $F_{1,75}=3.69$, $P=0.058$).

Although shrubland and grassland supported a similar richness and abundance of pit-resident seed, there was 3.5-times greater seed richness in pits in coarse-textured (4.47±1.1 species) than fine-textured (1.79±0.30 species) communities ($F_{1,75}=75.1$, $P<0.001$; Appendix S4). Seed abundance was about eight-times greater in pits in coarse-textured (23 700±4,272 seeds m⁻² pit) than fine-textured (3,154±894 seeds m⁻² pit; $F_{1,75}=72.4$, $P<0.001$) soils. Apart from the tarbush and

Table 2 Pit density, volume and surface area in relation to soil texture and encroachment status. Within a row, different superscripts indicate a significant difference in that attribute at $P<0.05$

Attribute	Coarse texture		Fine texture	
	Grassland	Shrubland	Grassland	Shrubland
Pit density (ha ⁻¹)	2566 ^a	2246 ^a	428 ^b	469 ^b
Pit volume (m ³ ha ⁻¹)	6.89 ^a	4.46 ^a	0.21 ^b	3.26 ^a
Pit surface area (m ² ha ⁻¹)	79.56 ^a	68.42 ^a	5.17 ^b	24.64 ^a

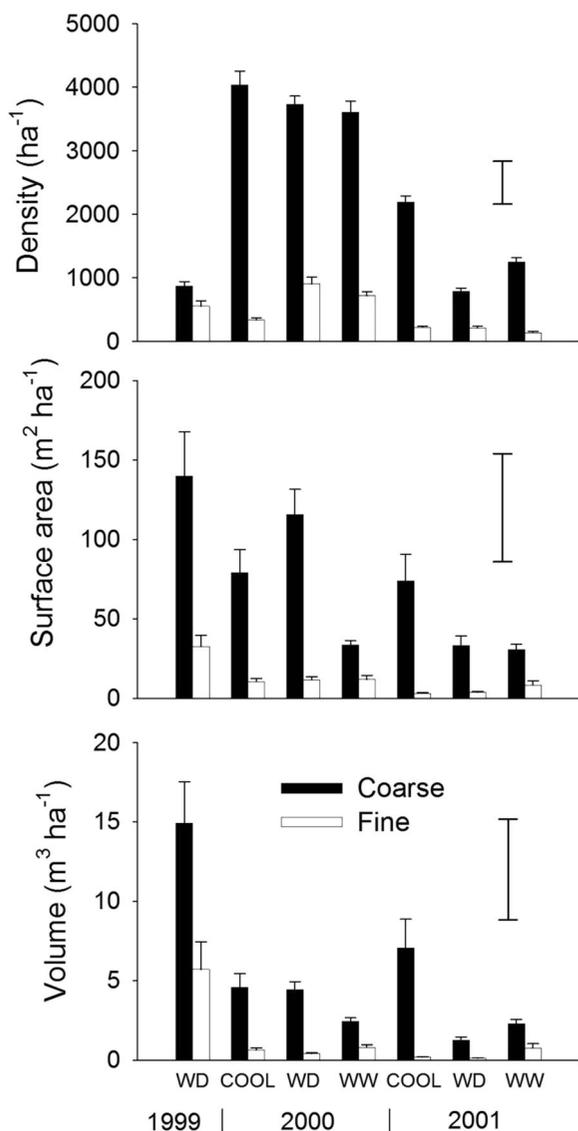


Fig. 1 Mean (\pm SE) density, surface area and volume of rodent pits on coarse- and fine-textured soils in relation to season and year. *WD* warm dry season, *WW* warm wet, *COOL* cool season. The tree bars indicate the 5 % LSD for the Period by Texture interaction. We have added the following to the captions. Data are based on 36 quadrats in each of 1999 and 2000, and 27 quadrats in 2001, for each of coarse- and fine-textured soils

tobosa grass playa, the composition of pit-captured seed differed significantly among communities (Pseudo $F_{5,75}=5.59$, P (perm)=0.001), with a clear separation between grassland, mesquite and creosotebush communities on the first CAP axis and between coarse- and fine-textured sites on Axis 2 (Fig. 2). Overall, seeds of *Larrea tridentata* and *Dassiochloa pulchellum* were more abundant in pits in the creosotebush shrublands,

while *Eriogonum abertianum* and *Aristida purpurea* were more abundance in pits in the black grama grasslands.

Rodent foraging pits as germination sites

More species germinated on coarse- than fine-textured soils, and in grasslands than shrublands, but the difference in germinant richness between grassland and shrubland was more pronounced on coarse-textured soils (texture by encroachment interaction: $F_{1,12}=7.29$, $P=0.019$, Fig. 3a; Appendix S5). There were also about 55 % more species in the pits (8.2 ± 1.69 species) than on a similar area of the surface (5.3 ± 1.29 species), consistently across textures and shrubland-grassland sites ($F_{1,12}=9.17$, $P=0.011$).

Although the composition of germinants differed between coarse- and fine-textured soils (Pseudo $F_{1,12}=9.32$, P (perm)=0.004) and grassland and shrubland (Pseudo $F_{1,12}=5.12$, P (perm)=0.001), there were

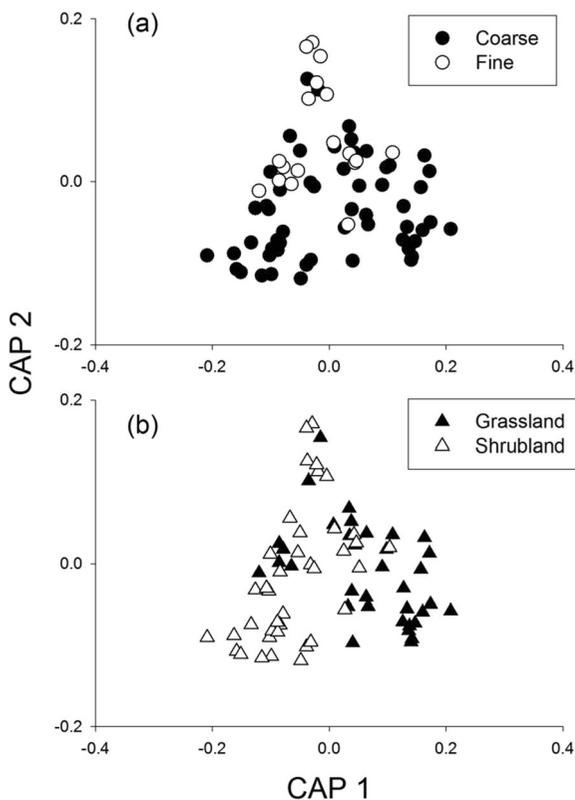


Fig. 2 The first two dimensions of the CAP biplot based on seeds found in the pits. Biplots are coded for (a) soil texture and (b) shrubland-grassland. Data based on 81 pits recorded within a 100 m² in each of six plots

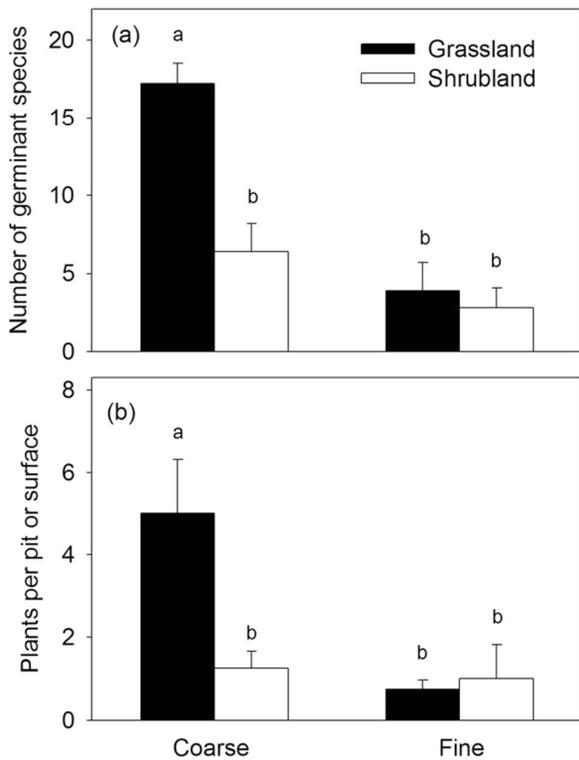


Fig. 3 Mean (\pm SE) (a) richness and (b) abundance of germinants (averaged over pit and non-pit surfaces) in relation to soil texture and encroachment. Different superscripts indicate a significant difference in richness or abundance at $P < 0.05$. Data are based on 10 pit/non-pit pairs within one 1 ha plot within each community

no differences between pits and surfaces (P (perm)=0.07). Results for abundance were similar to richness, with more plants in the grassland than shrubland, but only in coarse-textured soils (texture by encroachment interaction: $F_{1,12}=8.29$, $P=0.014$, Fig. 3b), and consistently 2 to 4-times more seedlings in the pits than on the surface ($F_{1,12}=13.25$, $P=0.003$). Differences between grassland and shrubland were most pronounced in the coarse-textured soils, but only in the pits ($F_{1,12}=4.75$, $P=0.050$).

Discussion

The effect of animal disturbance on soil and ecosystem processes has been a topic of considerable interest over the past decade (e.g. Nieminen 2008). This is due partly to the increased recognition of their functional roles in resource flows (e.g. Bardgett and Wardle 2010) and their potential roles in the restoration of degraded ecosystems (Byers et al. 2006; Eldridge and James 2009; Eldridge

et al. 2009). Our study demonstrated the strong effect of soil texture on surface disturbances by rodents, with substantially more disturbances, a greater diversity of disturbance types, and greater richness and abundance of pit-resident seed on coarse- than fine-textured soils. This compares with only a slight effect of woody encroachment on disturbances. We stress, however, that although the soil texture effect was strong, texture effects should not be considered in isolation from other environmental variables such as soil moisture or depth to the water table, which are likely to covary with texture. Our results suggest that any effect of woody encroachment on soil disturbance by vertebrates will be small compared with the differences that occur in relation to different soil textures across landscapes. Further, given the close links between soil texture and landscape position e.g. position on the slope (Burke et al. 1995), the ecosystem effects of disturbances are likely to be highly landscape-specific.

We recorded about three-times more rodent foraging pits on coarse- (734 pits ha^{-1}) than fine-textured (201 pits ha^{-1}) soils, but similar densities in grasslands and shrublands, providing support for our first hypothesis but not the second. Most of the pits were spatially dispersed, shallow cache sites excavated by heteromyid rodents. The relatively low density of cache pits on fine-textured soils is consistent with the sparse rodent populations inhabiting plant communities on fine-textured soils (Whitford 2002). The strongly seasonal variability in pit opening and reopening reflects the temporal variability in the supply of higher quality resources such as fresh grass tillers (Kerley et al. 1997) or seeds that provide the most energy per time and effort spent in harvesting them (Schoener 1971; Reichman 1984), thereby increasing the reliance of rodents on cached seed (Pyare and Longland 2000). Finer-textured communities may also have lower densities of preferred cache species such as creosotebush, mesquite, and black grama grass, and thus fewer cache pits. The energy costs of excavating scatter hoards are higher in finer-textured soils, which are often highly compacted (Kerley and Whitford 2000). Rodent seed caches in fine-textured soils are exposed to moist conditions for longer than those in sandy soils (Hoover et al. 1977), increasing the likelihood of seed spoilage by bacteria and fungi (Reichman 1988). Seed spoilage will also alter the

olfactory cues used by rodents to locate caches. Thus seed caches in fine-textured soils are likely to be excavated less frequently than those in coarse soils.

Although we detected similar densities of rodent pits in shrublands and grasslands, many rodents (e.g. deer mice *Peromyscus* spp., kangaroo rats, *Dipodomys* spp.) focus their burrowing (e.g. Nagorsen and Museum 2005) and foraging (Kerley and Whitford 2000) close to shrub canopies and are therefore highly reliant on shrub patches (Stapp and van Horne 1997), even in grasslands where shrubs are widely spaced. Seed caches in the Chihuahuan Desert tend to be concentrated around the base of shrubs (Giannoni et al. 2001) where nitrogen-rich mesquite seed pods are abundant. Indeed, more than half of all rodent foraging pits in our study area occurred within 20 cm of a shrub canopy (Eldridge et al. 2011). Similarly, removal of cached acorns was greater from under shrubs and out in the open in a Mediterranean Oak woodland (Smit et al. 2007), presumably to minimize the risk of predation (Parmenter and Macmahon 1983; Sivy et al. 2011). The clustering of pits around the edges of shrubs could explain why annual plants tend to be concentrated under the canopies of perennial shrubs (Parker et al. 1983).

Irrespective of differences in surface texture, plants establishing in animal-created foraging pits are likely to have a greater survival and growth than those growing in non-pit surface soils (James et al. 2011; Travers et al. 2012). In our study, pits in coarser soils contained not only more litter, but three-times greater seed richness, eight-times greater seed abundance, and markedly different species composition to that on the finer soils. This partly supports our fourth hypothesis, given that we did detect a slight encroachment effect, i.e. greater litter mass in shrubland than grassland. Both the higher ANPP of shrublands (Gibbens et al. 1996) and the tendency for shrub foliage to decompose more slowly than grasses (Throop and Archer 2007, 2009) would account for the greater mass of litter in the shrublands. At the landscape level, germination and establishment of cached or trapped seed is likely greater on coarser soils because of the greater *per-capita* density of pits on these soils. Germinating seeds would likely also have a competitive advantage on coarser soils because of the greater water availability in an environment where the majority of rainfall events

are of short duration, water penetration is greater and levels of evaporative losses are lower from coarser soils, consistent with the ‘inverse texture’ phenomenon (Noy-Meir 1979).

The ability of pits to retain litter and seed depends on surface characteristics such as soil roughness, but also has a soil textural component. Sediment and seed are more likely to blow into the pits in coarse-textured landscapes due to the more disaggregated nature of the surface material (i.e. sands), particularly around the margins of creosotebush and mesquite shrubs where wind erosion is high and fetch lengths are long (Li et al. 2009). Pit shape may also be influential. Larger, narrower pits that were typical of coarser soils (Eldridge et al. 2011) may be more effective at retaining resources than shallow, basin-shaped depressions dug into finer-textured soils. Pits constructed in coarse material are also likely to disintegrate more rapidly, trapping their litter and seed in situ (James et al. 2011). Interestingly, we found that, with encroachment, declines in richness and abundance of plants germinating in pits were more pronounced on coarser soils. This suggests to us that the consequences of encroachment on plant germination are likely to be more pronounced on coarser soils. This could relate to the fact that coarser soils have a lower water holding capacity and, combined with the fact that coarse material is highly mobile, a greater tendency to smother pit-resident germinants.

Our study reinforces the notion that the effects of small mammals on soils and plants are strongly texture-dependent, with higher rates and volumes of soil turnover in landscapes characterised by coarse soils and strong effects on plant richness, abundance and litter mass. While much has been written about the likely ecosystem effects of encroachment on organisms and thus the processes that they mediate (e.g. Hernandez et al. 2005), our research in the Chihuahuan Desert suggests that any responses of surface-disturbing biota to encroachment are likely to be more strongly driven by differences in soil texture than by changes in the structure of the vegetation associated with woody plant density increases. Overall, given the effect of rodent pits on trapping and providing ‘safe sites’ for the seeds of the dominant encroaching species, the effect of surface foraging

may be to reinforce the persistence of shrubs in already woody-dominated landscapes at the expense of grasses.

Acknowledgments We acknowledge support from the International Arid Lands Consortium, thank Terry Koen for undertaking the statistical analyses, and Santiago Soliveres, Matthew Bowker and Heather Throop for comments on earlier drafts. Chris Havstad provided office space to DJE while this work was carried out. This is a contribution to the Jornada Long-Term Ecological Research Program.

References

- Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA + for PRIMER: guide to software and statistical methods. PRIMER-E, Plymouth
- Bardgett RD, Wardle DA (2010) Aboveground-belowground linkages: biotic interactions, ecosystem processes, and global change. Oxford University Press, New York
- Bucini G, Hanan NP (2007) A continental scale analysis of tree cover in African savannas. *Global. Ecol Biogeogr* 16:593–605
- Burke IC, Elliott ET, Cole CV (1995) Influence of macroclimate, landscape position, and management on soil organic-matter in agroecosystems. *Ecol Appl* 5:124–131
- Byers JE, Cuddington K, Jones CG, Talley TS, Hastings A, Lambrinos JG, Crooks JA, Wilson WG (2006) Using ecosystem engineers to restore ecological systems. *TREE* 21: 493–500
- Dodd MB, Lauenroth WK, Burke IC, Chapman PL (2002) Associations between vegetation patterns and soil texture in the shortgrass steppe. *Plant Ecol* 158:127–137
- Eldridge DJ, James AI (2009) Soil-disturbance by native animals plays a critical role in maintaining healthy Australian landscapes. *Ecol Manag Restor* 10:S27–S34
- Eldridge DJ, Whitford WG (2009) Soil disturbance by native animals along grazing gradients in an arid grassland. *J Arid Environ* 73:1144–1148
- Eldridge DJ, Whitford WG, Duval BD (2009) Animal disturbances promote shrub maintenance in a desertified grassland. *J Ecol* 97:1302–1310
- Eldridge DJ, Bowker MA, Maestre FM, Roger E, Reynolds JF, Whitford WG (2011) Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecol Lett* 14:709–722
- Giannoni SM, Dacar M, Taraborelli P, Borghi CE (2001) Seed hoarding by rodents of the Monte Desert Argentina. *Austral Ecol* 26:259–263
- Gibbens RP, Hicks RA, Dugas WA (1996) Structure and function of C-3 and C-4 Chihuahuan Desert plant communities. Standing crop and leaf area index. *J Arid Environ* 34:47–62
- Gibbens RP, McNeely RP, Havstad KM, Beck RF, Nolen B (2005) Vegetation changes in the Jornada Basin from 1858 to 1998. *J Arid Environ* 61:651–668
- Havstad KM, Huenneke LF, Schlesinger WH (2006) Structure and function of a Chihuahuan Desert ecosystem. The Jornada basin long-term ecological research site. Oxford University Press, Oxford
- Hernandez L, Romero AG, Laundre JW, Lightfoot D, Aragon E, Portillo JL (2005) Changes in rodent community structure in the Chihuahuan Desert Mexico: comparisons between two habitats. *J Arid Environ* 60:239–257
- Hoover KD, Whitford WG, Flavill P (1977) Factors influencing the distributions of two species of *Perognathus*. *Ecology* 58: 877–884
- James AI, Eldridge DJ (2007) Reintroduction of fossorial native mammals and potential impacts on ecosystem processes in an Australian desert landscape. *Biol Conserv* 138:351–359
- James AI, Eldridge DJ, Hill BM (2009) Foraging animals create fertile patches on an Australian desert shrubland. *Ecography* 32:723–732
- James AI, Eldridge DJ, Koen TB, Moseby KE (2011) Can the invasive European rabbit (*Oryctolagus cuniculus*) assume the soil engineering role of locally-extinct natives? *Biol Invasive* 13:3027–3038
- Johnson RA (1992) Soil texture as an influence on the distribution of the desert seed-harvester ants *Pogonomyrmex-rugosus* and *Messor-pergandei*. *Oecologia* 89:118–124
- Kerley GIH, Whitford WG (2000) Impact of grazing and desertification in the Chihuahuan Desert: plant communities, granivores and granivory. *Am Midl Nat* 144:78–91
- Kerley GIH, Whitford WG, Kay FR (1997) Mechanisms for the keystone status of kangaroo rats: granivory rather than granivory? *Oecologia* 111:422–428
- Krasnov BR, Shenbrot GI, Rios LE, Lizurume ME (2000) Does food-searching ability determine habitat selection? Foraging in sand of three species of gerbilline rodents. *Ecography* 23: 122–129
- Lane SN, Reaney SM, Heathwaite AL (2009) Representation of landscape hydrological connectivity using a topographically driven surface flow index. *Water Resour Res* 45:W08423
- Li M, Li Z, Yao W, Liu P (2009) Estimating the erosion and deposition rates in a small watershed by the Cs-137 tracing method. *Appl Radiat Isot* 67:362–366
- Muñoz A, Bonal R, Díaz M (2009) Ungulates, rodents, shrubs: interactions in a diverse Mediterranean ecosystem. *Basic Appl Ecol* 10:151–160
- Nagorsen DW, Museum RBC (2005) Rodents and Lagomorphs of British Columbia. Royal BC Museum
- Nieminen JK (2008) Soil animals and ecosystem processes: how much does nutrient cycling explain? *Pedobiol* 51:367–373
- Noy-Meir I (1979) Structure and function of desert ecosystems. *Israel J Bot* 28:1–19
- Parker LW, Miller J, Steinberger Y, Whitford WG (1983) Soil respiration in a Chihuahuan desert rangeland. *Soil Biol Biochem* 15:303–309
- Parmenter RR, MacMahon JA (1983) Factors determining the abundance and distribution of rodents in a shrub-steppe ecosystem - the role of shrubs. *Oecologia* 59:145–156
- Payne RW, Harding SA, Murray DA, Soutar DM, Baird DB, Glaser AI, Channing IC, Welham SJ, Gilmour AR, Thompson R, Webster R (2008) The guide to GenStat release 11, Part 2: statistics. VSN International, Hemel Hempstead, United Kingdom
- Payne RW, Lane PW, Digby PGN, Harding SA, Leech PK, Morgan GW, Todd AD, Thompson R, Tunnicliffe Wilson

- G, Welham SJ, White RP (1993) Genstat 5 Release 3 Reference Manual. Oxford University Press, New York
- Price MV, Podolsky RH (1989) Mechanisms of seed harvest by heteromyid rodents - soil texture effects on harvest rate and seed size selection. *Oecologia* 81:267–273
- Price MV, Reichman OJ (1987) Distribution of seeds in Sonoran desert soils - implications for Heteromyid rodent foraging. *Ecology* 68:1797–1811
- Pyare S, Longland WS (2000) Seedling-aided cache detection by heteromyid rodents. *Oecologia* 122:66–71
- Reichman OJ (1979) Desert granivore foraging and its impact on seed densities and distributions. *Ecology* 60:1085–1092
- Reichman OJ (1984) Spatial and temporal variation of seed distributions in Sonoran Desert soils. *J Biogeogr* 11:1–11
- Reichman OJ (1988) Caching behavior of eastern wood rats *Neotoma floridana* in relations to food perishability. *Anim Behav* 36:1525–1532
- Rosenzweig ML, Winakur J (1969) Population ecology of desert rodent communities: habitats and environmental complexity. *Ecology* 50:558–572
- Roth GA, Whitford WG, Steinberger Y (2007) Jackrabbit (*Lepus californicus*) herbivory changes dominance in desertified Chihuahuan desert ecosystems. *J Arid Environ* 70:418–426
- Schoener TW (1971) Large-billed insectivorous birds - precipitous diversity gradient. *Condor* 73:154–161
- Schooley RL, Bestelmeyer BT, Kelly JF (2000) Influence of small-scale disturbances by kangaroo rats on Chihuahuan Desert ants. *Oecologia* 125:142–149
- Sivy KJ, Ostoja SM, Schupp EW, Durham S (2011) Effects of rodent species, seed species, and predator cues on seed fate. *Acta Oecol* 37:321–328
- Smit C, Vandenberghe C, den Ouden J, Mueller-Schaerer H (2007) Nurse plants, tree saplings and grazing pressure: changes in facilitation along a biotic environmental gradient. *Oecologia* 152:265–273
- Stapp P, van Horne B (1997) Response of deer mice (*Peromyscus maniculatus*) to shrubs in shortgrass prairie: linking small-scale movements and the spatial distribution of individuals. *Funct Ecol* 11:644–651
- Throop H, Archer S (2009) Resolving the dryland decomposition conundrum: some new perspectives on potential drivers. *Progress in Botany*. In: U. Lüttge, W. Beyschlag, B. Büdel, D. Francis (eds), pp. 171–194. Springer Berlin Heidelberg
- Throop HL, Archer SR (2007) Interrelationships among shrub encroachment, land management and litter decomposition in a semidesert grassland. *Ecol Appl* 17:1809–1823
- Travers SK, Eldridge DJ, Koen SB, Soliveres S (2012) Animal foraging pit soil affects the growth of a native grass. *Plant Soil* 352:341–351
- Whitford WG (2002) *Ecology of desert systems*. Elsevier Science, London
- Whitford WG, Kay FR (1999) Biopedurbation by mammals in deserts: a review. *J Arid Environ* 41:203–230
- Woinarski JCZ, Palmer C, Fisher A, Southgate R, Masters P, Brennan K (1999) Distributional patterning of mammals on the Wessel and English Company islands Arnhem Land, Northern Territory, Australia. *Aust J Zool* 47:87–111