Badger (*Taxidea taxus*) disturbances increase soil heterogeneity in a degraded shrub-steppe ecosystem

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ABSTRACT

In the western United States, overgrazing, weed invasion and wildfire have resulted in the conversion of shrub-steppe to annual grasslands, with substantial effects on ecosystem function. In these landscapes, badgers disturb large areas of soil while foraging for fossorial animals. Mounds created by badgers contained the lowest concentrations of total carbon, nitrogen and sulphur, mineral nitrogen and mineralizable nitrogen, inter-mound soils had the highest concentrations, and excavation pits had intermediate levels. Soil C:N ratio and pH were greater, and electrical conductivity and soluble Ca^{2+}, Mg^{2+} and K^+ were lower on mound soils compared with either pit or inter-mound soils. Larger pits generally trapped more litter, and increased litter mass equated with greater concentrations of active carbon, but only at the burned sites. Older mounds supported more vascular plants and cryptogamic crusts. Our results demonstrate reduced levels of nutrients and a higher C:N ratio on the mounds compared with either the pits or inter-mounds. Alteration to the homogeneous post-fire landscape by badgers contributes to patchiness in soils and vegetation, which is critical to the functioning of arid systems. Given their effect on soil C:N ratios, mounds may be important sites for recovery of indigenous shrub-steppe plant species.

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1. Introduction

Many organisms, including terrestrial vertebrates, interact positively with other organisms by changing their physical environment, thereby altering the availability of resources to either themselves or other organisms (ecosystem engineering *sensu* Jones et al., 1997). Ecosystem engineers have far reaching direct and indirect effects on ecosystems such as altering soil nutrient relationships, shifting the allocation of resources from roots to reproductive structures, dispersing or consuming seed and fruit, or changing the dominant plant growth form by grazing (Chew, 1974; Whitford, 2002). While these interactions might initially be negative, for example when grizzly bears (*Ursus arctos horribilis*) forage for, and consume, the below-ground bulbs of glacier lilies (*Erythronium grandiflorum*), they are often positive over longer timescales, as for example when those lilies surviving in the foraging pits have tissue of a higher nitrogen content and produce more seeds (Tardiff and Stanford, 1998). Ecosystem theory suggests that the impact of this engineering is likely to be greatest in environments of reduced productivity (Wright and Jones, 2004); thus we would expect substantial engineering effects in arid and semi-arid environments where essential resources such as water and nutrients are not only limiting, but are distributed heterogeneously in both space and time.

A number of studies have demonstrated that animals are important moderators of soil biogeochemical processes and influence the functioning of terrestrial ecosystems (e.g. Miller et al., 1994). Soil disturbance by animals (biopedturbation; Whitford and Kay, 1999), is a widespread form of engineering whereby animals alter the physical and chemical arrangement of soil patches directly through their activities (Huntly and Inouye, 1988; Schooley et al., 2000). Animal-induced disturbance creates microsites that differ in biophysical and chemical characteristics from the surrounding soil matrix. For example, nutrient-laden sediment mobilized by wind or water after mound construction by banner-tailed kangaroo rats (*Dipodomys spectabilis*) leads to a localized depletion of carbon and nitrogen in the vicinity of the mound. Caching of food by kangaroo rats within their subterranean larders and the breakdown of stored seed leads to patches of enhanced nutrients, 'safe sites' for germinating plants and hot spots of biological activity (Krogh et al., 2002).

The American Badger (*Taxidea taxus*) is an important vertebrate of shrub-steppe ecosystems in the western United States (Messick

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and Hornocker, 1981), changing a large mass of soil from an undisturbed soil matrix to disturbed mounds and pits (Eldridge, 2004). Badgers are significant predators of fossorial mammals such as ground squirrels (*Spermophilus* spp.), as well as burrowing owls (*Athene cunicularia*) that nest in their abandoned digs (Desmond et al., 2000). While preying on ground squirrels, badgers excavate small squirrel burrows, creating pits up to 15 cm across and 60 cm deep, and large fan-shaped mounds up to 1 m long and 0.5 m high at the entrance to the pit (Desmond et al., 2000; Eldridge, 2004; Green and Anthony, 1989; Platt, 1975). In the Snake River Birds of Prey National Conservation Reserve (BOPNCR) in west-central Idaho, badger digging has resulted in the creation of an extensive patchwork of scratchings, pits and mounds of various age and configuration across 5–8% of the landscape (Eldridge, 2004). Badgers are known to dramatically affect plant species dynamics, with changes persisting for many decades (Platt, 1975). There are few data, however, on the impact of badgers on soil processes (e.g. Voslamber and Veen, 1985; Yensen et al., 1992), nor any reliable estimates of *per capita* mound construction. Population estimates of 3.2–5 badgers km^{-1} (Messick and Hornocker, 1981) suggest that conservatively, each badger constructs 1100–1700 mounds yr^{-1}, given that 7% of mounds are recently constructed (Eldridge, 2004). The landscape-level effects of this substantial soil disturbance by badgers are therefore likely to be considerable.

During the past century, the structure and composition of North American shrub-steppe communities have been irreversibly modified by unrestricted grazing by European animals and invasion by Eurasian weeds (Mack, 1981). The increased frequency of wild-fire has resulted in the conversion of extensive areas of *Artemisia* shrub-steppe to alien annual grasslands dominated by cheatgrass (*Bromus tectorum*), which now burn at intervals of <10 years rather than 50–100 years (Brooks et al., 2004). Changes in landscape structure have had major impacts on biodiversity including loss of flora, declines in many faunal populations, and invasion of exotic species (Wambolt et al., 2001).

We speculate that badgers play an important role in these shrub-steppe ecosystems, even in the presence of cheatgrass. To examine this broad proposition we sought to test the following three specific hypotheses about the effects of badgers on the distribution of resources at landscape scales. Consistent with results for other semi-fossorial animals worldwide (e.g. Whitford and Kay, 1999), we predicted that (1) pits excavated by badgers would trap larger amounts of organic matter (litter) and fine sediment (silt and clay) compared with the intervening soil matrix, and the extent of this resource capture would increase with increasing pit size, and (2) increases in the mass of litter captured in the pits would correspond with increased concentrations of carbon and nitrogen in pit soils compared with adjacent mound and inter-mound soils. Further, given that subsoil is transported to the surface during mound excavation, we predicted that (3) the surface of badger mounds would be physically and chemically depauperate compared with the pits and inter-mound soil matrix, and mound chemistry would vary between burned and unburned treatments, given the effects of burning on soil chemistry. We did not expect

major differences in chemistry however between the two communities, given their similar structure and preferred habitats.

The first two hypotheses relate to the importance of badger-constructed pits as resource traps, an important function in land-scapes where the naturally-occurring shrub-interspace patchiness has been eliminated by grazing and wildfire, and where pits and mounds may provide the only form of semi-permanent patches. The third hypothesis is important, as a physico-chemically depauperate mound surface could affect resource availability and therefore plant regeneration on the mounds, and this would be expected to vary between burned and unburned sites. We tested these hypotheses by comparing litter loads and soil nutrient concentrations within their associated foraging pits with mounds and adjacent inter-mound surfaces across an extensive area of shrub-steppe.

2. Methods

2.1. The study site

The study was conducted in a sagebrush shrub-steppe community in the BOPNCR on the western Snake River Plain, west-central Idaho, about 40 km south-west of Boise (43°27′ N, 116°26′ W, 884–914 m above sea level). The soils are predominantly fine silty Xerollic Haplargids (Aridisols, Collett, 1980) formed on loess and sedimentary deposits covering basalt lava flows. In the inter-mound locations, soils are characterized by increasing concentrations of soluble cations, particularly after 40 cm depth, declines in total N and silt, and increases in sand (mainly fine sand) with depth (Table 1). The climate is semi-arid, with hot, dry summers and cool, wet winters. Annual precipitation ranges from 178 to 305 mm, with less than 35% of the moisture occurring between April and September. Mean daily temperatures range from −1 °C in January to 24 °C in July. The topography of the area is generally flat, with small basalt outcrops or remnants of volcanic activity.

The study was conducted across 20 sites within two distinct shrub-steppe community types, characterized by either sagebrush (*Artemisia* spp.) or winterfat (*Krascheninnikovia lanata*). Wyoming big sagebrush (*Artemisia tridentata* ssp. *tridentata*) occurs as a dominant shrub over large areas at variable densities with a perennial herbaceous understorey of Sandberg's bluegrass (*Poa secunda* J. Presl.) and bottletail squirreltail (*Elymus elymoides* Raf. Swezey). Extensive areas of the BOPNCR have been burned by wildfire, with burned and unburned sites varying markedly in structure and composition. We were interested in exploring potential differences in relation to burning because fire destroys shrub patches and reduces vegetation patchiness. Consequently our study used both burned or unburned sites. Burned sagebrush and winterfat sites were dominated by cheatgrass and scattered Russian thistle (*Salsola kali* var. *kali* L.), with occasional bluebunch wheatgrass (*Pseudoroegneria spicata* Pursh A. Love) and Thurber's needlegrass (*Achnatherum thurberianum* Piper Barkworth), and scattered clumps of forage kochia (*Kochia prostrata* L.) that had been artificially sown into some areas or had spread from seeded areas nearby.

Table 1
Soil physical and chemical features of a representative soil profile in the Birds of Prey Conservation Reserve, west-central Idaho.

Depth (cm)	Particle size (%)			pH (1:5)	EC (dS m^{-1})	Total nutrients (%)			Soluble cations (cmol (+) kg^{-1})			
	Clay	Silt	Sand			C	N	S	Ca	Mg	Na	K
0–5	11.1	31.6	57.3	7.6	0.21	0.012	0.219	0.012	0.54	0.22	0.51	0.02
10–20	24.2	28.5	47.3	8.5	0.13	n.d.	0.078	<0.01	0.48	4.30	1.20	1.20
40–50	16.0	19.1	64.9	8.4	0.08	n.d.	0.092	<0.01	n.d.	7.00	12.70	0.30
80–90	10.8	15.2	74.0	8.1	0.20	n.d.	0.039	0.5	n.d.	14.30	15.30	0.30

n.d. – no data available.

2.2. Field measurements

Ten of the 20 sites were dominated by sagebrush and 10 by winterfat. Five sites of each vegetation community were burned and five unburned. Sites were widely spread over an area of about 300 km^2 of the BOPNCR and separated from each other by distances of 3–10 km. Sites were therefore statistically independent and chosen in order to sample the variability of landscapes dominated by the two shrub communities while confining the study to a single soil type. The 20 sites were selected *a priori* by examining vegetation maps and consulting local experts on the location of burned and unburned sites from each vegetation community. All burned sites had been burned only once, 7–10 years before our study and were located at least 4 km from the nearest unburned patch. At each site, a 50 m by 10 m plot was systematically located about 200 m from the main access track, but away from power lines, tracks, easements and obvious areas of disturbance from off-road vehicles. All badger diggings and mounds within the plot were measured. Fieldwork was carried out during September and October 2002.

Badger mounds consist of a fan-shaped deposit of soil around a pit, the point of excavation. Mounds can be classified as active, crusted or recovering. Active mounds had been excavated within the past 2–3 weeks and comprised loose, powdery soil with no evidence of physical crusting. Crusted mounds showed signs of the development of a thin physical (raindrop-impact) crust, and recovering mounds were dominated by an organic (biological) soil crust (cryptogamic crust) and/or partially colonized by vascular plants, depending on their age (Eldridge, 2004). At each of the 20 sites we assessed the average cover of cryptogamic crusts, litter and bare soil on the different types of mounds. Litter accumulating in the pits was assessed as being either shallow (<0.5 cm deep), deep (>0.5 cm deep) or absent. We have been monitoring changes in badger mound morphology with age since 2002 at a number of sites in the BOPNCA. Over the 6-year period we have not found any evidence that mounds remain in a crusted stage for more than a year.

2.3. Litter and soil nutrient sampling

A random sub-sample of three of the five replicate sites by two levels of burning by two vegetation communities (*n* = 12) was chosen to test our hypotheses. Data from Eldridge (2004) indicated that 12 sites was sufficient to sample the variability in cover and soil nutrients across the area, and this sampling intensity was considered feasible given the large distances involved and measurements required. At each of the 12 sites, five pits were selected spanning the full range of pit sizes encountered at that site. To ensure that the selection process was unbiased, we sampled the full range of pit sizes (using mean diameter) encountered at that site, and selected five pits for detailed sampling. The procedure for selecting pits was to walk along one 50 m edge of the plot until the first pit (of a particular size class) was encountered within the plot. The procedure was repeated, by walking slowly up and down the plot until a total of five pits of the required size had been selected.

We collected all litter trapped within each pit, and a sample of soil (~20 g; termed the 'pit' sample) from immediately beneath the litter (within 5 mm). We also collected soil samples at two microsites adjacent to each of the five selected pits: (i) on top of a 'crusted' mound associated with the pit, or the nearest 'crusted' mound (termed 'mound') which was always found within 3 m; and (ii) adjacent to the 'crusted' mound but on an undisturbed soil surface (termed 'inter-mound'). The presence of a lichen-dominated cryptogamic crust indicated a relatively undisturbed surface. Sampling was restricted to crusted mounds for two reasons. First, about 70% of the mounds across the 12 sites were crusted and were therefore

proportionally more important than the other mound types. Second, we could not be sure of the exact age of recovering mounds. Our inability therefore to separate old recovering mounds from inter-mound surfaces might have compromised the study. Nonetheless, we recognize that some control soils may have been old mounds many years ago, given that mounds are thought to last for up to 15 years (Whitford and Kay, 1999).

2.4. Soil chemical analyses

The pit, mound and inter-mound soil samples described above were air-dried, passed through a 2 mm sieve and assayed for total N, C and S using a high temperature combustion method (LECO 2000 CNS system). Soils were also analysed for pre-existing inorganic (mineral) nitrogen ($NH_4^+ + NO_3^-$) and mineralizable N, according to Method 4 of Gianello and Bremner (1986). This method measures the amount of N mineralized over 16 h of anaerobic digestion at 100 °C, providing an index of the potential pool of N available to plants (i.e. an index of available N), and present at the time of sampling. Although this index cannot be compared numerically with NH_4^+ and NO_3^-, the values should be highly correlated with exhaustive aerobic soil incubation for N mineralization (Gianello and Bremner, 1986). Active (labile) C was determined using a simplified laboratory method whereby slightly alkaline, dilute $KMnO_4$ reacts with the readily oxidizable (active) carbon, converting Mn(VII) to Mn(II), and lowering the absorbance of 550 nm light (Weil et al., 2002). Soluble and exchangeable Ca^{2+}, K^+, Mg^{2+} and Na^+ were determined using inductively coupled plasma spectroscopy (Perkin Elmer Optima 3000 DV ICP-OES). Electrical conductivity and pH were determined on a 1:5 soil water extract. In total 180 samples were analysed representing two vegetation communities (sagebrush, winterfat) by two levels of burning (burned, unburned) by three microsites (pit, mound, inter-mound) by three sites each with five replicate samples per site. One of the five replicate samples used for determination of soil nutrient concentrations at each site was chosen randomly *a priori* for determination of the particle size distribution of mound, pit and inter-mound soils (<2 mm fraction) using the hydrometer method with dispersed samples.

2.5. Data analyses

Relationships between pit size, litter mass and nutrient concentrations (Hypothesis 1) were examined using regression analysis with a range of linear and non-linear models to maximize the degree of fit. Differences in the cover of bare soil, litter and cryptogams on active, crusted and recovering mounds (Hypothesis 3) were examined at all 20 sites using General Linear Models (GLM; Minitab, 2003). Data were transformed, where necessary, after examination of diagnostic plots and homogeneity of variance tests (Levene's tests) The GLM model was a split-plot design with two error terms; the whole-plot stratum considered vegetation community and burning (and their interactions), and the sub-plot stratum partitioned mound type and its two- and three-way interactions with vegetation community and burning. For these analyses, individual mounds at a site were not considered to be true replicates in a statistical sense, as cover is likely driven by landscape-level factors such as landuse and grazing effects. Accordingly, cover data were averaged for each of the three mound types before statistical analysis. Differences in soil physical and chemical properties in relation to burning, vegetation community and microsite (mound, inter-mound, pit) and their interactions at the 12 sites (Hypotheses 1 and 3) were also examined using GLM, but with the inclusion of an additional error term to account for the fact that microsites were clustered (blocked) at each site. For soil nutrients and litter accumulation, individual mounds were the subject of

study, and as the attributes measured were considered to vary across small spatial scales, were treated as statistically independent. In all cases Tukey's Least Significant Difference (LSD) testing was used to examine differences in all means.

3. Results

3.1. Pits as resource traps

Three-quarters of pits adjacent to recovering mounds contained deep litter, while 71% of pits adjacent to active mounds contained no litter ($F_{2,24} = 28.5$, $P < 0.001$, Fig. 1). There was no effect of burning nor vegetation community on the proportion of pits containing any class of litter, i.e. nil, shallow, deep. The spectrum of soil particle sizes differed between pits, mounds and inter-mounds. Pit soil had a two- to three-times greater percentage of clay and silt and very low percentages of coarse and fine sand compared with the mound and inter-mound soils, which were themselves not significantly different ($P < 0.001$; Fig. 2).

Across the 60 locations (12 sites each with five pits), larger pits tended to trap a greater mass of litter ($F_{1,28} = 37.2$, $P < 0.001$, $R^2 = 0.38$). When the data were partitioned between burned and unburned sites, and sagebrush and winterfat sites, increases in pit size were associated with large increases in litter mass at all but the unburned winterfat sites ($F_{2,12} = 8.07$–14.8, $R^2 = 0.50$–0.66, $P < 0.01$; Fig. 3).

Concentrations of total N, S and C, and active C in the pits were intermediate between those from either mound or inter-mound surfaces ($F_{2,112} = 21.9$–100.4, $P < 0.01$). The increased concentrations of active C from inter-mound soils were more pronounced in unburned soils than burned soils (burning by microsite interaction: $F_{2,112} = 6.03$, $P = 0.003$; Fig. 4). Overall, concentrations of mineral N ($NH_4^+ - NO_3^-$) were greatest in the pit soils than with mound (75% greater) or inter-mound (45% greater) soils ($F_{2,112} = 51.5$, $P < 0.001$). Differences among mounds and the other microsites were more pronounced in the burned soils (burning × microsite interaction: $F_{2,112} = 5.22$, $P = 0.007$; Fig. 5a).

3.2. Litter effects on soil nutrients

There were strong positive relationships between the mass of litter trapped in the pits and the concentration of active C in the soil immediately beneath the litter, but only on the unburned sites ($F_{1,13} = 13.0$, $R^2 = 0.50$, $P = 0.003$ for sagebrush, and $F_{2,12} = 51.5$, $R^2 = 0.85$, $P < 0.001$ for winterfat). For a given mass of litter, soil from pits in sagebrush communities contained about twice the
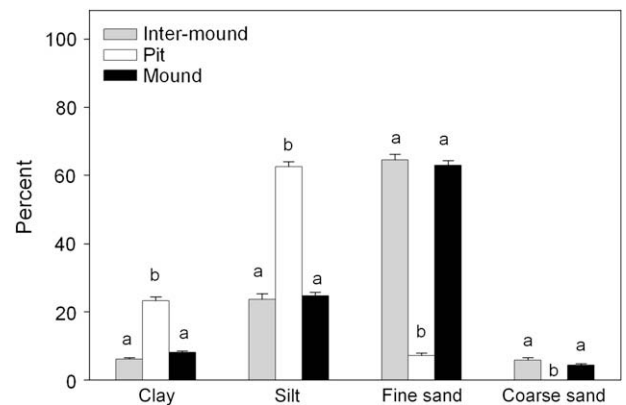
Fig. 2. Particle size analyses of soils taken from three microsites. Different letters within a particle size class indicate a significant difference at $P < 0.05$. Bars indicate standard error of the mean.

concentration of active carbon compared with those from winterfat communities. There were no significant relationships between the mass of litter trapped in the pits, or the size of the pit openings, and either mineral N or mineralizable N ($P > 0.40$).

3.3. Mounds as physically depauperate, resource-depleted patches

The cover of cryptogams ($F_{2,12} = 278.1$, $P < 0.001$) and litter ($F_{2,12} = 12.5$, $P = 0.001$) increased, and bare soil decreased ($F_{2,12} = 237.5$, $P < 0.001$) with increasing mound age, i.e. from active mounds through crusted to recovering mounds (Fig. 6). The treatment by mound surface interaction for cryptogam cover indicated generally greater cryptogam cover on unburned sites, but not for active mound types ($F_{2,12} = 15.1$, $P = 0.001$). There were no differences in cryptogam, litter or bare soil cover in relation to vegetation community or burning ($P > 0.05$).

Concentrations of active C, and total N, S and C were 43, 32, 25 and 52% lower, respectively, in mound soils compared with inter-mound soils. The C:N ratio of mound soils ($\sim 25:1$) was significantly larger ($F_{2,112} = 28.4$, $P < 0.001$) than that of either pit or inter-mound soils ($\sim 15:1$; Fig. 4). Mineralizable (available) N concentrations were lowest in the mound soils ($F_{2,112} = 16.8$, $P < 0.001$), and differences among microsites were more pronounced in the unburned treatments (burning × microsite interaction: $F_{2,112} = 3.76$, $P = 0.026$; Fig. 5b). The three-way burning × vegetation community × microsite interaction ($F_{2,112} = 5.08$, $P = 0.008$) resulted from a substantially greater concentration of mineralized N in inter-mound and pit soils compared with mound soil within the unburned sagebrush community. When we scaled total N and C concentrations up from the scale of individual mounds and pits to the landscape scale by taking into account the relative cover of pits, mounds and inter-mound surfaces at each site (data presented in Eldridge 2004), we found no significant differences in the total stocks of C nor N in the surface 2 cm of the soil in relation to burning (burned, unburned), vegetation community (sagebrush, winterfat), nor their interaction ($P > 0.43$).

Mound soils were significantly more alkaline (by 0.8 pH units) compared with inter-mound or pit soils ($F_{2,112} = 112.8$, $P < 0.01$; Fig. 4), and had a physico-chemical profile comparable to soil from a depth of 40–80 cm (Table 1). Electrical conductivity was significantly lower in mound soils compared with pit or inter-mound soils ($F_{2,112} = 57.6$, $P < 0.01$; Fig. 4).

Concentrations of the soluble cations Ca^{2+}, K^+ and Mg^{2+} were generally significantly lower on mound soils compared with pit or inter-mound soils ($P < 0.01$; Table 1). Further, both soluble and exchangeable Na^+ were greater on the mounds ($F_{2,112} = 10.3$–10.9,
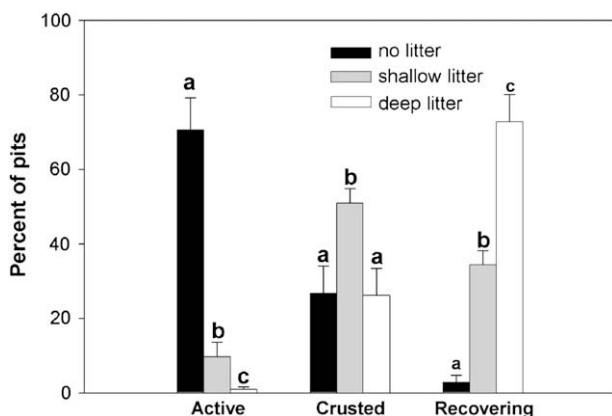

Fig. 1. Percentage of pits associated with active, crusted and recovering mounds containing three levels of litter. Within each mound type, different letters indicate a significant difference at $P < 0.05$. Bars indicated standard error of the mean.
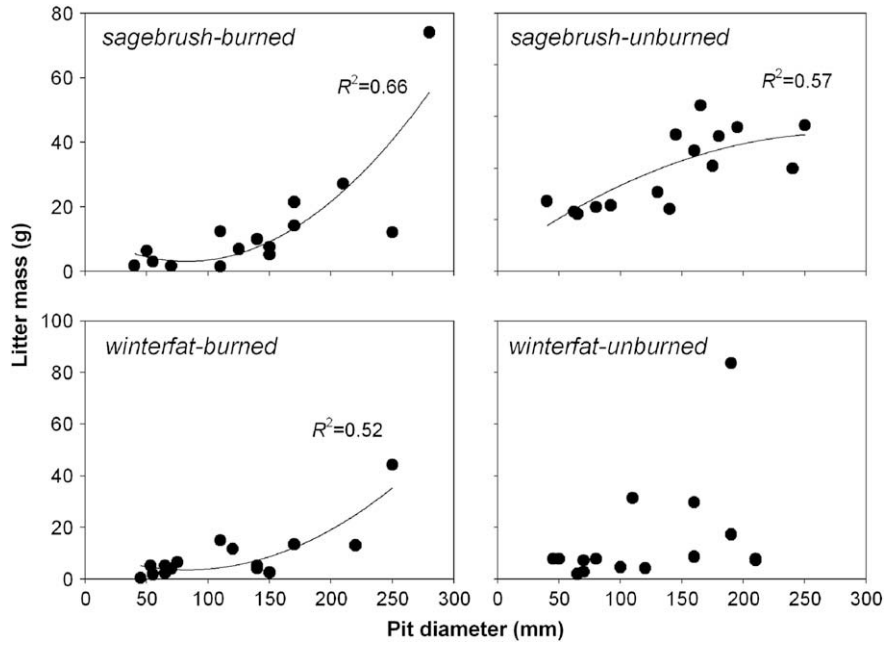
Fig. 3. Relationships between the diameter of the pit opening (mm) and the mass of trapped litter (g) for burned and unburned sagebrush and winterfat communities.
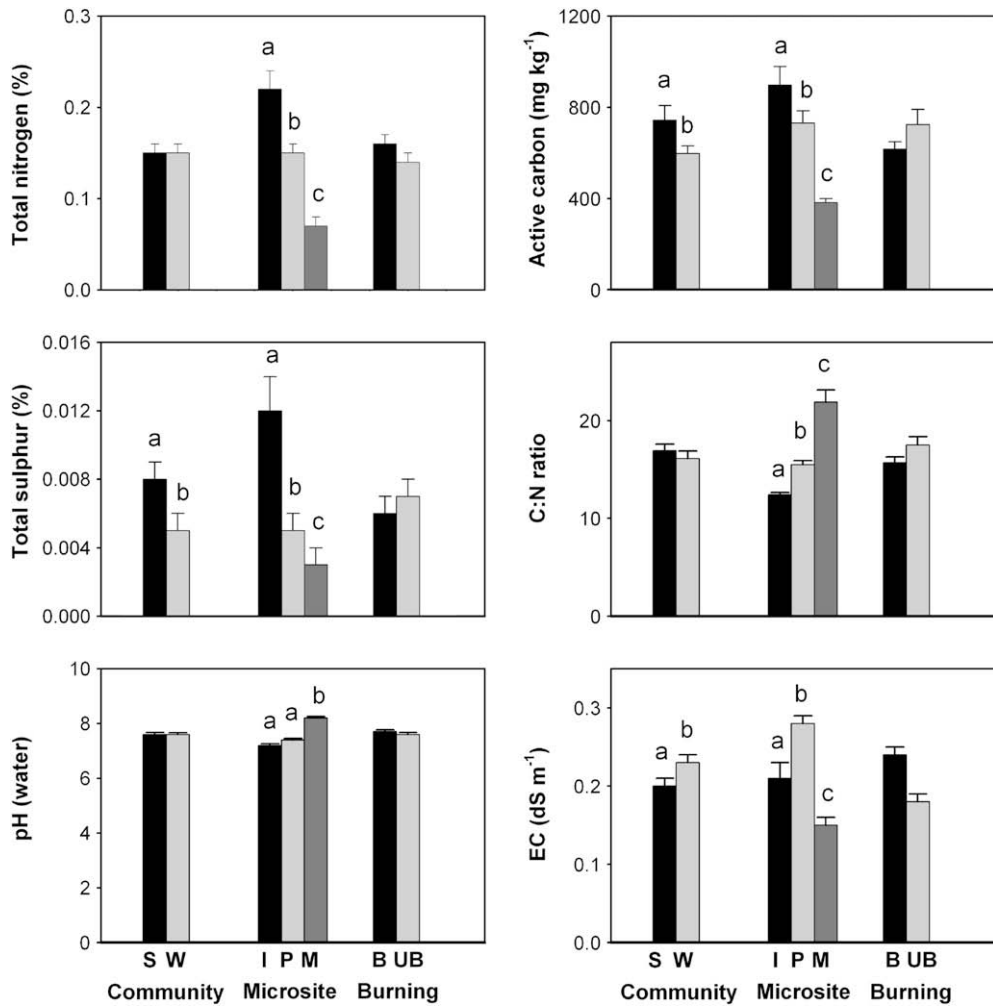

Fig. 4. Total nitrogen (%), active carbon (mg kg^{-1}), total sulphur (%), C:N ratio, pH and EC (dS m^{-1}) of soils in relation to vegetation community, microsite, and burning status. Community: S = sagebrush, W = winterfat. Microsite: I = inter-mound, P = pit, M = mound. Burning status: B = burned, UB = unburned. Different letters within a community, microsite or burning status indicate a significant difference at $P < 0.05$. Letters for non-significant comparisons have been omitted. Bars indicate standard error of the mean.
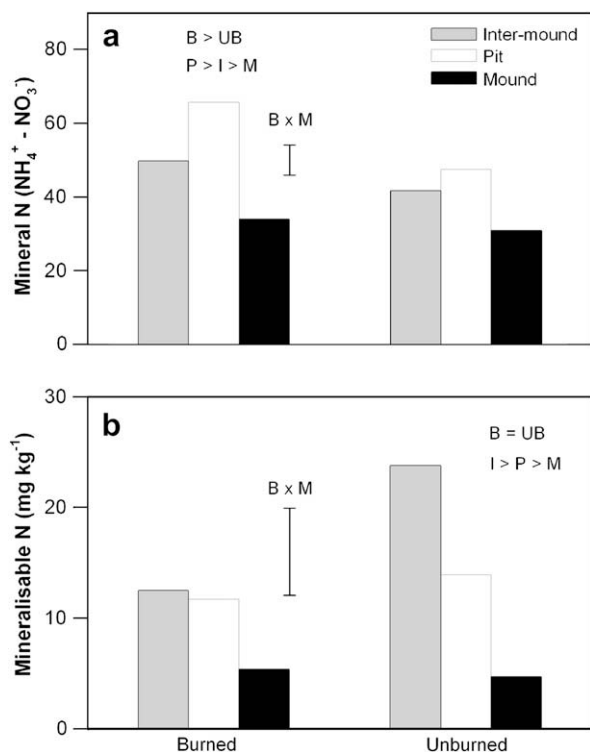
Fig. 5. Mineral N ($NH_4^+ - NO_3^-$) and mineralizable (available) N concentrations in relation to burning treatment (B) and microsite (M). Burning status: B = burned, UB = unburned. Microsite: I = inter-mound, P = pit, M = mound. The 5% LSD for the burning by microsite (B × M) interaction is shown.

$P = 0.001$, Table 2) consistent with an increase in Na^+ concentration with depth (Table 1). Concentrations of exchangeable Ca^{2+} were greater in the mound and pit soils compared with inter-mounds soils ($F_{2,112} = 15.9$, $P < 0.001$). However, while this difference was quite marked in sagebrush soils, there was little difference in winterfat soils (vegetation community × microsite interaction: $F_{2,112} = 7.16$, $P < 0.001$). Exchangeable K^+ declined from mound to inter-mound soils ($F_{2,112} = 4.42$, $P = 0.014$), particularly in sagebrush, but less so in winterfat soils (vegetation community × microsite interaction: $F_{2,112} = 3.75$, $P = 0.027$). There were no significant differences in exchangeable Mg^{2+} in relation to microsite, vegetation community or burning treatment (Table 2).
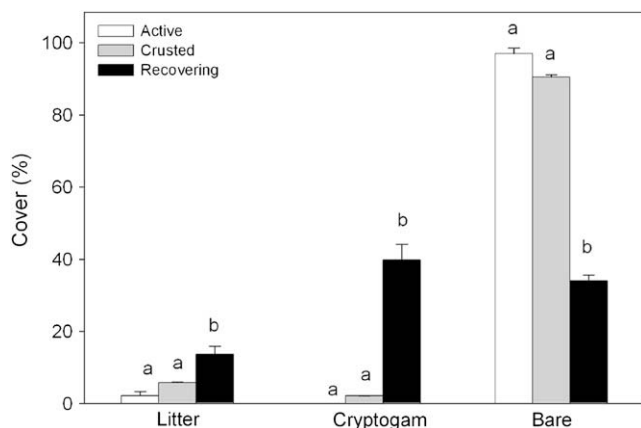

Fig. 6. Mean (±SEM) cover (%) of litter, cryptogamic crusts and bare soil on active, crusted and recovering mounds. Within a cover component, different letters indicate a significant difference in cover at $P < 0.05$.

4. Discussion

Soil disturbance by mammals is an important ecosystem process that reinforces spatial heterogeneity, particularly in arid areas where essential resources such as water and nutrients are distributed in patches within an infertile matrix (Boeken et al., 1995; Kinlaw, 1999; Whitford and Kay, 1999). Digging by badgers enhanced the deposition of litter and fine soil particles, and altered soil physico-chemical properties across the shrub-steppe landscape. Mounds had lower levels of biologically-derived nutrients, and active mounds supported a reduced cover of cryptogams and vascular plants compared with the older recovering mounds or inter-mound surfaces.

Reductions in total, mineral and mineralizable N in mound soils are attributed to the translocation of N-poor subsoil (Table 1) to the surface, consistent with observations of lower concentrations of N and C in the mounds of many fossorial and semi-fossorial animals worldwide (Eldridge and Koen, 2008; Eldridge and Myers, 2000; Whitford and Kay, 1999). Differences in available N were more pronounced in the unburned treatments, consistent with our third hypothesis, and largely as a result of the greater levels of available N in the unburned, inter-mound soils. However, while more litter corresponded with more total N, it was not a significant predictor of mineral N or mineralizable N, only partly supporting our second hypothesis. The poor relationship between litter mass, mineral N and mineralizable N could be attributed to complex mineralization processes in the pits and the leaching of nitrate resulting from melting snow trapped in the pits.

Mound soil had a spectrum of particle sizes comparable to soil at depths of 40–80 cm, supporting our third hypothesis. Apart from the direct effects of digging on soil nutrients (e.g. Inouye et al., 1997), lower concentrations of mineralizable N in animal mounds have been attributed to the incorporation of calcareous subsoil transported to the surface by animals (Carlson and White, 1988). The smooth, concave surface of the mounds with few surface cracks more than a few millimeters wide, combined with the extensive sealing of the mound surface, would have mitigated against any retention of organic matter on the mound surface.

Exchangeable Ca^{2+} and Na^+ concentrations were greater in crusted mound soils compared with inter-mound soils (Table 2), similar to observations of the mounds of pocket gophers (Thomomys spp., Kerley et al., 2004). Badgers readily penetrate layers of indurated calcrete while excavating their prey (Chew, 1979), transporting Ca^{2+}-adsorbed soil to the surface, thereby increasing Ca^{2+} ion concentrations. The greater exchangeable Ca^{2+} and K^+ in mound soils in the sagebrush community (inconsistent with our third hypothesis) could be related to inherent differences in soils or the depth to calcrete horizons between the two communities. Increased exchangeable Na^+ in mound soils is consistent with an increase in Na^+ concentrations with depth (Table 1) and could also be due to redistribution by wind and water (Schlesinger et al., 1996) from beneath shrub canopies. Higher base saturation, i.e. a greater concentration of exchangeable Na^+ and Ca^{2+} in mound soils would also account for the higher pH levels observed in the mound soils. Increasing surface pH could also result from the effects of digging on soil aeration, mixing of litter, and increased microbial activity (Malizia et al., 2000), though this could have been offset by higher respiration rates. Higher pH is likely to have flow on effects to soil mineralization processes and plant composition on the warrens, favoring some species that require higher pH soils. Potassium is a very mobile monovalent cation and is easily leached in soils with a high infiltration capacity (Kerley et al., 2004). Given the low levels of infiltration recorded on badger mounds (Eldridge, in press), low concentrations of soluble and exchangeable K on the mounds are not unexpected.

Notwithstanding the observations of low nutrient concentrations in mounds soils, many studies have reported higher nutrient

Table 2
Mean (±SEM) soluble and exchangeable soil cations for the mounds by vegetation community, microsite and burning treatment.

| | Vegetation community | | | | Microsite | | | | | | Burning treatment | | | |
| | Sagebrush | | Winterfat | | Inter-mound | | Pit | | Mound | | Burned | | Unburned | |
	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
Soluble cations														
Ca (cmol (+) kg^{-1})	0.573[a]	0.023	0.641[a]	0.041	0.537[a]	0.072	0.800[b]	0.114	0.484[a]	0.049	0.684[a]	0.041	0.530[b]	0.021
K (cmol (+) kg^{-1})	0.215[a]	0.013	0.320[a]	0.021	0.303[a]	0.045	0.309[a]	0.055	0.191[b]	0.042	0.334[a]	0.021	0.201[a]	0.011
Mg (cmol (+) kg^{-1})	0.236[a]	0.009	0.243[a]	0.011	0.224[a]	0.023	0.306[b]	0.031	0.197[c]	0.016	0.268[a]	0.011	0.217[a]	0.008
Na (cmol (+) kg^{-1})	0.244[a]	0.044	0.157[a]	0.029	0.065[a]	0.013	0.188[b]	0.070	0.349[c]	0.155	0.226[a]	0.042	0.176[a]	0.033
Exchangeable cations														
Ca (cmol (+) kg^{-1})	14.010[a]	0.353	13.165[a]	0.203	12.865[a]	0.743	13.751[b]	0.727	14.149[b]	0.872	14.275[a]	0.286	12.900[a]	0.278
K (cmol (+) kg^{-1})	1.607[a]	0.069	2.013[b]	0.087	1.948[a]	0.185	1.790[b]	0.181	1.692[b]	0.282	2.158[a]	0.092	1.463[b]	0.044
Mg (cmol (+) kg^{-1})	3.674[a]	0.106	2.998[a]	0.061	3.296[a]	0.191	3.276[a]	0.224	3.437[a]	0.330	3.244[a]	0.061	3.428[a]	0.116
Na(cmol (+) kg^{-1})	0.279[a]	0.058	0.142[a]	0.026	0.080[a]	0.012	0.140[a]	0.036	0.410[b]	0.201	0.230[a]	0.056	0.190[a]	0.032

For each mound attribute, differences letters within a community, mound type or burning treatment indicate a significant difference at $P < 0.05$.

concentrations in areas where fossorial animals congregate (Whitford and Kay, 1999). However, increased nutrients are generally restricted to either soil types where nutrient concentrations or cation exchange increase with depth, or foraging pits and diggings used regularly by animals for bedding, nesting or feeding (Dean and Milton, 1991; Eldridge and Rath, 2002; Huntly and Inouye, 1988). Badgers occasionally cache food within their digs (Michener, 2000), but this is infrequent, and is unlikely to lead to prolonged buildup of nutrients. Bedding sites, however, will naturally contain fecal accumulations and decomposing plant and animal tissue, and are therefore likely to generate greater concentrations of soil organic matter and biologically-derived nutrients. However, as badger mounds are not occupied by the animals themselves, nutrient concentrations are unlikely to reach levels found within structures used by colonial fossorial animals, which may be many decades old (e.g. Dean and Milton, 1991; Kinlaw, 1999).

Ground squirrels, the principal prey item of badgers, also cache material in their burrows (Yensen et al., 1992). Excavation of ground squirrel holes and their larders by badgers, and the scattering of larder material could potentially increase levels of soil nutrients in the pits, though the extent of this can only be speculated upon. Nevertheless, ground squirrel burrow entrances occurred at an average density of about 1500 holes ha^{-1} in the inter-mound areas (Eldridge, 2004), and the combined effect of their burrowing entrances and inter-mound vegetation could be to enhance the chemical fertility of the inter-mound areas and heighten the differences between badger mound and inter-mound soils. Similarly, burrowing owls gather dung and distribute it in and around their nests in badger burrows and this is known to attract dung beetles (*Phanaes* spp. Levey et al., 2004). Recent research from the Snake River Plain in west-central Idaho has shown that dung affects the microclimate in burrowing owl burrows dug into badger pits through its effect on decreased CO_2 concentrations (James Beltoff, personal communication, 2006). Dung may also represent local accumulations of nutrients from ingested beetles and regurgitated owl pellets, and the contribution to local nutrient pools could be substantial across small spatial scales, particularly where natural soil nutrients are already low.

Consistent with our first hypothesis, pits trapped a substantial mass of litter. Pits with larger openings trapped more litter, particularly on the burned sites, suggesting to us that pits are important for retaining litter in areas that would otherwise be resource-poor. Despite the dense cover of cheatgrass, which is known to produce large quantities of litter (Norton et al., 2004), surface-resident litter was sparse at the burned sites. Our observations at burned sites indicate that, apart from a few residual shrubs and their associated hummocks that had escaped fire, there were few surface obstructions available to trap and retain organic

material on-site. Thus although less litter was trapped in pits at the burned (890 g m^{-2}) compared with the unburned (1459 g m^{-2}) sites, pits at burned sites were crucial sites of resource accumulation. The extent to which pits contribute to landscape-level differences in litter production is amplified when one considers *per capita* pit construction, estimated conservatively at 1100–1700 year^{-1} (Eldridge, 2004), and their longevity. Alometric relationships between pit size and longevity for a range of fossorial mammals suggest that average sized pits will persist for up to 4 years (Whitford and Kay, 1999). We maintain therefore that, along with mounds, pits are important long-lived structures in dysfunctional landscapes, and in fire-ravaged shrub-steppe ecosystems, their contribution to the development of spatial patchiness could be substantial.

Soil directly beneath litter in the pits contained approximately twice the concentrations of active C and total N, 75% more mineral N, and 150% more mineralizable N compared with mound soils, consistent with our first hypothesis. The trapping of litter in pits will likely lead to short-term, to immobilization of N (Zaady et al., 1996), though decomposition over longer periods will provide a slow release of N, unlike the rapid short-duration flush of N following rainfall in desert systems. Thus pit-resident litter may sustain soil microbial biomass for longer periods, allowing plant growth to persist later into the season (Zaady et al., 1996). Similarly, higher levels of soil moisture, due in part to greater water storage after rainfall and snow melt in pits (e.g. Laundré, 1993) will likely extend the period over which microbial decomposition of organic matter is maximized (Steinberger and Whitford, 1983).

A direct effect of digging was to increase the erodible fraction of the soil by breaking relatively large non-erodible aggregates into highly erodible micro-aggregates (<0.84 mm in diameter). Recently excavated mounds remain erodible until the first rains or heavy frost harden the surface into a physical, raindrop-impacted crust. Although wind storms probably winnow fine material (<250 μm) from mound soils, our data suggest that these particle sizes accumulate in the pits, which, we argue, represent the only substantial resource traps at many sites. Digging by badgers also destroys the stable, biological soil crusts that dominate the inter-mound surfaces (Hilty et al., 2004), and would be expected to change crust composition from one dominated by mosses and lichens to one dominated by cyanobacteria. While cyanobacteria provide some soil protection against raindrop impact, recovery of the lichen- and moss-dominant surface is likely take many years (Hilty et al., 2004).

Overall, our results demonstrate a depletion of essential resources (nutrients, sediment) on mounds compared with either the pits or inter-mound surfaces. We argue that badger mounds and their associated pits provide the only substantial structure in post-fire sagebrush steppe, where shrubs and their associated

hummocks have largely been eliminated, and believe that they may have a role in the restoration of degraded shrublands. In burned environments, pits obstruct the flow of resources, trapping wind-borne organic matter and fine soil particles such as silt and clay, which would normally be captured by shrubs and their hummocks. Pits also trap water and are likely sites of fungal decomposition (Cortinas and Seastedt, 1996; Sherrod and Seastedt, 2001). Finally, preliminary observations suggest that the density and biomass of *Bromus tectorum* are substantially lower on mounds compared with inter-mounds, and that older recovering mounds are sites of reestablishment of *Krascheninnikovia* and *Poa secunda*. It is logical to expect that native plants will have a competitive advantage over exotic annuals such as *Bromus tectorum* on mound soils where nitrogen is immobilized (*sensu* Paschke et al., 2000) by the relatively high soil C:N ratio ($\sim$25:1).

Acknowledgements

References

Boeken, B., Shachak, M., Gutterman, Y., Brand, S., 1995. Patchiness and disturbance: plant community responses to porcupine diggings in the central Negev. Ecography 18, 410–422.

Brooks, M.L., D'Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.M., DiTomaso, J.M., Hobbs, R.J., Pellant, M., Pyke, D.A., 2004. Effects of invasive alien plants on fire regimes. BioScience 54, 677–688.

Carlson, D.C., White, E.M., 1988. Effects of prairie dogs on mound soils. Soil Science Society of America Journal 51, 389–393.

Chew, R.M., 1974. Consumers as regulators of ecosystems: an alternative to energetics. Ohio Journal of Science 74, 359–370.

Chew, R.M., 1979. Mammalian predation on honey ants, *Myrmecocystus* (Formicidae). The Southwestern Naturalist 24, 677–682.

Collett, R.A., 1980. Soil survey of Ada County area, Idaho. U.S. Department of Agriculture, Soil Conservation Service.

Dean, W.R.J., Milton, S.J., 1991. Disturbances in semi-arid shrubland and arid grassland in the Karoo, South Africa: mammal diggings as germination sites. African Journal of Ecology 29, 11–16.

Desmond, M.J., Savidge, J.A., Eskridge, K.M., 2000. Correlations between burrowing owl and black-tailed prairie dog declines: a 7-year analysis. Journal of Wildlife Management 64, 1067–1075.

Eldridge, D.J., 2004. Mounds of the American Badger (*Taxidea taxus*): significant features of North American shrub-steppe ecosystems. Journal of Mammalogy 85, 1060–1067.

Eldridge, D.J., Badger (*Taxidea taxus*) mounds affect soil physical and hydrological properties in a degraded shrub-steppe. American Midland Naturalist (in press).

Eldridge, D.J., Koen, T.B., 2008. Formation of nutrient-poor soil patches in a semi-arid woodland by the European rabbit (*Oryctolagus cuniculus* L.). Austral Ecology 33, 88–94.

Eldridge, D.J. Myers, C.A., 2000. The impact of warrens of the European rabbit (*Oryctolagus cuniculus* L.) on soil and ecological processes in a semi-arid Australian woodland. Journal of Arid Environments 47, 325–337.

Eldridge, D.J., Rath, D., 2002. Hip holes: kangaroo resting sites enhance the physical and chemical environment of woodland soils. Austral Ecology 27, 527–536.

Gianello, C., Bremner, J.M., 1986. Comparison of chemical methods of assessing potentially available nitrogen. Communications in Soil Science and Plants 17, 215–236.

Green, G.A., Anthony, R.G., 1989. Nesting success and habitat relationships of burrowing owls in the Columbia River Basin, Oregon. Condor 91, 347–354.

Hilty, J.H., Eldridge, D.J., Rosentreter, R., Wicklow-Howard, M.C., Pellant, M., 2004. Recovery of biological soil crusts following wildfire on the Snake River Plain, Idaho. U.S.A. Journal of Range Management 57, 89–96.

Huntly, N., 1988. Pocket gophers in ecosystems: patterns and mechanisms. BioScience 38, 786–793.

Inouye, R.S., Huntly, N., Wasley, G.A., 1997. Effects of pocket gophers (*Geomys bursarius*) on microtopographic variation. Journal of Mammalogy 78, 1144–1148.

Jones, C.G., Lawton, J.H., Shachak, M., 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78, 1946–1957.

Kerley, G.I.H., Whitford, W.G., Kay, F.R., 2004. Effects of pocket gophers on desert soils and vegetation. Journal of Arid Environments 58, 155–166.

Kinlaw, A., 1999. A review of burrowing by semi-fossorial vertebrates in arid environments. Journal of Arid Environments 41, 127–145.

Krogh, S.N., Zeisset, M.S., Jackson, E., Whitford, W.G., 2002. Presence/absence of a keystone species as an indicator of rangeland health. Journal of Arid Environments 50, 513–519.

Laundré, J.W., 1993. Effect of small mammal burrows on water infiltration in a cool desert environment. Oecologia 94, 43–48.

Levey, D.J., Duncan, R.S., Levins, C.F., 2004. Animal behaviour: use of dung as a tool by burrowing owls. Nature 431, 39.

Mack, R.N., 1981. Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. Agro-Ecosystems 7, 145–165.

Malizia, I., Kittlein, M.J., Busch, C., 2000. Influence of subterranean herbivorous rodent (*Ctenomys talarum*) on vegetation and soil. Zeitschrift für Säugetierkunde 65, 172–182.

Messick, J.P., Hornocker, M.G., 1981. Ecology of the Badger in southwestern Idaho. Wildlife Monographs, 5–53.

Michener, G.R., 2000. Caching of Richardson's ground squirrels by North American badgers. Journal of Mammalogy 81, 1106–1117.

Miller, B., Ceballos, G., Reading, R., 1994. The prairie dog and biotic diversity. Conservation Biology 8, 677–681.

Minitab, 2003. References Manual, Release 14. Minitab Inc., State College Pennsylvania.

Norton, J.B., Monaco, T.A., Norton, J.M., Johnson, D.A., Jones, T.A., 2004. Soil morphology and organic matter dynamics under cheatgrass and sagebrush-steppe plant communities. Journal of Arid Environments 57, 445–466.

Paschke, M.W., McLendon, T., Redente, E.F., 2000. Nitrogen availability and old-field succession in a shortgrass steppe. Ecosystems 3, 144–158.

Platt, W.J., 1975. The colonization and formation of equilibrium plant species associations on badger disturbances in a tall-grass prairie. Ecological Monographs 45, 285–305.

Schlesinger, W.H., Raikes, J.E., Hartley, A.E., Cross, A.F., 1996. On the spatial pattern of soil nutrients in desert ecosystems. Ecology 77, 364–374.

Schooley, R.L., Bestelmeyer, B.T., Kelly, J.F., 2000. Influence of small-scale disturbances by kangaroo rats on Chihuahuan Desert ants. Oecologia 125, 142–149.

Sherrod, S.K., Seastedt, T.R., 2001. Effects of the northern pocket gopher (*Thomomys talpoides*) on alpine soil characteristics, Niwot Ridge, CO. Biogeochemistry 55, 195–218.

Steinberger, Y., Whitford, W.G., 1983. The combination of rodents to decomposition processes in a desert ecosystem. Journal of Arid Environments 6, 177–181.

Tardiff, S.E., Stanford, J.A., 1998. Grizzly bear digging: effects on subalpine meadow plants in relation to mineral nitrogen availability. Ecology 79, 2219–2228.

Voslamber, B., Veen, A.W.L., 1985. Digging by badgers and rabbits on some wooded slopes in Belgium. Earth Surface Processes and Landforms 10, 79–82.

Wambolt, C., Walhof, K., Frisina, M., 2001. Recovery of big sagebrush communities after burning in south-western Montana. Journal of Environmental Management 61, 243–252.

Weil, R.R., Islam, K.R., Stine, M.A., Gruver, J.B., Samson-Liebig, S.E., 2002. Estimating active carbon for soil quality assessment: a simplified method for laboratory and field use. American Journal of Alternative Agriculture 18, 1–15.

Whitford, W.G., 2002. Ecology of Desert Ecosystems. Academic Press, San Diego.

Whitford, W.G., Kay, F.R., 1999. Biopedturbation by mammals in deserts: a review. Journal of Arid Environments 41, 203–230.

Wright, J.P., Jones, C.J., 2004. Predicting the effects of ecosystem engineers on patch-scale species richness from primary productivity. Ecology 85, 2071–2081.

Yensen, E., Quinney, D.L., Johnson, K., Timmerman, K., Steenhof, K., 1992. Fire, vegetation changes and population fluctuations of Townsend's ground squirrels. American Midland Naturalist 128, 299–312.

Zaady, E., Groffman, P.M., Shachak, M., 1996. Litter as a regulator of N and C dynamics in macrophytic patches in the Negev desert soils. Soil Biology and Biochemistry 28, 39–46.