Soil Disturbance by Invertebrates in a Semi-arid Eucalypt Woodland: Effects of Grazing Exclusion, Faunal Reintroductions, Landscape and Patch Characteristics

David J. Eldridge[1], Niki Huang[1], Jocelyn Bentley[2] and Matthew W. Hayward[2]

[1]Evolution and Ecology Research Centre, Office of Environment and Heritage, c/- School of Biological, Earth and Environmental Sciences, University of NSW, Sydney, NSW, 2052, Australia. d.eldridge@unsw.edu.au
[2]Australian Wildlife Conservancy, Scotia Sanctuary, c/- P.O. Wentworth, NSW 2648, Australia

Published on 28 August 2012 at http://escholarship.library.usyd.edu.au/journals/index.php/LIN

Eldridge, D.J., Huang, N. and Hayward, M.W. (2012). Soil disturbance by invertebrates in a semi-arid eucalypt woodland: effects of grazing exclusion, faunal reintroductions, landscape and patch characteristics. *Proceedings of the Linnean Society of New South Wales* **134**, A11-A18.

Soil disturbing invertebrates are common elements of arid and semi-arid landscapes. Disturbances such as burrows, nest entrances, emergence holes and mounds of ejecta soil have large, but often poorly understood, effects on ecosystem properties and processes as broad as pedogenesis, soil movement and water infiltration. We examined disturbances created by a range of invertebrates in a semi-arid eucalypt woodland in eastern Australia in relation to three levels of disturbance varying from areas currently grazed by domestic herbivores to those where domestic herbivores have been removed, with and without the reintroduction of locally-extinct omnivorous native mammals. Overall, the tunnels and ejecta soil from ant nests comprised 80% of all invertebrate disturbances across all sites and treatments. There were significantly more invertebrate disturbances at sites where domestic herbivores had been excluded, more disturbances on dunes and in the swales than on plains, and more under shrubs than under trees. The cover of disturbances by invertebrates tended to increase with increasing cover of disturbance by native vertebrates, but only under exclosure where no locally-extinct native mammals had been reintroduced. Our results indicate that invertebrate-created disturbances are a common feature of semi-arid woodland soils, and that management activities, such as grazing and the reintroduction of locally-extinct vertebrates, will affect their density, potentially influencing a range of ecosystem processes.

Manuscript received 4 November 2011, accepted for publication 22 December 2011.

KEYWORDS: biogeomorphology, bioturbation, eucalypt, foraging, soil disturbance, invertebrates, shrubland, soil movement.

INTRODUCTION

Arid and semi-arid landscapes function most effectively when limited resources, such as water, seed, sediment and nutrients, are concentrated within patches (fertile patches; Noy-Meir 1973). This patchiness exists at a range of spatial scales, from landscapes to microsites, with smaller patches often nested within larger patches within a hierarchy (Kotliar and Weins 1990). Different organisms respond to these different scales of patchiness, consistent with their body size and behaviour (e.g. foraging and reproductive; Vanbergen et al. 2007). Thus larger animals generally respond to coarse or intermediate scales (Jackson et al. 2003) while smaller animals, such as invertebrates, are more responsive to changes at finer scales (e.g. Martin and Major 2001; Whitehouse et al. 2002). Similarly, habitat complexity is known to affect insect diversity (Barton et al. 2010) and has been shown to alter the foraging success of ants across a range of environments (Gibb and Parr 2010).

Animals respond not only to changes in patch size and configuration but also create and maintain their own patches. For example, depressions in the soil surface created by burrowing vertebrates can trap seed, litter and animal faeces, which are often subsequently covered by eroded soil (Whitford and Kay 1999). The construction of burrows, pits and mounds by both vertebrates and invertebrates can alter soil physical and chemical properties such as texture, structure, fertility and infiltration rate (Whitford 2002) and enhance the germination and establishment of vascular plants (James et al. 2011), creating new patches or expanding existing patches (Whitford and Kay 1999). The burrows and emergence holes of soil surface-active invertebrates can act as macropores, enhancing the infiltration of water into the subsoil, and affecting landscape–level differences in soil moisture (Elkins et al. 1986, Holt et al. 1996), soil and nutrient redistribution (Nkem et al. 2000), and the development of substantial soil biomantles (Johnson 1990).

Changes in soil surface environments resulting from the activity of vertebrates can also influence the spatial distribution and abundance of other organisms such as invertebrates (Huntly & Inouye 1988; Whicker & Detling 1988; Ceballos et al. 1999; Kretzer & Cully 2001). Alteration of the physical and chemical environment of the soil surface may extend the habitat of other animals, such as occurs when, for example, prairie dog (*Cynomys* spp.) engineered soil surfaces advantage foraging by tenebrionid beetles (Bangert and Slobodchikoff 2006). Soil disturbance by vertebrates may benefit smaller animals such as ants by creating open habitat (e.g. Borchard and Eldridge 2011). Similarly, grazing-induced disturbance by livestock can affect the distribution, abundance, and diversity of soil-disturbing organisms, often in unknown directions (Nash et al. 2001).

We compared soil disturbances created by a broad suite of surface-active invertebrates at sites ungrazed by domestic livestock (with and without the reintroduction of locally–extinct soil foraging animals), with sites that are currently and heavily grazed by sheep, cattle and goats. Specifically, our objective was to determine how three different land management practices influenced soil disturbance by invertebrates, and whether this varied among different landforms (dune, swale, plain), patch types (shrub, tree) and positions within a patch type, i.e. sites ranging from close to the canopy to the open. Our three predictions were that: (1) density of disturbances created by invertebrates (mounds, depressions, emergence holes and burrows of ants, termites, scorpions, spiders, termites, ant lions, cicadas and beetles) would vary very little across the land management gradient; (2) the density of invertebrate disturbances would be most responsive to changes at small spatial scales (e.g. patch type, e.g. shrub *vs* tree) and position within the canopy than in relation to larger landscape – scale differences (e.g. dune vs swale). Given that native insectivorous vertebrates are known to prey on epigeal invertebrates such as scorpions and lycosid spiders (e.g. Southgate 1990, we expected that (3) there would be relatively strong relationships between the densities of invertebrates and their vertebrate predators. We tested these predictions in a mallee eucalypt woodland across three grazing-induced treatments.

METHODS

The study site

The study was carried out at the Scotia Sanctuary and adjacent grazing properties. Scotia is a 64, 653 ha property approximately 150 km south-west of Broken Hill, Australia (33°12'S, 141°10'E). We restricted our study to three different landscapes characterised by 1) linear dunes dominated by eucalypts; 2) inter-dunal swales; 3) plains with a variable cover of trees. The dunes were predominantly west-east trending, of Quaternary alluvium, and characterized by calcareous and siliceous sands (Rudosols). They were separated by inter-dunal swales and plains, up to 500 m wide, of loamy, calcareous soils (Calcarosols). Vegetation on the dunes is dominated by open mallee (*Eucalyptus* spp.) woodland with a spinifex (*Triodia scariosa* ssp. *scariosa*) understorey and a variable cover of shrubs such as punty bush (*Senna artemisioides*) and narrow-leaved hopbush (*Dodonaea viscosa).* The plains vegetation is dominated by scattered belah (*Casuarina pauper*) and sugarwood (*Myoporum platycarpum*), and a variable cover of punty bush, hopbush, turpentine (*Eremophila sturtii*), pinbush wattle (*Acacia burkittii*) and assorted bluebushes (*Maireana* spp.). The climate is semi-arid, with cool winters (mean ≤ 17°C) and hot summers (mean 30°C). Rainfall over the period 1996 to 2011 averaged 244 mm yr^{-1}.

Experimental design

In December 2006, we surveyed all soil surface disturbances created by animals that forage in the soil or create burrows, nests or resting sites on the surface. Our survey was carried out within two large exclosures at the Scotia Sanctuary, Stage I (termed '*Reintroduction*') and Stage II (*'Exclosure'*), both of which are feral animal free and ungrazed by domestic livestock. A third treatment was located on adjoining pastoral properties, which are grazed by sheep and cattle and contained variable populations of rabbits (*Oryctolagus cuniculus*) and foxes (*Vulpes vulpes*; termed *'Pastoral'*). At the time of the study, locally-extinct mammals such as the greater bilby (*Macrotis lagotis*) and the burrowing bettong (*Bettongia lesueur*) had been reintroduced into Stage I but not Stage II. All three treatment types, however, contained variable populations of the short-beaked echidna (*Tachyglossus aculeatus*) and Gould's sand goanna (*Varanus gouldii*), both of which also disturb the soil while foraging for food. European rabbits also occurred in the *Pastoral* sites. Because there is only one example of *Reintroduction* and *Exclosure* and it was not possible to replicate the treatments elsewhere, the design is therefore pseudoreplicated, and does not allow generalisation about the effects of ecosystem engineers beyond the study site. Nevertheless, this single site represents a valuable opportunity to gain information about the effects of locally extinct native animals on the structures created by invertebrates.

Field measurements

Within these three treatment areas, we assessed all animal disturbances on three landform elements (dunes, swales, plains) and within two patch types (tree, shrub) along 2–m wide transects extending from the base of each tree or shrub. Each transect was adjusted to be three times the radius of the canopy to account for different-sized trees and shrubs. Along this transect, we identified four zones: 1) trunk (0.25 x canopy radius), 2) mid-canopy (0.5 x canopy radius), 3) canopy edge (1 x canopy radius) and 4) open (1.75 x canopy radius). A total of 126 transects was measured, representing the three treatments by three landform elements (dune, swale, plain) by two macro-patch types (tree, shrub), with seven replicate transects. Measurement sites were selected so that they were evenly distributed over each of the three treatments and within 200 m of roads (for ease of access). Sites in the *Pastoral* treatment were at least 5 km from water, and other areas of excessive stock trampling were avoided e.g. near holding paddocks.

For each disturbance type, we measured the following: length and width of all pits, burrows and depressions, and the type of animal that created each disturbance (bilby/bettong, goanna, echidna, rabbit, ant, ant lion, beetle, kangaroo, scorpion, skink, spider, termite) in relation to the various nested patch types in which the disturbances occurred. Litter was carefully removed from the soil surface in order to record any animal disturbances that might have been present below the litter. These measurements were used to calculate the density of structures and their areas. While the emphasis in this paper is on invertebrate disturbances, we also report data on the density of vertebrate disturbances (Eldridge et al. 2011b) in order to examine possible relationships between vertebrate and invertebrate disturbances.

Statistical analyses

Differences in the density and cover of disturbances of the total suite of invertebrates, in relation to the three treatments, landform element, patch type and position in relation to the canopy, were analysed using a mixed-models General Linear Models ANOVA with three error terms. The first stratum considered treatment, landform element and their interaction, the second stratum patch and its two- and three-way interactions with treatment and landform, and the third stratum distance from the trunk and its two-, three- and four way interactions with the other factors. Data were transformed to a density per square metre of canopy location in order to standardise between the different sampling areas beneath the canopies of the various sized trees and shrubs. Data were checked for homogeneity of variance and normality (Minitab 2007) prior to analysis, and in most cases, $\log_{10}(X+1)$ or √–transformed to standardise the residuals prior to ANOVA. We used linear regression analyses (Minitab 2007) to determine possible relationships between the density of invertebrate and vertebrate disturbances for all factors, averaged across the four canopy locations (*n*=126).

RESULTS

We recorded significantly more disturbances by invertebrates in Scotia Stages I (*Reintroduction*) and II (*Exclosure*), where domestic livestock had been excluded, than where domestic grazing animals occurred (Pastoral: $F_{2,54}$=8.64, P=0.001). We also recorded more disturbances on dunes and in the swales than on plains ($F_{2,54}$=6.40, P=0.003; Figure 1A), and more disturbances around and under shrubs than trees ($F_{1,54}$=48.68, P<0.001; Figure 1B). The number of disturbances increased with increasing distance from the trunks of trees, but there were no clearly-defined trends out from the trunks of shrubs (Patch type x Distance from trunk interaction: $F_{3,324}$=10.91, P<0.001, Figure 1B). Overall, trends in relation to cover of disturbances under shrub and tree canopies were the same as for density (data held by the senior author and not shown). Further, most of the effects were due to differences in the number of disturbances by ants, which constituted about 80% of all invertebrate structures across all sites and treatments. We expected that some invertebrate burrows might occur within foraging pits or mounds of soil ejected from the pits of vertebrates, suggesting a shared habitat preference. Over all sites and quadrats,

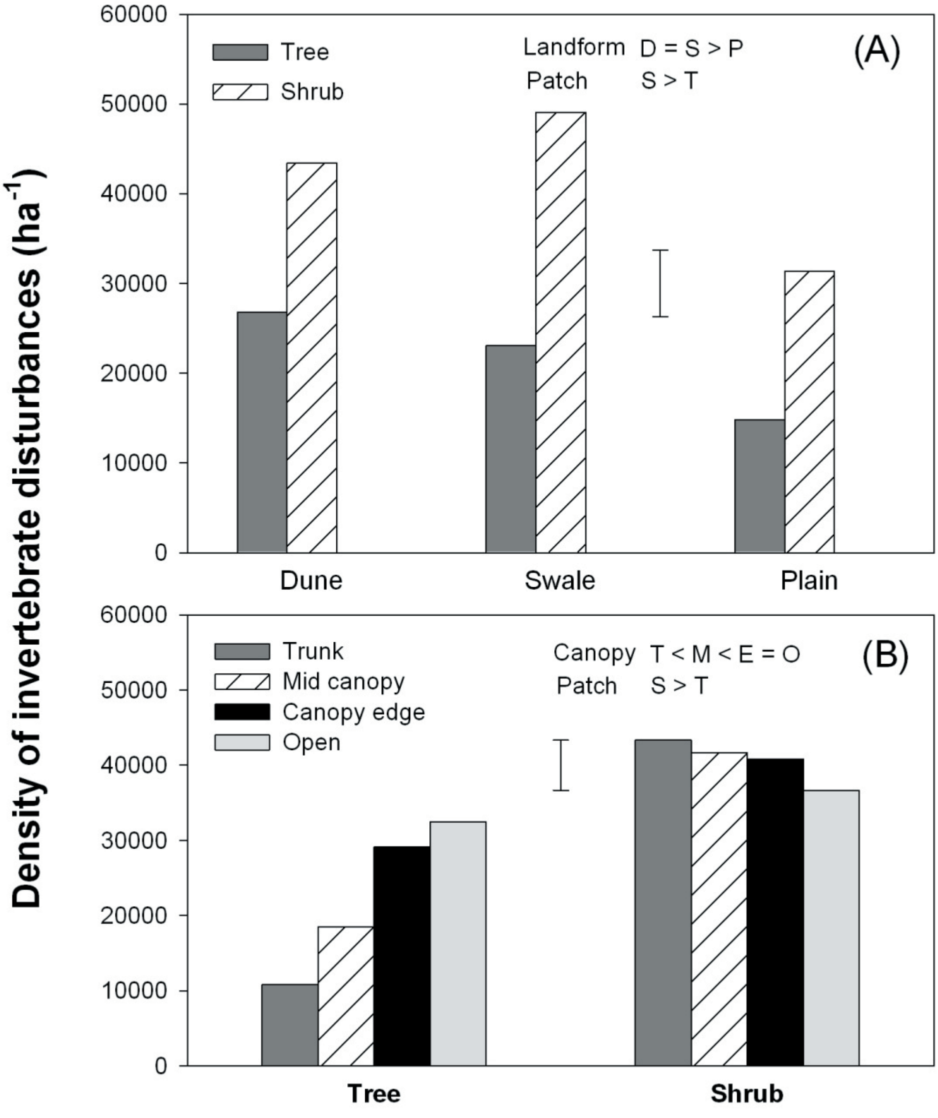

Figure 1. Mean density of disturbances (ha^{-1}) created by invertebrates in relation to (A) Landform (D = dune, S = swale, O = open) and Patch type (T = tree, S = shrub), and (B) Patch type (T = tree, S = shrub) and location within the canopy (T = trunk, M = mid-canopy, C = canopy edge, O = open). Bars indicate the 5% least significant difference (LSD) for (A) Landform x Patch type interaction and (B) the Canopy location x Patch type interaction.

however, we detected only five burrows, all from small body-sized ants, in the foraging pits of bettongs, and none from those of rabbits or echidnas. There were no significant relationships between vertebrate and invertebrate disturbances when we pooled the data for the three positions along the gradient (P=0.123), and no relationships for either *Reintroduction* or *Pastoral* when data were analysed separately. However, for the *Exclosure* sites, increasing cover of vertebrate disturbances was associated with increasing cover of invertebrate disturbances, thus:

$$I = 1.103 \text{ x } V^{0.036} \quad (1)$$

where I = cover of invertebrate disturbances, V = cover of vertebrate disturbances (R^2=0.24; P=0.001).

DISCUSSION

Many studies have demonstrated marked changes in biotic and abiotic environments in relation to grazing-induced disturbance, with sites grazed by domestic livestock characterised by a more degraded soil surface and reduced ecosystem function and stability (Nash et al. 2004; Eldridge et al. 2011b). Our gradient was characterised by a decline in the health of the soil surface from *Exclosure* to *Pastoral*, indicated by reduced plant diversity, declines in soil surface stability and increases in the cover of bare soil (Howard 2011). It is not surprising, therefore, that we recorded fewer invertebrate disturbances at sites grazed by domestic livestock, given their generally lower plant diversity and probably lower productivity (Howard 2011). Many invertebrates construct similar-shaped burrows on the surface, and often with markedly different depths and shapes below the surface. Our focus was on surface soil disturbance, and we were unable to identify the specific organism responsible for their construction other than to place structures into broad orders. We acknowledge that this is a shortcoming of our study. More information on the residents of these structures would have enabled us to make more definitive statements about the species-specific effects across the gradient.

The finding that the density of invertebrate disturbances was greatest under *Exclosure* could be related to the generally more favourable biophysical conditions within the Stage II exclosure at Scotia (e.g. greater shrub and grass cover, more litter, more extensive cryptogamic soil crust cover; Huang 2007) compared with the other treatments. Differences could also be due simply to lower rates of predation, given that only echidnas and goannas were present in Stage II at the time of the study. Bilbies are largely omnivorous, preying on a range of epigeal invertebrates and small skinks (Southgate, 1990; Navnith et al. (2009). The cover of invertebrate disturbances at the landscape scale was lower at *Pastoral* than *Reintroduction* sites even though density showed the opposite trend. This suggests a difference in the frequency distribution of disturbance sizes among the different positions along the gradient, and a substantially reduced engineering effect of small animal disturbances under grazing.

Landscape- and patch-level effects

The cover of invertebrate disturbances, which was greatest in the dunes and least in the plains, is probably a function of soil texture. However, whereas the cover of disturbances by vertebrates, such as bilbies, bettongs and echidnas, responded only to large landform–level changes (e.g. among dunes/swales and plains; Eldridge et al. 2011b), the burrowing activity of invertebrates responded to smaller localised effects. While patch type had some affect on the composition of invertebrate disturbances, this was very weak. Such a result is unexpected, as other studies have shown that invertebrates tend to be strongly influenced by changes in habitat complexity (Kaspari and Weiser 1999, Bonte et al. 2002, Whitehouse et al. 2002, Jouquet et al. 2006, Mazia et al. 2006). We did not measure litter depth nor litter composition, factors that might be expected to influence the presence of surface-active invertebrates. However, litter loads under trees, averaged over dunes and swales, ranged from 505 and 565 g m^{-2} for *Pastoral* and *Recovering* sites, respectively, to 980 g m^{-2} for *Conservation* sites (unpublished data). We did not measure litter loads under shrubs. However, litterfall from shrubs at Scotia is not inconsiderable, ranging from 14 to 30 g m^{-2} yr^{-1} for *Senna* spp. and *Acacia* spp. respectively (Samantha Travers, unpublished data). Although litter loads under shrubs would have been substantially less than under trees, the shrub canopy environment would have been more heterogeneous. The variable cover of biological soil crusts, surface cracking and microclimatic differences in shade, radiation and protection would be more aligned with the spatial differences in invertebrate distribution.

Disturbance densities were higher in association with shrubs than in association with trees, but only in the swales and plains. The soil below shrub canopies is generally more porous, with greater levels of carbon and nitrogen than the interspaces (Eldridge et al. 2011a). Shrubs also moderate surface temperatures and facilitate the growth of understorey plants that may not be present in the community in the interspaces (Soliveres et al. 2011). Greater density of disturbances under shrubs, particularly in the swales and plains, has implications for the management of shrubby woodlands where the removal of encroaching shrubs ('woody weeds') is a common pastoral practice by land managers (Eldridge et al. 2011a). Our work suggests that shrub removal will reduce the burrowing activity of invertebrates given the observation of more burrows under shrubs. Shrub removal will also likely reduce small-scale patchiness due to the close link between shrub density and the density of vertebrate-created pits and depressions, which trap water, litter and sediment and therefore become fertile, productive microsites (Eldridge et al. 2011b). The greater cover of invertebrate disturbances under trees than shrubs in the dunes (data not shown), could be a response to extensive leaf litter loads under mallee eucalypts. We observed considerable volumes of ejecta material from the emergence holes of beetles and cicadas in litter-covered mallee woodlands. Much of this loose, poorly aggregated soil is highly wind erodible and would likely be redistributed short distances by wind erosion processes, contributing to the development of soil and moisture profiles around existing plants (Sarah 2004).

Ants are one of the main taxa responsible for soil movement in arid and semi-arid ecosystems (Whitford 1996), and in our study, comprised about 80% of all invertebrate disturbances. Generally the densities of ant nests tend to be greater where soils have sandy textures (James et al. 2008; Whitford and Eldridge 2010). It is not surprising, therefore, that disturbances by ants were a substantial component of soil disturbance in sandy mallee environments. Estimates of soil movement by ants vary widely, with average global rates of soil turnover at about 5,000 kg ha^{-1} yr^{-1} (Folgarait 1998). In arid environments, the rate of soil disturbance is expected to be related to differences in soil texture and density, which both affect the energy costs of nest excavation.

Many ant taxa are thermophilic (Muser et al. 2005), so their nests would be expected to be located in exposed environments. Structures created by ants were the most dominant in our study, but previous studies have failed to find strong relationships between the presence of ant nests and the make-up of the soil surface (Huang 2007). We expected that some species of ants would have been more common under the *Pastoral* land use. For example, *Rhytidoponera* spp. readily colonise disturbed pastoral areas (Andersen 1986), and has been found as a dominant of bare, disturbed areas in degraded woodlands (Bronham *et al.* 1999). Our result may reflect the fact that ant species richness has been shown to be negatively correlated with cattle grazing (Bouton et al. 2005). The most parsimonious explanation for this is that in the present study, ants building similar-sized nest structures were grouped into a single taxon. In reality, however, there were probably many functional groups of ants at our sites around Scotia, each with differing niche requirements and therefore idiosyncratic preferences for widely different habitat types at small spatial scales (Andersen 1986). The preference of invertebrates for open sites is probably related to the availability of relatively large areas of intact and compacted soils. For example, the burrows of lycosid spiders are generally found in the open, and often associated with intact soil crusts (Martin and Major 2001, Oberg et al., 2007). Scorpions, however, prefer to burrow in sandy soils (Locket 1993). This preference for open areas by invertebrates is in strong contrast to sites selected by native vertebrates, which are predominantly under the canopies of shrubs and trees (Eldridge et al. 2011b).

Invertebrate-vertebrate interactions

We detected a moderately strong correlation between the cover of vertebrate and invertebrate disturbances, but only for the *Exclosure* treatment (Scotia Stage II). It is reasonable to expect non-trophic effects of soil-disturbing native vertebrates on soil-active invertebrates given that they move a considerable mass of soil in the process of foraging and could be affecting patch conditions for the much smaller invertebrates (e.g. Schooley et al. 2000). Indeed, the decline in evidence of activity by invertebrates in areas of grazing could have been due to direct effects of animal disturbance through declines in the quality of habitat with grazing. For example, Howard (2011) showed that an index of soil stability declined from the Scotia Sanctuary to the adjoining grazing leases and this was due primarily to reductions in cryptogam cover and increases in soil compaction (Huang 2007). The effects could be due to changing the availability of resources for invertebrates i.e. making prey items more or less available, changing the abiotic environments to increase (or decrease) ease of movement by, for example, creating more bare soil surface, or conceivably, altering the competitive ability of different groups of organisms (e.g. seed harvesting vs. predatory ant species–trophic effect). It is possible that in more degraded landscapes such as those experienced at the *Pastoral* sites, all burrowing animals might avoid foraging in areas where the soil surface has been trampled by exotic grazers. Consequently, because vertebrates and invertebrates forage away from disturbed sites, their disturbances appear to be interrelated.

In summary, soil disturbance by invertebrates in our eucalypt woodland appears to be influenced by landscape- and local-scale factors. Soil movement is an important geomorphic process that is critical for the maintenance of functioning arid and semi-arid environments (Whitford 2002; Eldridge et al. 2011b). Reductions in the density, cover and composition of of invertebrate (and vertebrate) disturbances by overgrazing, for example, will lead to reductions in small-scale landscape heterogeneity, ultimately reducing stability and productivity of semi-arid systems.

ACKNOWLEDGEMENT

We thank all the staff at Scotia Sanctuary for assistance locating sites and logistical support. Terry Koen provided considerable input into the statistical analyses. We are grateful for the excellent comments provided by an anonymous reviewer.

REFERENCES

Andersen, A.N. (1986). Patterns of ant community organization in mesic southeastern Australia. *Australian Journal of Ecology* **11**, 87-97.

Bangert, R.K. and Slobodchikoff, C.N. (2006). Conservation of prairie dog ecosystem engineering may support arthropod beta and gamma diversity. *Journal of Arid Environments* **67**, 100-115.

Barton, P.S., Manning, A.D., Gibb, H., Lindenmayer, D.B. and Cunningham, S.A. (2010). Fine-scale heterogeneity in beetle assemblages under co-occurring *Eucalyptus* in the same subgenus. *Journal of Biogeography* 37, 1927-1937.

Bonte, D., Baert, L. and Maelfait, J.-P. (2002). Spider assemblage structure and stability in a heterogeneous coastal dune system (Belgium). *Journal of Arachnology* **30,** 331–343.

Boulton, A.M., Davies, K.F. and Ward, P.S. (2005). Species richness, abundance, and composition of ground-dwelling ants in Northern California grasslands: role of plants, soil, and grazing. *Environmental Entomology* 34, 96-104.

Borchard, P. and Eldridge, D.J. (2011). The geomorphic signature of bare-nosed wombats (*Vombatus ursinus*) and cattle (*Bos taurus*) in an agriculture riparian ecosystem. *Geomorphology* **130,** 365-373.

Bromham, L., Cardillo, M., Bennett, A. and Elgar, M. (1999). Effects of stock grazing on the ground invertebrate fauna of woodland remnants. *Australian Journal of Ecology* **24**, 1999-2007.

Ceballos, G., Pacheco, J. and List, R. (1999). Influence of prairie dogs (*Cynomys ludovicianus*) on habitat heterogeneity and mammalian diversity in Mexico. *Journal of Arid Environments* **41,** 161-172.

Eldridge, D.J., Bowker, M.A., Maestre, F.M., Roger, E., Reynolds, J.F. and Whitford, W.G. (2011a). Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecology Letters* **14**, 709-722**.**

Eldridge, D.J., Koen, T.B., Huang, N, Killgore, A. and Whitford, W.G. (2011b). Animal foraging as a mechanism for sediment movement and soil nutrient development: evidence from the semi-arid Australian woodlands and the Chihuahuan Desert. *Geomorphology* doi:10.1016/j.geomorph.2011.04.041

Elkins, N.Z., Sabol, G.V., Ward, T.J. and Whitford, W.G. (1986). The influence of subterranean termites on the hydrological characteristics of a Chihuahuan desert ecosystem. *Oecologia* **68,** 521-528.

Folgarait, P.J. (1998). Ant biodiversity and its relationship to ecosystem functioning: a review. *Biodiversity and Conservation* **7,** 1221-1244.

Gibb, H., and Parr, C.L. (2010). How does habitat complexity affect ant foraging success? A test using functional measures on three continents. *Oecologia* **164**, 1061-1073.

Holt, J.A., Bristow, K.L. and McIvor, J.G. (1996). The effects of grazing pressure on soil animals and hydraulic properties of two soils in semi-arid tropical Queensland. *Australian Journal of Soil Research* **34,** 69-79.

Howard, K. (2011). Plant-plant interactions in an arid shrubland: the role of shrubs as facilitators. Unpublished BSc (Hons.) thesis, University of NSW, Sydney. 58 pp.

Huang, N. (2007). Interrelationships between burrowing animals and arid landscapes. Unpublished BSc (Hons.) thesis, University of NSW, Sydney. 82 pp.

Huntly, N. and Inouye, R. (1988). Pocket gophers in ecosystems: patterns and mechanisms. *Bioscience* **38**, 786-793.

James, A. I., Eldridge, D. J. Koen, T. B. and Moseby, K. E. 2011. Can the invasive European rabbit (*Oryctolagus cuniculus*) assume the soil engineering role of locally-extinct natives? *Biological Invasions* **13**, 3027-3038.

James, A. I., Eldridge, D. J. Koen, T. B. and Whitford, W.G. (2008). Landscape position moderates how ant nests affect hydrology and soil chemistry across a Chihuahuan Desert watershed. *Landscape Ecology* **23,** 961-975.

Johnson, D. L. (1990). Biomantle evolution and the redistribution of earth materials and artifacts. *Soil Science* **149,** 84-102.

Jouquet, P., Dauber, J., Lagerlöf, J., Lavelle, P. and Lepage, M. (2006). Soil invertebrates as ecosystem engineers: intended and accidental effects on soil and feedback loops. *Applied Soil Ecology* **32,** 153-164.

Kaspari, M. and Weiser, M.D. (1999). The size-grain hypothesis and interspecific scaling in ants. *Functional Ecology* **13**, 530-538.

Kotliar, N.B. and Wiens, J.A. (1990). Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* **59,** 253-260.

Kretzer, J.E. and Cully, J.F. (2001). Prairie dog effects on harvester ant species diversity and density. *Journal of Rangeland Management* **54,** 11-14.

Lassau, S.A. and Hochuli, D.F. (2004). Effects of habitat complexity on ant assemblages. *Ecography* **27,** 157-164.

Martin, T.J. and Major, R.E. (2001). Changes in wolf spider (Araneae) assemblages across woodland-pasture boundaries in the central wheat-belt of New South Wales, Australia. *Austral Ecology* **26,** 264-274.

Mazía, C.N., Chaneton, E.J. and Kitzberger, T. (2006). Small-scale habitat use and assemblage structure of ground-dwelling beetles in a Patagonian shrub steppe. *Journal of Arid Environments* **67,** 177-194.

Minitab (2007). 'References Manual Release 15'. (Minitab Inc: State College Pennsylvania).

Muser, B., Sommer, S., Wolf, H. and Wehner, R. (2006). Foraging ecology of the thermophilic desert ant, *Melophorus bagoti*. *Australian Journal of Zoology* **53**, 301-311.

Nash, M.S., Bradford, D.F., Franson, S.E., Neale, A.C., Whitford, W.G. and Heggem, D.T. (2004). Livestock grazing effects on ant communities in the eastern Mojave Desert, USA. *Ecological Indicators* **4,** 199-213.

Nash, M.S., Whitford, W.G., Bradford, D.F., Franson, S.E., Neale, A.C. and Heggem, D.T. (2001). Ant communities and livestock grazing in the Great Basin, USA. *Journal of Arid Environments* **49,** 695-710.

Navnith, M., Finlayson, G.R., Crowther, M.S. and Dickman, C.R. (2009). The diet of the re-introduced greater bilby *Macrotis lagotis* in the mallee woodlands of western New South Wales. *Australian Zoologist* **35**, 90-95.

Nkem, J. N., de Bruyn, L. A. L., Grant, C. D., Hulugalle, N. R. (2000). The impact of ant bioturbation and foraging activities on surrounding soil properties. *Pedobiologia* **44,** 609-621.

Noy-Meir, I. (1973). Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* **4,** 25-51.

Öberg, S., Ekbom, B. and Bommarco, R. (2007). Influence of habitat type and surrounding landscape on spider diversity in Swedish ecosystems. *Agriculture, Ecosystems and Environment* **122,** 211-219.

Sarah, P. (2004). Nonlinearity of ecogeomorphic processes along Mediterranean-arid transect. *Geomorphology* **60,** 303-317.

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

Southgate, R.I. (1990). Habitat and diet of the greater bilby *Macrotis lagotis* Reid (Marsupialia: Peramelidae). In Seebeck, J.H., Brown, P.R., Wallis, R.I and Kemper C.M. (eds) 'Bandicoots and Bilbies' (Surrey Beatty & Sons: Sydney).

Vanbergen, A.J., Watt, A.D., Mitchell, R., Truscott, A.-M., Palmer, S.C.F., Ivits, E., Eggleton, P., Jones, T.H. and Sousa, J.P. (2007). Scale-specific correlations between habitat heterogeneity and soil fauna diversity along a landscape structure gradient. *Oecologia* **153,** 713-725.

Whicker, A.D. and Detling, J.K. (1988). Ecological consequences of prairie dog disturbances. *Bioscience* **38,** 778-785.

Whitehouse, M.E.A., Shochat, E., Shachak, M. and Lubin, Y. (2002). The influence of scale and patchiness on spider diversity in a semi-arid environment. *Ecography* **25,** 395-404.

Whitford, W.G. (2002). 'Ecology of Desert Systems'. (Academic Press: London).

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