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Desertification and biopedturbation in the northern Chihuahuan Desert

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We examined the relationship between biopedturbation (animal caused soil disturbance) and several vegetation and soil-based indicators of rangeland condition to evaluate the effects of desertification on animal soil disturbance. The area, volume, and abundance of various biopedturbation types were assessed at 117 sites in south-central New Mexico where vegetative cover and composition had been measured previously. There were significant relationships between biopedturbation and selected rangeland condition indicators. Increasing percentages of grass cover were positively associated with increasing total area of biopedturbation. Increasing percentages of shrub cover and mean bare patch size were negatively associated with total biopedturbation area. Biopedturbation area and volume were related to indicators of rangeland condition and percent shrub cover best predicts the area of soil disturbed by animals. This relationship, however, cannot reliably predict total biopedturbation area or the area of soil disturbance types.

Keywords: Chihuahuan Desert; biopedturbation; desertification; soil disturbance; rangeland condition indicators

Introduction

Desertification can be defined as 'the diminution or destruction of the biological potential of the land, and can lead ultimately to desert-like conditions' (Verstraete, 1986). In North America the primary symptom of desertification is the replacement of grassland or shrubland capable of supporting a livestock industry by shrubland that is of little use to livestock.

Desertification in Chihuahuan Desert rangelands has produced large changes in the structure and function of the desertified ecosystems. The most widespread structural changes resulting from desertification processes are shifts from desert grassland to several different shrubland configurations (Buffington & Herbel, 1965; Grover & Musick, 1990). Despite the well-documented changes in vegetation, there is a

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paucity of information on the effects of desertification on fauna and on soils (Whitford, 1997).

Animals provide essential ecosystem services by their effects on soils (biopedturbation). Animals affect soil properties such as texture, bulk density, macroporosity, nutrient heterogeneity and pedogenesis (Whitford & Kay, 1999; Whitford, 2000). If desertification negatively impacts keystone animal species as suggested by Whitford (1997), key biopedturbation processes may also be negatively impacted. This study was designed to examine the full range of structural animal biopedturbation in regional ecosystems of varying degrees of desertification. We hypothesized that the ecosystems exhibiting the greatest change in structure would have significant reductions in biopedturbation.

The importance of biopedturbation on soil properties and processes has long been recognized (Darwin, 1881). Biopedturbation is important for maintaining the spatial and temporal heterogeneity in arid and semi-arid ecosystems. Animal-generated soil disturbance has been shown to affect vegetation patch dynamics, seed germination and plant establishment, water infiltration and storage, nutrient cycling, soil nutrient heterogeneity, and pedogenesis (Hole, 1960; Johnson, 1990; Whitford & Kay, 1999, Whitford, 2000). The characteristics and effects of biopedturbation are dependent upon the behavior of the animals creating them. Some disturbances are the result of single events and others are the result of continuous use. In the Chihuahuan desert there are a number of animal species producing soil disturbances (Table 1).

There is a large body of literature dealing with biopedturbation (Lobry de Bruyn & Conacher, 1994; Whitford & Kay, 1999). The majority of biopedturbation studies focus on a single species or on a group of related species. Most of the literature is also limited spatially by studying biopedturbation over a limited geographic range.

Three indicators of rangeland condition (percent shrub cover, percent grass cover, and mean bare patch size) were used to evaluate the effects of desertification on biopedturbation at the landscape scale, and thereby to assess the value of biopedturbation as a potential indicator of rangeland condition. Additionally, this study looks at the relationship of biopedturbation area and volume among four different dominant vegetation types or life-form classes (bare, grass, grass+shrub, or shrub) and among plant community types, characterized by the dominant species of vegetation at a study site.

Methods

We used 117 study sites previously studied by Johnson *et al.* (2000) and Dappen (1999) in the south-central portion of New Mexico, ranging from 32·00°N–34·21°N and from 105° W to 107·78° W (Fig. 1). Soil disturbance data were collected from early June to mid-August 1999. Study sites were located using a Global Positioning System (Trimble Geoexplorer II, accuracy was within ±50 m). Johnson *et al.* (2000) and Dappen (1999) reported values of rangeland condition indicators such as bare ground cover, vegetation cover, and plant species composition (Whitford *et al.*, 1999).

At each study site, all types of biopedturbation were measured using a 1 ha nested-quadrat sampling scheme. Smaller biopedturbation such as rodent burrows, cache pits, rabbit resting forms, ant nests, spider burrows, and termite galleries were counted and measured within four 10 m × 10 m plots in the corners of the 1 ha plot. Larger disturbances such as banner-tail kangaroo rat mounds, badger excavations, and large *Pogonomyrmex rugosus* ant nests were counted and measured over the entire 1-ha plot. Measurements for each biopedturbation included two diameters and a depth or height measurement. Soil ejecta piles associated with soil disturbances were also measured and recorded if present.

Table 1. *Types of biopedturbation and species producing the soil disturbance in the northern Chihuahuan Desert*

Biopedturbation type	Species	Biological feedback	Reference
Large pits	Badger (*Taxidea taxus*)Skunks (*Mephitis* spp.)	Contribute to pedogenesis Pits trap seeds and litter to form nutrient-rich germination sites	Chew (1974) Steinberger & Whitford (1983) Longland (1995)
Small foraging pits	Kangaroo rats (*Dipodomys* spp.)Lizards (*Cnemidophorus* spp.)Ground squirrel (*Spermophilus spilosoma*)	Seeds and litter become trapped forming nutrient-rich seedling germination sites	Whitford & Kay (1999)
Foraging galleries	Subterranean termites (*Gnathamitermes tubiformans*)	Affect infiltration rates and contribute to soil mixing	MacKay & Whitford (1988)
Single burrows	Kangaroo rats (*Dipodomys* spp.)Pocket mice (*Perognathus* spp.)Ground squirrels (*Spermophilus spilosoma)*	Bring readily erodable soil to the surface, contributes to soil mixing. Abandoned burrows collect seeds and litter	Whitford & Kay (1999)
Resting forms	Jackrabbit (*Lepus californicus*)Desert cottontail (*Sylvilagus auduboni.*)	Usually under shrubs, facilitate seedling establishment and possibly contributes to island of fertility effect	Personal Observation
Burrow system	Banner-tail kangaroo rat (*Dipodomys spectabilis*) Pocket gophers (*Thomomys bottae and Geomys bursarius*)	Affect soil texture and structure, infiltration rates, mineralization rates, fertility, bulk density, erosion and biomantle evolution	Moorhead *et al.* (1988), Mun & Whitford (1990), Kinlaw (1999)
Emergence holes	Grass cicadas (*Cacama* spp.)	Contribute to soil macroporosity and increase water infiltration into soil.	Whitford *et al.* (1995),
Ant nests > 1 m deep	Ant Species: *Pogonomyrmex desertorum, Pogonomyrmex rugosus, Myrmecocystus* spp., *Trachymyrmex smithii*	Increase water infiltration rates and soil organic matter, contribute to textural homogenization of the soil profile	Whitford *et al.* (1995)
Ant nests > 1 m deep	Ant species: *Conomyrma insana, Forelius pruinosus, olenopsis* spp., *Pheidole* spp.	Bring readily erodable soil to the surface, contributes to soil mixing	Whitford *et al.* (1995)
Spider burrowss	*Geolycosa rafaelana*	Contribute to soil macroporosity and increase water infiltration into soil	Personal observation

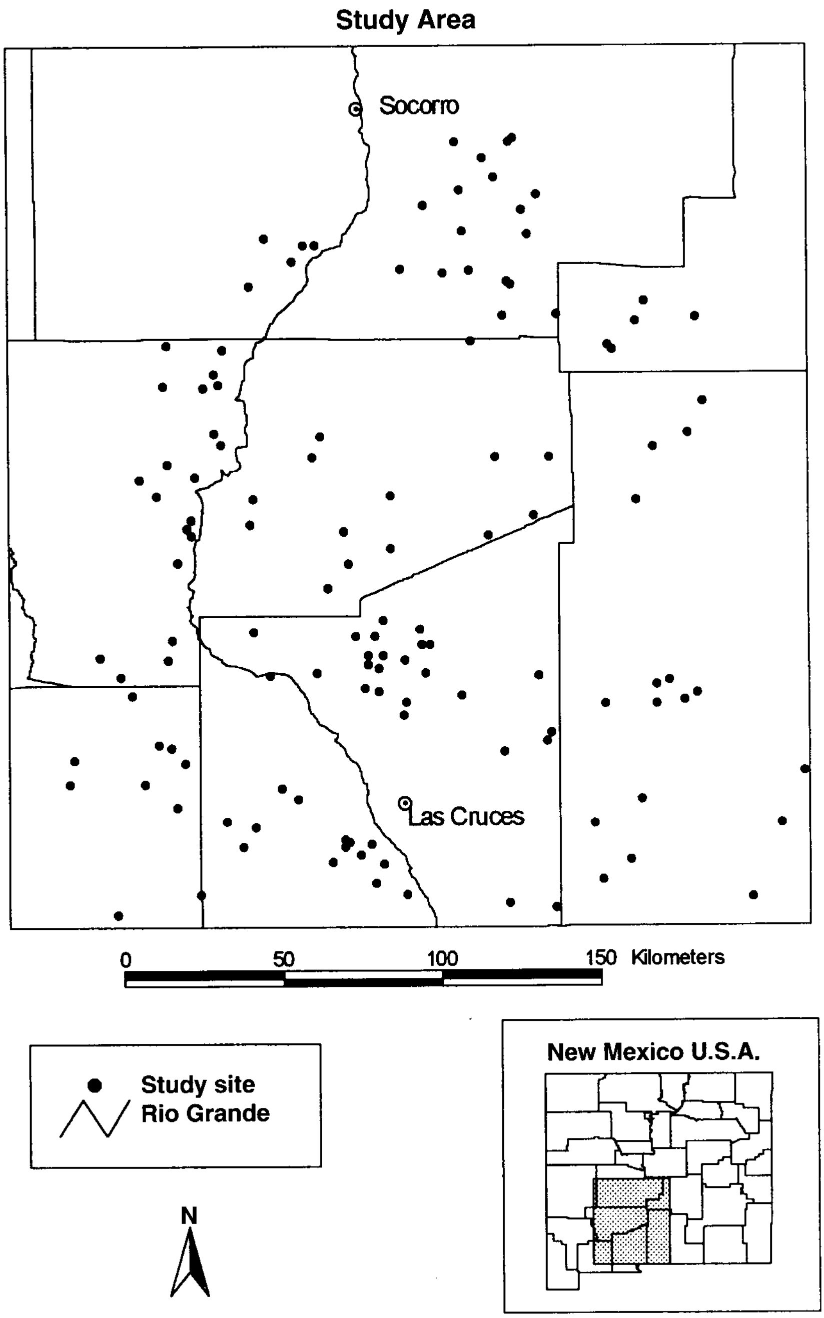

Figure 1. Map of study area.

To determine the area of each soil disturbance, the formula for the area of an ellipse was used. Several studies have assumed the area of an ellipse in calculating biopedturbation area (Carlson & Crist, 1999; Fields *et al.*, 1999). To model disturbances with three dimensions (e.g. a pit, foraging pit, kangaroo rat mound, ant mound, or soil ejecta mound) the volume formula of a spherical cap was used.

Data were scaled up from the 10 m × 10 m nested quadrats to obtain an estimate of the abundance, area, and volume of biopedturbation for each of the 117 1-ha study sites. Data analysis examined the relationships between biopedturbation and the chosen indicators of rangeland condition (e.g. mean bare patch size, percent grass cover, and percent shrub cover) for each study site. Data were analysed using forward stepwise regression, logistic regression, and a Kendall rank correlation test (McGrew & Monroe, 2000).

To further investigate the relationship between vegetation cover and biopedturbation area, study sites were categorized by dominant vegetation based on Johnson *et al.* (2000). Each site was assigned to one of four classes; grass, grass+shrub, shrub, or bare. Sites were assigned to a class as follows, a site with at least 10% grass cover was considered a grass site, a site with at least 10% shrub was a shrub site, a site with at least 10% of each would be a grass+shrub site, and sites with < 10% cover were classes as bare (DeSoyza *et al.*, 2000). Ten percent ground cover of a life form is generally indicative of the dominant life form in desert systems where 30% vegetation cover often represents maximum cover.

To examine the relationship between biopedturbation and vegetation community types, sites were classed as creosote bush, creosote+grass, grass, and mesquite, and mesquite+grass. Again, a minimum of 10% vegetation cover was used to determine plant community type. Sites where the dominant grass cover was tabosa grass (*Pleuraphis mutica*) or burro grass (*Slceropogon brevifolius*) were removed from the analysis. Neither of these grasses are considered good forage for domestic livestock and burro grass is often associated with rangeland disturbance. By excluding these species the grassland category is believed to be more representative of watershed areas minimally impacted by cattle grazing (Whitford, pers.comm.).

A Kruskal–Wallis test was used to look for significant differences among these vegetation cover classes or community type for each soil disturbance type. If a significant difference was detected, then a Mann–Whitney *U*-test was used to compare which of dominant vegetation type categories or vegetation community types were significantly different from each other.

Logistic regressions were used to predict the probability of the presence or absence of each soil disturbance type given the cover measurements of percent grass, percent shrub, and mean bare patch size. Logistic regression models were run for each disturbance type category using the presence/absence of soil disturbance types as the dependent variable and cover values as independent variables. To interpret overall model significance, the likelihood ratio test statistic was used. The likelihood ratio test statistic is essentially a chi-square statistic where small *p*-values indicate a good fit between the logistic regression equation and the data being tested. The threshold probability for positive classification was set at 0·50. Good models were classified as having greater than 50% correct classification rate and a low observed significance level or *p*-value for the overall model. The correct classification rate was obtained by comparing predicted and observed for presence and absence of soil disturbance types.

Results

A forward stepwise regression revealed that total biopedturbation area was best predicted by percent shrub cover ($p < 0{\cdot}001$, $r^2 = 0{\cdot}115$). Percent grass and mean bare patch size did not significantly add to the ability of the stepwise regression to predict biopedturbation area. However, because this r^2-value only explains 11·5% of the variation in the data, percent shrub is not a very good predictor of biopedturbation area.

The Kendall rank test yielded a significant positive cover relationship between biopedturbation area and percent grass cover indicating that high ranks of total

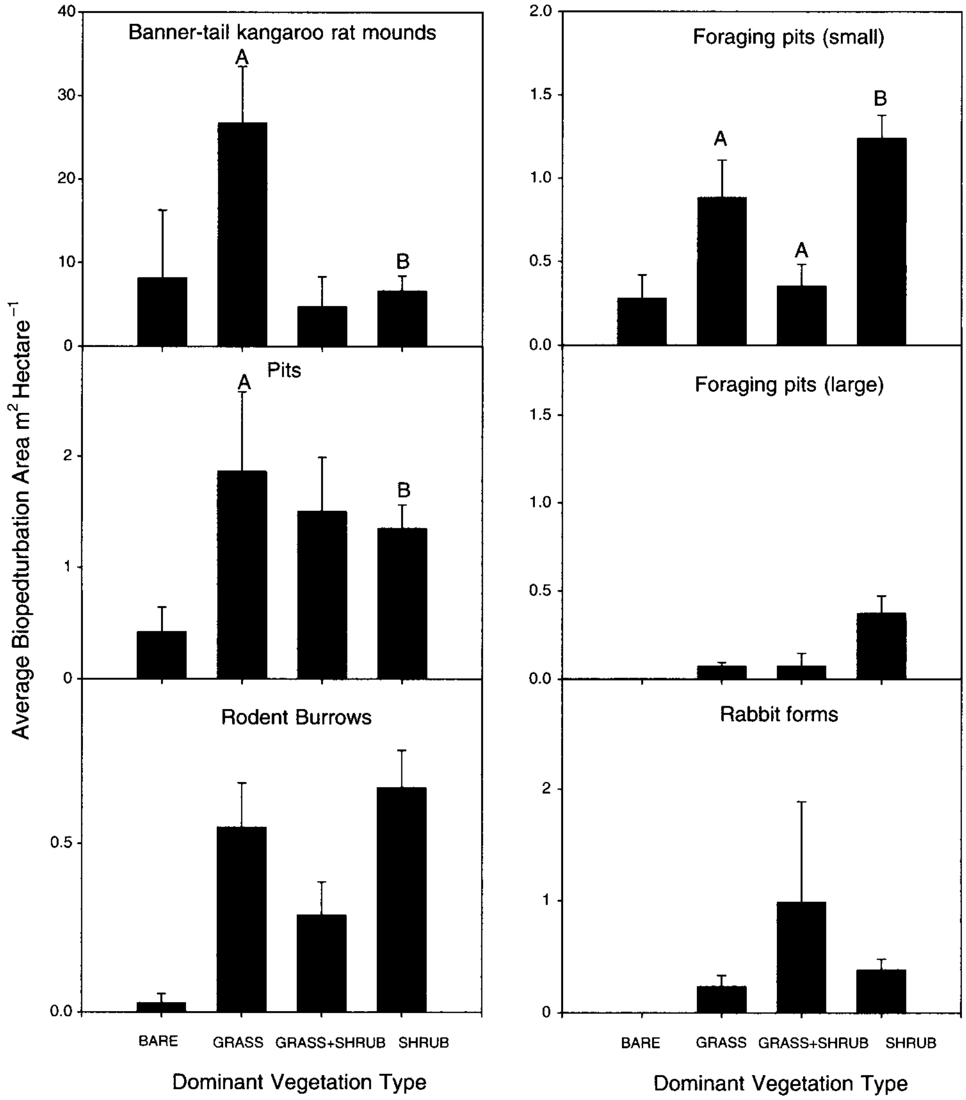

Figure 2. Average (±S.E.) biopedturbation area of disturbance types separated by dominant vegetation types. Different letters above the columns illustrate significant differences between those columns. Columns without a letter above them are not significantly different from any other column.

biopedturbation area occur with high ranks of grass cover. The values for percent shrub and mean bare patch size had a significant negative correlation with biopedturbation area. This indicates that high ranks of 1% shrub and mean bare patch size occur with low ranks of the biopedturbation (Fig. 2).

Only a few soil disturbance types yielded good logistic regression models (Table 2). Presence of ant disks had the greatest probability (63%) of being correctly predicted from mean bare patch size. Large foraging pits made good models with percent shrub (64%) and mean bare patch size (70%) as predictor variables. For kangaroo rat mounds, the model showed there was a 69% chance of accurately predicting presence from percent grass, a 66% chance of predicting presence of percent shrub, and a 67%

Table 2. *Summary of results from logistic regression models between presence or absence of soil disturbance types and each cover type*

Disturbance types	Vegetation cover type	Slope sign†	Overall chi-square	% Correct classification
Ant disks	% Grass	+	0·065	56·0%
	% Shrub	–	0·151	58·6%
	Mean bare patch size	–	0·009*	62·9%
Ant mounds	% Grass	–	0·811	63·0%
	% Shrub	+	0·279	63·0%
	Mean bare patch size	+	0·172	63·0%
Foraging pits (small)	% Grass	–	0·764	87·0%
	% Shrub	+	0·802	87·0%
	Mean bare patch size	–	—	—
Foraging pits (large)	% Grass	–	0·156	66·0%
	% Shrub	+	0·026*	63·8%
	Mean bare patch size	+	0·020*	70·0%
Foraging pit complexes	% Grass	–	0·610	75·9%
	% Shrub	+	0·122	75·9%
	Mean bare patch size	+	0·110	75·9%
Kangaroo rat mounds	% Grass	+	0·004*	69·0%
	% Shrub	–	0·001*	66·0%
	Mean bare patch size	–	0·001*	67·2%
Pits	% Grass	–	0·028*	83·6%
	% Shrub	+	0·001*	83·6%
	Mean bare patch size	+	0·028*	83·6%
Rodent burrows	% Grass	–	0·179	82·7%
	% Shrub	+	0·168	82·7%
	Mean bare patch size	+	0·687	82·7%
Rabbit forms	% Grass	–	0·108	71·5%
	% Shrub	–	0·220	71·5%
	Mean bare patch size	–	0·206	71·5%
Spider holes	% Grass	+	0·309	76·7%
	% Shrub	–	0·071	76·7%
	Mean bare patch size	–	0·923	76·7%
Termite galleries and sheeting	% Grass	+	0·134	67·2%
	% Shrub	–	0·026*	69·0%
	Mean bare patch size	–	0·034*	69·0%

†Sign of estimated slope coefficient. A positive slope implies that as the independent variable increases, the likelihood of observing the type of disturbance also increases. The inverse of this is true for negative slopes.
*Indicates that the model is significant ($p<0{\cdot}05$).

chance of predicting presence from mean bare patch size. Termite gallery presence was correctly classified at 69% for percent shrub and at 69% for mean bare patch size. The best overall models generated were for pits. For all three independent variables,

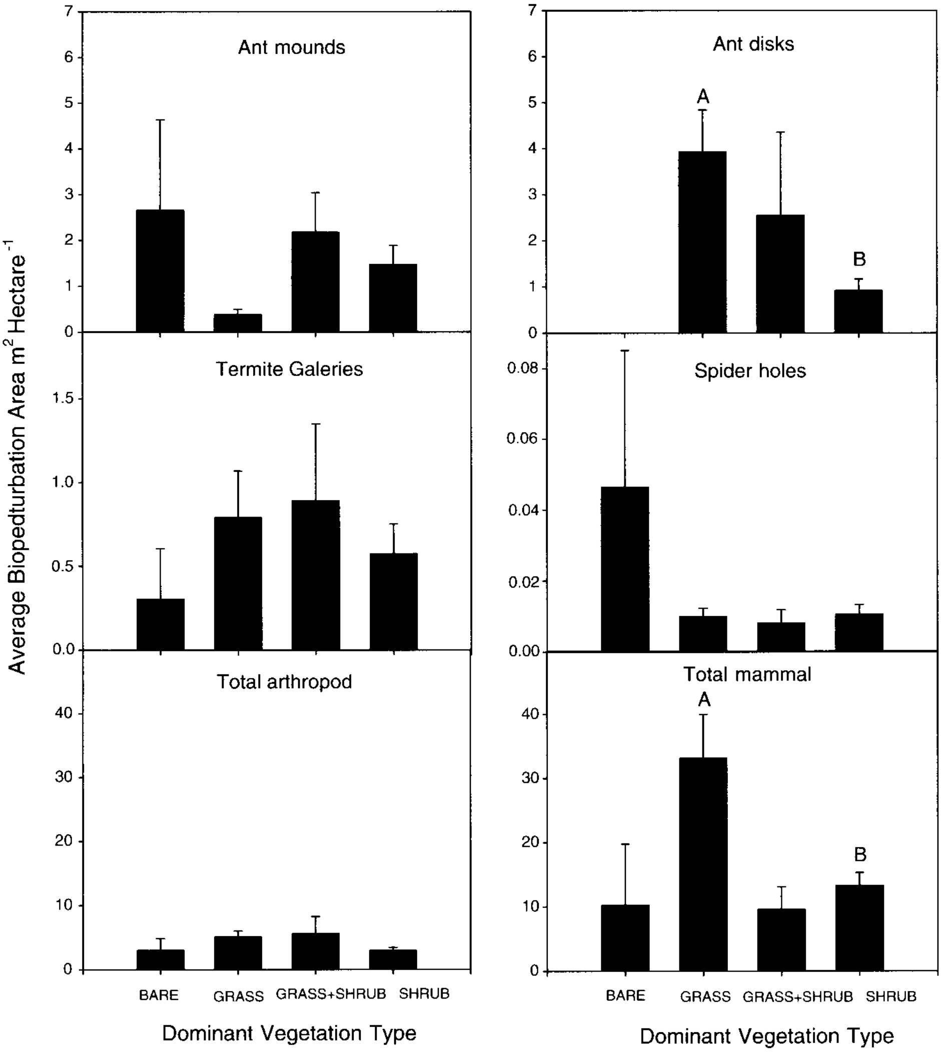

Figure 3. Average (±S.E.) biopedturbation area of more disturbance types separated by dominant vegetation types. Different letters above the columns illustrate significant differences between those columns. Columns without a letter above them are not significantly different from any other column.

pits had an 84% correct classification rate. The most commonly found disturbances, such as small foraging pits and ant mounds, did not make good models. Relationships of small foraging pits and mean bare patch size were not statistically significant. .

Biopedturbation area was calculated in square meters. As a result of stratifying the study sites by dominant vegetation type, sample sizes were unevenly distributed between the categories. Consequently, when stratified at the 10% level the bare category only contained three sites. Because of this small sample size, the bare category was excluded from statistical analysis and is included only as a reference (Fig. 2–4).

Comparisons of biopedturbation area by disturbance type with dominant vegetation categories had varied results (Figs 3 & 4). The area of pits and banner-tail kangaroo

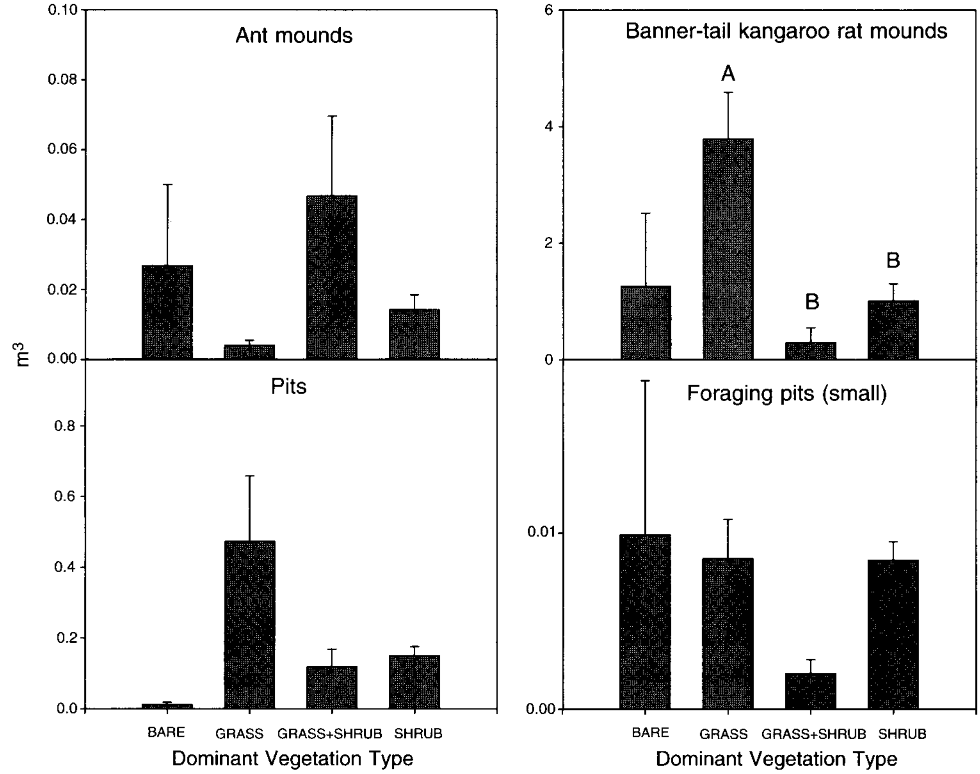

Figure 4. Average (±S.E.) volume of four soil disturbance types separated by dominant vegetation types. Different letters above the columns illustrate significant differences between those columns. Columns without a letter above them are not significantly different from any other column.

rat mounds were significantly higher in grass areas than shrub areas. The area of smaller foraging pits were significantly higher in shrub sites than in grass or grass+shrub sites. The larger size class of foraging pits was highest in shrub sites, but not significantly so. Ant disks made by harvester ants (*Pogonomyrmex rugosus*) were significantly higher in grass sites than in shrub sites. Total mammal disturbance was significantly higher in grass sites than shrub sites. Again, this finding is attributed primarily to the large area of banner-tail kangaroo rat mounds.

The volume of soil disturbance was calculated in cubic meters. Total volume calculations include measurements for ant mounds, pits, foraging pits, and banner-tail kangaroo rat mounds. The average total biopedturbation volume was also significantly higher in grass sites than in shrub sites for each minimum cover class of dominant vegetation types (Fig. 4). The Kruskal–Wallis test showed significant differences ($p<0\cdot05$) between kangaroo rat mound volume and dominant vegetation types (Fig. 5). Mann–Whitney *U* pair wise comparisons showed that there were significant differences between kangaroo rat mound volume in grassland sites compared to grass+shrub and shrub sites.

At the plant community level, there were similar associations between disturbance types as there were with dominant vegetation types (Figs 5 & 6). Smaller foraging pits was significantly higher in mesquite-dominated areas than in creosote or

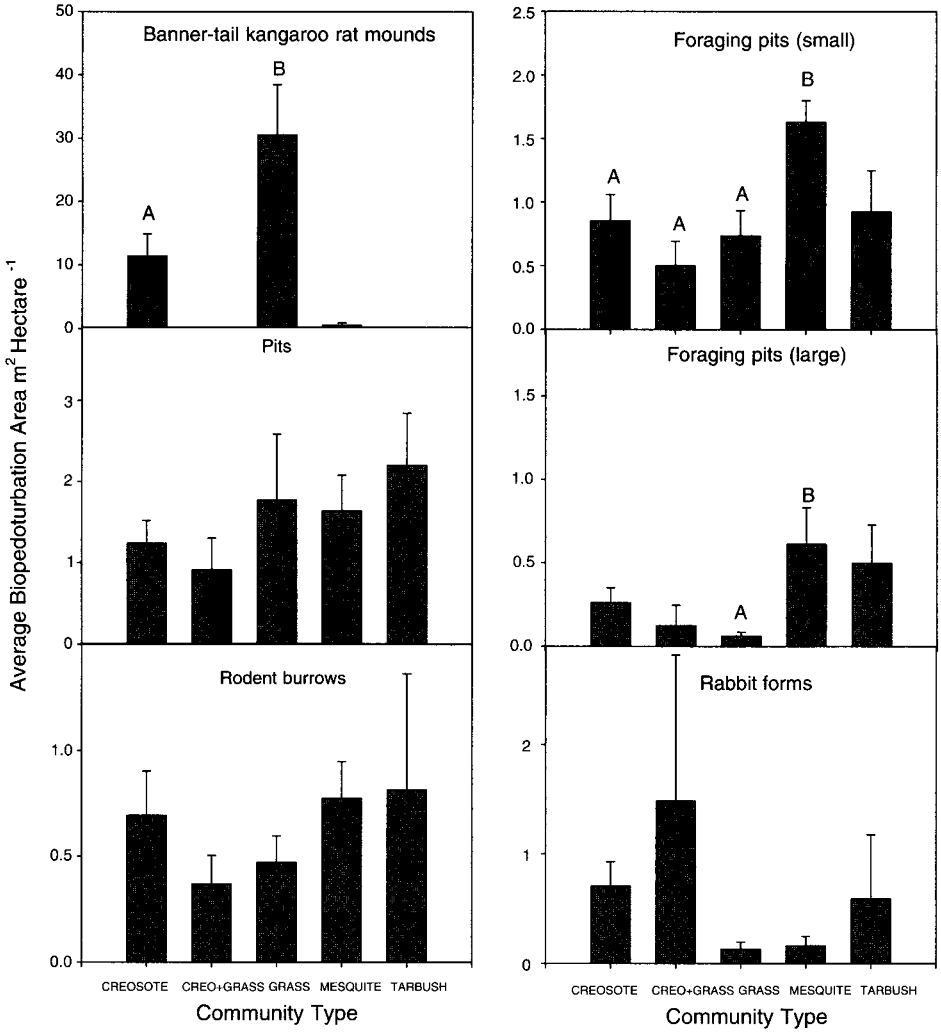

Figure 5. Average (±S.E.) biopedoturbation area of disturbance types separated into community type categories. Different letters above the columns illustrate significant differences between those columns. Columns without a letter above them are not significantly different from any other column.

creosote+grass dominated areas. The larger foraging pits were significantly higher in mesquite-dominated sites than in grass sites. Banner-tail kangaroo rat mounds were again dominant in grassland sites and were not present in areas dominated by tarbush or creosote+grass. Kangaroo rat mounds were significantly higher in grassland sites than in creosote-dominated sites. Ant disks were also significantly higher in grassland sites than in either creosote+grass or mesquite-dominated shrub sites.

Both total area and total volume measurements were heavily influenced by the presence of banner-tail kangaroo rat mounds which have been shown to be more abundant in grassland areas (Krogh *et al.*, in press). The large area and volume of these mounds heavily influence these results for total biopedturbation.

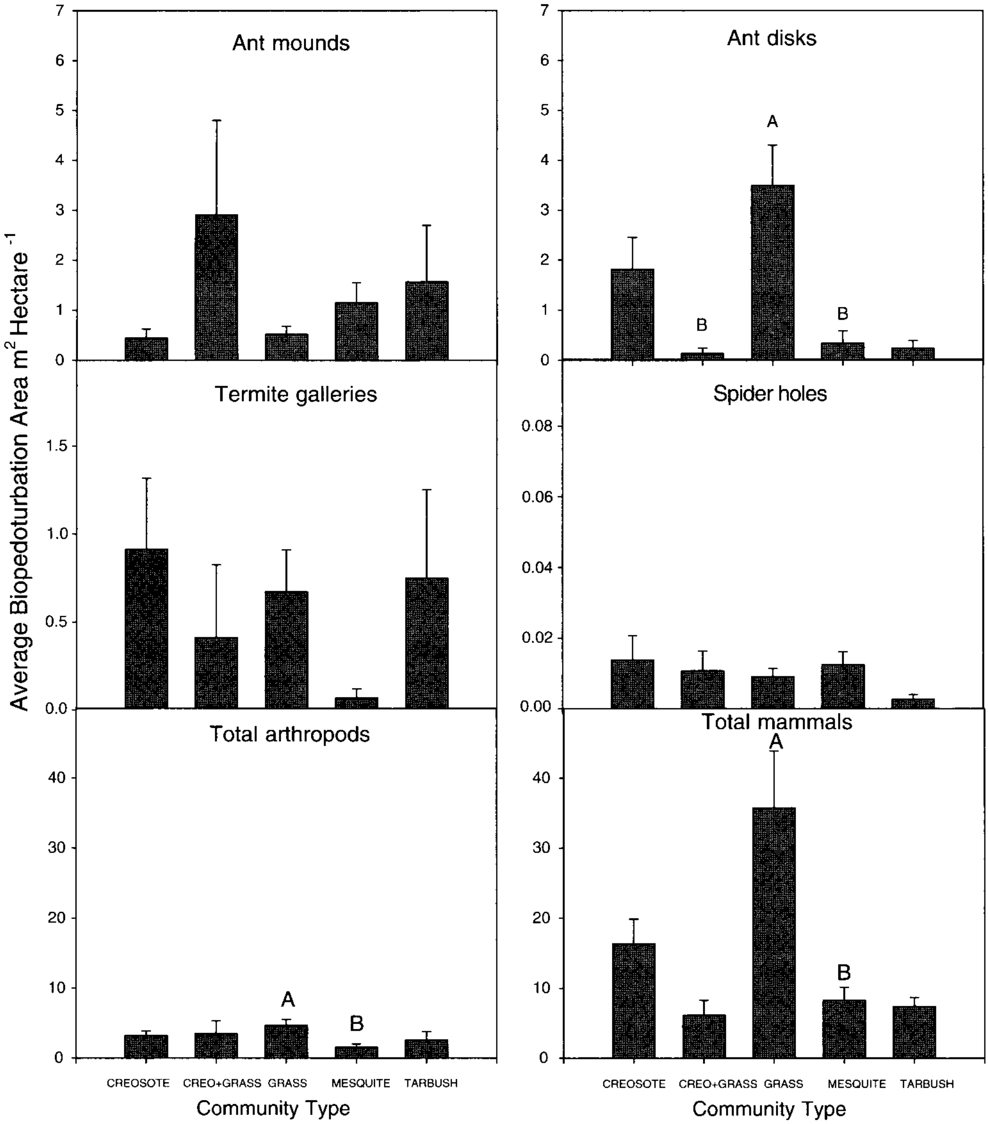

Figure 6. Average (±S.E.) biopedoturbation area of more disturbance types separated into community-type categories. Different letters above the columns illustrate significant differences between those columns. Columns without a letter above them are not significantly different from any other column.

Discussion

The relationship between total area of biopedturbation and the indicators of desertification or ecosystem degradation supports the hypothesis that degradation of desert grassland negatively impacts soil processes. The largest total area of soil disturbance by animals was in the grasslands. Total area of soil disturbance was lower on shrub-dominated plots and on plots with large bare patches. However, since the contribution of various classes of soil disturbance to ecosystem processes and soil genesis is dependent upon the animal taxon producing the disturbance, total area of soil disturbed is not the most robust variable for assessing the impact of degradation on soil properties and processes. The largest areas of soil disturbance in desert grassland that were absent or sparse in bare soil areas, shrub–grass mosaic, or shrubland were the mounds of banner-tail kangaroo rats (*Dipodomys spectabilis*). The importance of Chihuahuan Desert grasslands as habitat for this keystone species is well documented (Schroeder, 1987; Anderson & Kay, 1999; Krogh *et al.*, in press). Banner-tail kangaroo rat mounds have been shown to increase areas of soil nutrient concentration and patches with high water infiltration (Mun & Whitford, 1990). Thus, the reduction or loss of *D. spectabilis* mounds in degraded areas represents the loss of an important component of soil heterogeneity.

Although there were significant relationships between biopedturbation area and indicators of rangeland condition, these indicators explained only a small part of the variation in total biopedturbation area. Indicators based on animal populations and diversity were not suitable for assessing the condition of Chihuahuan Desert rangelands (Whitford *et al.*, 1998,1999). Although total area of soil disturbed by animals was hypothesized to decrease as a result of desertification, the changes in species composition of animal communities during and following desertification appear to exhibit redundancy with respect to biopedturbation (Whitford, 1997). Since several species of the same family of animals produce similar types of soil disturbance, changes in species composition and abundance of animal species has minimal effect on total area of disturbed soil.

The logistic model prediction for biopedturbation area of ant nest disks from mean bare patch size is related to the preference of *Pogonomyrmex rugosus* for patches of bare soil for location of nests. *P. rugosus* nest disks located in bare patches allow this species to incubate larvae and pupae in nest chambers close to the surface characterized by temperatures that are optimum for growth and development (Whitford *et al.*, 1976). Large foraging pits are the result of digging by ground squirrels (*Spermophilus spilosoma*), skunks (*Mephitis* spp.) and foxes (*Vulpes* spp.). The logistic model relationship of area of large foraging pits and shrub cover or mean bare patch area probably reflects the wide range of habitats that are used by these species and the availability of insect larvae and pupae in the soil. The logistic model predictions for kangaroo rat mounds, and termite galleries reflect the wide distribution of these animals in all habitats (Whitford, 1997; Nash *et al.*, 1999). A long-term study of termite activity documented no significant differences in relative abundance and/or activity of termites in degraded and non-degraded ecosystems (Nash *et al.*, 1999).

The relationship between various types of soil disturbance and growth form of the dominant vegetation was similar to the abundance patterns of the animals generating the soil disturbance. For example, the significantly greater abundance of small foraging pits in shrubland is related to the higher densities of heteromyid rodents in shrubland compared to grassland (Whitford, 1997; Kerley & Whitford, 2000). Foraging pits are not randomly distributed on the landscape. Foraging pits are more abundant under shrub canopies in shrub-dominated habitats (Steinberger & Whitford, 1983, Dean & Milton, 1991). Since litter accumulates and decomposes in these pits, the concentration of foraging pits under shrub canopies contributes to the shrub 'fertile island' effect (Whitford, 1993). High rates of small mammal biopedturbation may reinforce the dominance of shrubs and contribute to the resistance of shrublands to restoration efforts.

Rabbits are generally more abundant in shrubland and in grass–shrub mosaic habitats than in desert grasslands (unpublished data, Jornada LTER Program) and the total area/volume of rabbit forms reflect that pattern. Abundance of ants and termites is relatively similar in most Chihuahuan Desert habitats (Nash *et al.*, 1999; Whitford *et al.*, 1999). The differences in abundance of species of animals that generate soil disturbance affect the functional significance of biopedturbation in different habitats

(Whitford, 2000). Ant colonies may contribute nutrient-rich, high water infiltration patches or contribute to textural homogenization of the soil profile. Termites affect infiltration rates and contribute to soil mixing. Pits trap litter and seeds contributing to nutrient-rich patches and safe germination sites. The variety and spatial extent of biopedturbation affect the structural properties and ecosystem processes thereby affecting the long-term structure and function of desert landscapes.

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