Soil disturbance by animals at varying spatial scales in a semi-arid Australian woodland

David J. Eldridge[A,C] *and Alan B. C. Kwok*[B]

[A]Department of Environment and Climate Change, School of Biological, Earth and Environmental Sciences,
  University of New South Wales, Sydney, NSW 2052, Australia.
[B]School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney,
  NSW 2052, Australia.
[C]Corresponding author. Email: d.eldridge@unsw.edu.au

Abstract.   We studied soil disturbance by rabbits, echidnas, goannas, ants and termites at three different spatial scales across four vegetation communities (dense woodland, open woodland, shrubland, grassland) in semi-arid rangeland in western NSW. For analyses, bare and litter-covered surfaces (micro-scale) were nested within canopy and open patches (intermediate scale), which were nested within vegetation communities (landscape scale). Landscape-scale disturbances (rabbit warrens) were six and three times more abundant in open woodlands and shrublands, respectively, than in dense woodlands. Although individual warrens had a similar mass of excavated soil across all vegetation communities, in total, more soil was excavated in the grasslands than in the dense woodlands or shrublands. There were four times as many intermediate-sized disturbances (foraging pits and resting sites) under canopies than out in the open, and this was consistent across all vegetation communities. Echidna foraging pits and kangaroo resting sites dominated the canopy patches. Intermediate-sized disturbances scaled up to the landscape scale were marginally more abundant in the dense and open woodlands than in grasslands and shrublands. However, total mass of soil moved by all species did not differ among vegetation communities. The density of small-scale disturbances (ant nests, termite foraging galleries) did not differ at the landscape-, intermediate- or micro-scales. Our study documents the extent of animal activity in the semi-arid woodlands, and reinforces the notion that, as soil disturbance is scale-dependent, differences among species, habitats and communities will depend on the scale at which disturbances are examined.

Additional keywords: biopedturbation, echidna, foraging pits, goanna, patch dynamics, soil properties.

Introduction

During the past decade there has been increasing recognition of the importance of spatial scale in ecological studies (e.g. Wiens 1989; Wiens and Milne 1989; Levin 1992; Peters and Havstad 2006). Many ecological processes and attributes are scale-dependent. These include the structure and dynamics of ecological communities (Bossdorf *et al*. 2000; Pandolfi 2002), habitat selection by organisms (Sapir *et al*. 2004; Murray *et al*. 2008), eco-hydrology of catchments (Ludwig *et al*. 2005), aeolian processes of sediment redistribution (Okin *et al*. 2006), the distribution of microbial processes, and the effects of soil fungi on vegetation (Lucero *et al*. 2006).

Spatial heterogeneity or patchiness is critical in arid and semi-arid environments, and varies at scales ranging from the landscape or watershed scale (e.g. Dunkerley and Brown 1995), down to the scale of the individual plant (Bochet *et al*. 1999). This patchiness results in major differences in the distribution of soil water, soil biogeochemistry and plant productivity at all scales, resulting in the creation of 'fertile islands' or 'islands of fertility' (Garner and Steinberger 1989; Schlesinger *et al*. 1996). These patches of

greater soil fertility, soil moisture, plant productivity and animal activity typically occur around long-lived woody vegetation at small and intermediate spatial scales, i.e. at the scale of single shrubs and trees or groups of shrubs and trees (Bochet *et al*. 1999; Bossdorf *et al*. 2000). Patches are initiated and maintained by abiotic processes of resource redistribution (e.g. wind and water movement), as well as biotic processes such as soil disturbance by animals (Whitford 2002). Across whole landscapes, processes operate at different scales within a hierarchy, are highly inter-dependent, and affect processes at greater levels of organisation. Thus, for example, greater rates of decomposition under individual plants at small spatial scales may result in greater concentrations of nutrients, but may also effect the distribution of invertebrate herbivores and therefore the distribution of predators at larger scales (e.g. Saab 1999).

Spatial heterogeneity of arid and semi-arid landscapes also results from the activities of soil disturbing animals. Soil disturbance by animals results from activities such as digging for food (Whitford 1998; Eldridge and Mensinga 2007), burrowing (Whitford and Kay 1999), and creating resting sites (Gutterman

1997; Eldridge and Rath 2002). Such disturbances change the physical and chemical properties of soils, altering water infiltration (Garkaklis *et al.* 2000; Jackson *et al.* 2003), nutrient distribution (Nkem *et al.* 2000; Garkaklis *et al.* 2003), and a range of other soil properties (Whitford and Kay 1999). Increased nutrient availability that results from the greater accumulation and mineralisation of organic matter is very important in arid landscapes because such environments are often nutrient limited (Whitford 2002). With increased access to nutrients and water, diggings become 'safe sites' for germination (Jackson *et al.* 2003), with a greater probability of successful germination and establishment compared with less favourable microsites (Gutterman *et al.* 1990). In the Negev Desert Highlands, for example, depressions created by the Nubian Ibex support larger numbers of annual plants (Gutterman 1997). Similarly, Indian crested porcupine diggings have been shown to improve plant germination (e.g. Yair and Rutin 1981; Gutterman *et al.* 1990). In fertile patches, increased nutrient levels result in increased plant productivity (e.g. Boeken *et al.* 1998), and this exacerbates the differences between the patch and the surrounding soil matrix, thus, enhancing spatial heterogeneity.

The study of soil disturbance by animals in Australia is in its infancy, and research to date has focused on the physical and ecological effects of ground-foraging animals. In south-western Australia, the foraging pits of woylies (*Bettongia penicillata*) have significant soil and ecological effects, including the development of subsurface water repellency (Garkaklis *et al.* 2000) and fine-scale patterning in soil nutrient distribution (Garkaklis *et al.* 2003). In the woodlands of west-central NSW, the resting forms of kangaroos ('hip holes') contain greater concentrations of nitrogen, organic carbon, and total carbon and sulfur than undisturbed areas (Eldridge and Rath 2002), and in arid South Australia, small foraging digs by a range of animals act as resource traps and contain greater nutrient loads than undisturbed areas (James and Eldridge 2007). Such studies have been invaluable in providing insights into the effects of disturbance at a single spatial scale (e.g. single vegetation community or patch), but we are unaware of any studies that have considered soil disturbance across multiple spatial scales or different vegetation communities.

In terms of animal disturbances, spatial scale is important because, not only does it influence the way we view the effects of organisms on landscapes, but it also helps us to understand how different suites of organisms, usually of differing body size, might differ in the way they affect landscapes and landscape processes. Spatial scale is also important as invertebrate disturbances would be distributed differently to those of vertebrates. The semi-arid woodlands of eastern Australia are spatially heterogeneous (patchy), varying widely in soil physical and chemical characteristics often across small distances (Greene 1992). Resource-rich patches such as mulga log mounds (Tongway *et al.* 1989) and perennial grass tussocks typically occur adjacent to resource-poor patches such as runoff plains dominated by cryptogams. Different sized patches are used by different organisms, often with widely varying body size. Thus, although large-bodied organisms typically respond to changes at larger scales (e.g. different levels of plant utilisation brought about by grazing across large paddocks), medium-sized animals respond at meso-scales such as around individual trees (Dean *et al.* 1999) or

in the grassy bands adjacent to run-on zones (Whitford 1998), and microorganisms and micro-arthropods respond to a finer scale of patchiness such as around litter or clumps of perennial grasses (Gibb *et al.* 2008). Because different sized organisms will be driven by differences in relation to their body size, it is important to consider scale when assessing their impact on ecosystems.

Our aim in this study was to assess the magnitude of soil disturbance by a range of woodland-active animals in four different vegetation communities. Because the soil disturbances of different woodland animals are known to differ between different patch types (e.g. resting sites of kangaroos under trees, Eldridge and Rath 2002), our intention was to sample a range of patch types that would reflect the distribution of these disturbances. Consequently, we conducted this study at three spatial scales: (1) among four different vegetation communities across an area of ~60 000 ha (landscape scale), (2) between the timbered (tree canopy) and open sites within each vegetation community (intermediate scale), and (3) between bare- and litter-covered soils within trees and open areas (microsite scale; Fig. 1). Disturbances (warrens) constructed by European rabbits (*Oryctolagus cuniculus*) were assessed within large plots because of their size (15–30 m across). Similarly, smaller disturbance types such as ant burrows and termite sheeting were measured within small quadrats; scales commensurate with their size.

We tested three predictions about soil disturbance by woodland-active animals: (1) given the overwhelming evidence on the importance of large trees as focal points for animals (e.g. Dean *et al.* 1999; Cooper and Whiting 2000; Fischer and Lindenmayer 2002), we expected that the magnitude of disturbances (i.e. cover, density and mass of excavated soil) created by medium-sized animals such as echidnas, rabbits and goannas would be greater under tree canopies than in the open (Hypothesis 1). As an extension of Hypothesis 1, we expected that the level of animal activity, and therefore the number and magnitude of disturbances, would not only increase with increases in tree density, because of a greater number of favourable sites for excavation, but that the trend would be consistent among the four vegetation communities (Hypothesis 2). Finally, given that our four communities varied markedly in overall structure and composition of patch types (trees, shrubs, open areas), we anticipated that the spectrum of animal disturbances would be different among the different vegetation communities (Hypothesis 3).

Materials and methods

Study site

The study was conducted between December 2004 and March 2005 at Yathong Nature Reserve (107 241 ha), which is located ~130 km south of Cobar (32°37′S, 145°34′E) in west-central NSW, Australia. Our study site in the eastern section of the reserve lies on the Cobar Peneplain, and is mainly low ridges and lowlands (Ongley 1974). Yathong is semi-arid, receiving ~325–350 mm of rainfall per year, though there may be substantial variation among years (Leigh *et al.* 1989). Temperatures in July reach a mean minimum of 4.5°C, and a mean maximum of 33.2°C in January (McCullough and McCullough 2000). The soils are classified as Typic Haplargids or Kandosols (Isbell 1996). Typical soil profiles consist of a loamy clay loam surface horizon up to 1 m
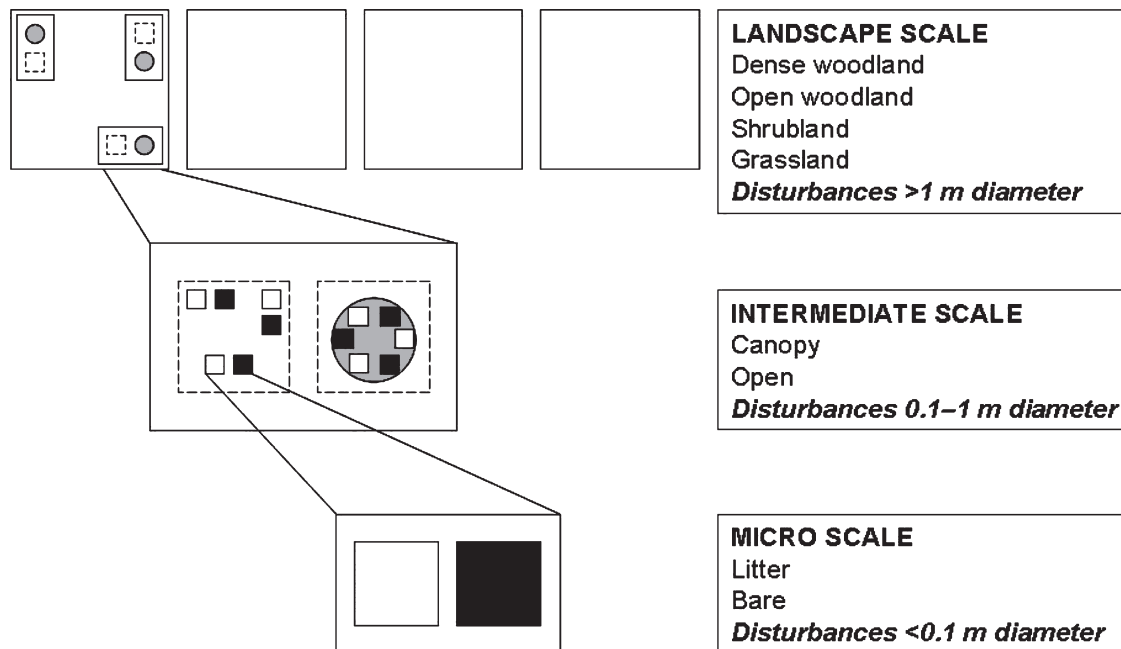
Fig. 1. Schematic diagram of the experimental design of the study. Each vegetation community was replicated at three sites, there were three replicate canopy (circle) and open (square) patches within each site, and three replicate litter-bare quadrats within each canopy-open patch.

deep overlying a light-medium clay B horizon. Detailed profile descriptions are given in Eldridge and Greene (1994). Although grazing by domestic stock ceased in 1971, substantial numbers of feral goats (*Capra hircus*) and European rabbits are active throughout the reserve. Eastern grey kangaroos (*Macropus giganteus*) and western grey kangaroos (*Macropus fuliginosus*) are present in large numbers within the reserve, with up to 40 kangaroos per km^2 (McCullough and McCullough 2000).

This study was confined to four vegetation communities varying in complexity and structure, as defined by their physiognomy (e.g. dense woodland to grassland). The four communities were: (1) dense woodlands – dominated by thick patches of white cypress pine (*Callitris glaucophylla* J. Thomps. & L.A.S.Johnson), with scattered individual trees of western red box (*Eucalyptus intertexta* R.T. Baker) and poplar box (*Eucalyptus populnea* F. Muell.). The inter-tree distance was typically <15 m. The understorey comprised speargrasses (*Austrostipa* spp.), wiregrasses (*Aristida* spp.) and scattered forbs; (2) open woodlands – characterised by *E. intertexta* and *E. populnea* as the dominant tree species, an open canopy (<30% cover), and inter-tree distances of 75–100 m. The understorey was similar in composition to the dense woodland; (3) shrublands – dominated by shrubs usually less than 2 m in height (including various species of wattle – *Acacia brachybotrya* Benth., *Acacia colletioides* Benth.) and scattered western red box and belah (*Casuarina cristata* Miq.) at low densities. The understorey was dominated by speargrasses and wallaby grass (*Austrodanthonia caespitosa* (Gaudich.) H.P.Linder); (4) grasslands – dominated by perennial grasses (wiregrasses, wallaby grass and speargrasses) and with large western red box scattered at distances of many hundreds of metres.

In Yathong Nature Reserve several different animals create soil disturbances of different sizes, which are, therefore, apparent at different spatial scales, and this formed the basis for our study. At the landscape (vegetation community $\sim \times 10^4 m^2$) scale, European rabbits, exotic herbivores, create extensive above-ground warrens with associated burrow systems which may cover several hundred square metres (Eldridge and Myers 2001). At intermediate ($\times 10^1 m^2$) scales, native species such as goannas (*Varanus gouldii*, *Varanus varius*) and echidnas (*Tachyglossus aculeatus*) and the European rabbit create pits in the soil while foraging for invertebrates and plant roots, respectively, and eastern and western grey kangaroos and the red kangaroo (*Macropus rufus*) excavate shallow depressions in the soil surface which they use as diurnal resting beds. At the finest ($\times 10^{-1} m^2$) scale, ants (*Rhytidoponera* spp., *Camponotus* spp.) and a range of spiders excavate burrow entrances and harvester termites (*Drepanotermes* spp.) excrete developmental cellulose which they mix with soil to form impervious circular pavements devoid of herbage (Noble *et al.* 1989). Foraging galleries of epigaeic termites are common in all communities along with carton, which is used as a protective covering for the termites while they are foraging above-ground (Whitford 2002).

Sampling design

Measurements were made at 12 sites comprising three replicates each of dense woodlands, open woodlands, shrublands and grasslands (Fig. 1). Sites measured 500×500 m (25 ha), and were separated by distances ranging from 5 to 10 km. The largest form of animal disturbance, rabbit warrens, which range from 15 to 30 m in diameter, were sampled across the entire 25 ha at each site.

Within each 25 ha site we selected three large plots of 10×10 m at predetermined locations near the corners of each site. Each plot centred upon a mature *Eucalyptus* tree ('canopy'), which were typically up to 15 m high and with a canopy radius of 15 m. An adjacent paired 'open' plot was located 20 m from the edge of the canopy plot. Within these paired 100 m^2 plots, all disturbances of intermediate size (0.1–1.0 m in diameter) i.e. kangaroo hip holes, foraging pits and diggings of echidna, goanna and rabbits, and above-ground capping of subterranean termite galleries were recorded. The smallest forms of animal disturbance (<0.1 m in length), generally burrows of ants, emergence holes of termites and spiders, and carton produced by termites (hereafter referred to as 'microsite-scale disturbances') were recorded within six 0.5×0.5 m quadrats that were placed in three pairs within each 10×10 m plot. A quadrat from each pair was placed on one of two surface types, a litter-dominated surface ('litter') and a bare-dominated surface ('bare').

The study, therefore, comprised a factorial combination of four vegetation communities (each replicated three times), by two intermediate-level patches (canopy, open) by two microsite types (litter, bare; Fig. 1). Each spatial scale is linked with an appropriate vegetation pattern. The landscape scale is linked with tree density, the intermediate scale with canopy or open locations, and the microsite scale linked with the cover of leaf litter and bare soil. The nested-quadrat sampling scheme allowed us to examine soil disturbance at different spatial scales and determine whether animals were showing preference for certain patches or surface types. It also allowed us to investigate how vegetation processes operating at multiple spatial scales might affect soil disturbance by animals.

Field measurements

For each animal disturbance we recorded its dimensions (length, width, depth or height) and the animal creating the disturbance (i.e. rabbit, echidna, goanna, kangaroo, ant, spider or termite). Over the past decade we have learnt to recognise the range of morphologies of pits and resting forms created by vertebrates in the semi-arid woodlands. Echidnas create a range of disturbances (nose pokes, shallow to deep digs, extensive tracts of bull-dozing) while foraging for macro-invertebrates (Rismiller 1999). Echidna pits are generally circular-shaped, and surrounded by a small accumulation of soil, which is generally very rough or cloddy. Rabbits create elongated pits, with a sharp face at the proximal end and a small mound of finely-crushed soil at the distal end. Rabbit pits are typically shallower (<10 cm deep) than echidna pits (15–20 cm deep). Goanna pits range from narrow, ellipsoid excavations dug at an angle of ~30% to the horizontal, to wedge-shaped excavations, which are similar, though generally larger, than rabbit pits. The floor of the pits often show evidence of two deep scratch marks where the soil has been excavated by the reptiles' strong forelimbs. Kangaroo hip holes are generally reniform- to subcircular-shaped depressions to 2 m long, and 0.5 m wide and deep, located close to the trunks of trees and shrubs (Eldridge and Rath 2002). The outer edge of the hip holes (further from the trunk) is more sharply angled than the inner edge, which slopes towards the original ground level. Termite pavements are roughly circular, ~45 cm in diameter, with concave, but sometimes slightly convex surfaces. Termite carton

is a thin surface layer of decomposing soil mixed with organic matter and occurs in small patches less than 20 cm across. Ground-foraging fossorial spiders such as the Lycosids and *Ariadna* spp. have permanent burrows (York Main 2001) up to 1 cm in diameter, often with an almost invisible trapdoor.

The volume of soil contained within rabbit warrens was calculated using the formula for a prolate sphere, and the mass determined by multiplying soil volume by 1.38, the bulk density of soils at Yathong (Eldridge and Myers 2001). The area of soil disturbed in pits and burrows was calculated using the formula for the area of a circle. The area and volume of soil disturbed by kangaroo hip holes was calculated using the formula for an ellipse. The volume of each echidna, goanna and rabbit pit was calculated by the product of its width, length and depth using an equation by James and Eldridge (2007).

Statistical analyses

Differences among the four vegetation communities in the density and area ($\log_e$) of rabbit warrens and the mass of soil they contained ($\log_e$), were tested using one-way ANOVA after diagnostic tests of residual and normal plots and Levene's homogeneity of variance test using Minitab (1997). Data for intermediate-sized disturbances were scaled up to the landscape scale by adjusting for the density of large trees at each site. Tree density was assessed using current aerial photographs.

For intermediate-scale data on density $[\log_e (x+1)]$, soil excavation $[\log_e (1000x+1)]$ and cover $[\log_e (x+1)]$ of disturbances, we used a mixed models ANOVA to test for differences among the four vegetation communities and the two patch types, and their interactions, using the GenStat 7.1 (VSN International Ltd, Hertz, UK) statistical package (Payne *et al.* 1993). The main plot stratum considered the effects of vegetation community, and the subplot stratum patch type and its interaction with vegetation community. A third stratum accounted for the effects of replicate trees within a community. Disturbances at the microsite scale were analysed for differences in density $[\log_e (x+1)]$ and cover of disturbed soil $[\log_e (x+1)]$ in relation to vegetation community, patch type, microsite type and their interactions. Because of the large number of zero values within the dataset, i.e. many quadrats showed no evidence of microsite-scale disturbances, data were averaged across each site for each patch type by litter type combination. The data were again analysed using a mixed models ANOVA with a similar structure as above, but with an additional stratum which considered microsite, and its two- and three-way interactions with community and patch type. For all analyses, *post-hoc* differences in means were compared using Tukey's least significant difference (l.s.d.) tests.

Multivariate analyses were used to explore possible differences in the complement of disturbances from different types of animals to total disturbance among vegetation communities or patch types (and their interaction). The data matrix comprised the mean number of diggings created by four animals (echidnas, goannas, kangaroos, termites) in each replicate patch by vegetation community. This resulted in a matrix of four columns (animals) by 24 rows (four communities each with three replicates each of canopy and open). Similar matrices were created for cover and mass of soil excavated. Each matrix

was converted to a similarity matrix using the square-root transformation and the Bray Curtis similarity coefficient within the Primer (Version 5; PRIMER-E Ltd, Ivybridge, UK) statistical package (Clarke and Gorley 2001). Non-metric multidimensional scaling (MDS) was then performed on each similarity matrix. Analysis of similarities (ANOSIM) was used to test, *a priori*, defined hypotheses of differences among vegetation communities or between patch types in the relative number of disturbances created by different animals, mass of excavated soil, and cover of disturbances. Finally, similarity analysis (SIMPER) was used to rank the relative importance of each animal to the average dissimilarity among groups.

Results

Landscape-scale disturbances – rabbit warrens

There were six times as many warrens in the open woodland, and three times as many in the shrublands compared with the dense woodland ($F_{3,8} = 5.69$, $P = 0.022$; Table 1). Similarly, warrens in the grasslands were twice the size of those in the other communities ($F_{3,8} = 4.74$, $P = 0.035$, Table 1). Although the average mass of soil per warren (3300–4500 kg) was similar among communities ($P > 0.05$), the total soil mass of warrens on a per hectare basis was greater in the grasslands than in the dense woodlands and shrublands ($F_{3,8} = 3.79$, $P = 0.059$). This trend was similar for the cover of warrens ($F_{3,8} = 4.64$, $P = 0.037$, Table 1). In all communities except the grasslands, warrens tended to occur within 10 m of a tree.

Intermediate-sized disturbances created by goannas, echidnas, kangaroos, rabbits and termites

Disturbances by echidnas and kangaroos dominated the canopy patches, and although echidna and goanna, and to a lesser extent termite, disturbances were co-dominant in the open (Fig. 2). Only termite pavements were more abundant in the open than under the canopy, and kangaroo hip holes were almost absent from the open areas (Fig. 2). Surprisingly, only three rabbit foraging pits were recorded across all the sites (all in the open). Consequently, they were excluded from consideration. Echidna pits (22–25 cm long, 16–21 cm wide) were of a similar size to goanna pits (18–26 cm long, 12–22 cm wide), though considerably shallower (Table 2). Kangaroo hip holes averaged ~70 × 53 cm, with an average mass of 6.3 kg of excavated soil (Table 2).

Across the four vegetation communities there were four times as many disturbances by native animals under canopies (19.4 pits per 100 m^2 of canopy) compared with out in the open (3.8 pits per

100 m^2 open; $F_{1,16} = 38.8$, $P < 0.001$ on $\sqrt{}$-transformed data; Fig. 2). Cover of disturbances under the canopies was nine times greater (9.4%) than out in the open (1.0%; $F_{1,16} = 144.0$, $P < 0.001$ on $\sqrt{}$-transformed data), and ~30 times greater mass of soil removed from disturbances from beneath the canopy (119 kg per 100 m^2) compared with that disturbed in the open (6 kg per 100 m^2; $F_{1,16} = 62.5$, $P < 0.001$ on $\sqrt{}$-transformed data). On a per-canopy basis (i.e. per 100 m^2 of canopy), there were no significant differences in either the density, cover or mass of soil disturbances among the four vegetation communities ($P > 0.05$). There were no significant community × patch type interactions ($P > 0.05$) for any attributes, indicating that trends in relation to canopy and open patch types were consistent across the four vegetation communities.

For density, soil mass and cover, there was a significant difference in the composition of disturbances created by different animals between canopy and open patch types (Global $R = 0.55$–0.77, $P = 0.001$), but no difference among vegetation communities (Global $R < 0.003$, $P > 0.05$; Fig. 3). Similarity analyses (SIMPER) for cover data indicated that 73% of the dissimilarity between the canopy and open patch types was related to a greater abundance of kangaroo hip holes beneath the tree canopies.

When we scaled the intermediate-sized disturbances up to the landscape scale using tree density data for the four communities, disturbances were marginally more abundant in the dense (693.1 ± 380 disturbances/ha) and open (904.5 ± 225/ha) woodlands compared with either the shrublands (238.2 ± 12.2/ha) or grasslands (235.1 ± 72.5/ha; $F_{3,8} = 3.95$, $P = 0.05$, Fig. 4). However, the relative contribution of the canopy to total density was greatest in the dense woodlands (52%) and shrublands (48%), and less in the open woodlands (23%) and grasslands (12%; Fig. 4). Echidna foraging pits were more abundant in dense and open woodlands, termite pavements were most abundant in open woodland, and goanna foraging pits in dense and open woodland (Fig. 5). However, although kangaroo hip holes were dominant in all communities at the patch scale, when scaled up to the landscape scale, they were less dominant in those communities where tree density was low i.e. grasslands and shrublands, and tended to increase with increases in tree density (see data below). The total mass of soil disturbed by all animals ranged from 490 ± 170 kg/ha for the grassland to 2770 ± 1250 kg/ha for the dense woodland and was not significantly different among communities ($F_{3,8} = 3.50$, $P = 0.069$ on $\log_{10}$ transformed data). Despite the importance of tree canopies as sites for concentrated foraging, we found no significant relationships between

Table 1.   Rabbit warren size, cover, density and mass of soil excavated for the four vegetation communities
Within an attribute, different lower case letters indicate a significant difference at $P < 0.05$

| Attribute	Grassland		Shrubland		Open woodland		Dense woodland	
	Mean	s.e.m.	Mean	s.e.m.	Mean	s.e.m.	Mean	s.e.m.
Warren length (m)	11.7a	0.60	6.0b	0.49	5.4b	0.24	5.5b	0.54
Warren cover (%)	1.26a	0.38	0.28b	0.19	0.46ab	0.14	0.08b	0.02
Warren density (per ha)	1.28ab	0.19	0.92bc	0.47	1.97a	0.23	0.32c	0.14
Warren soil mass (kg/warren)	3290a	2250	3800a	1210	4270a	290	4470a	1040
Soil excavated (kg/ha)	29 400a	13 100	3200b	1640	8400ab	3040	1400b	250
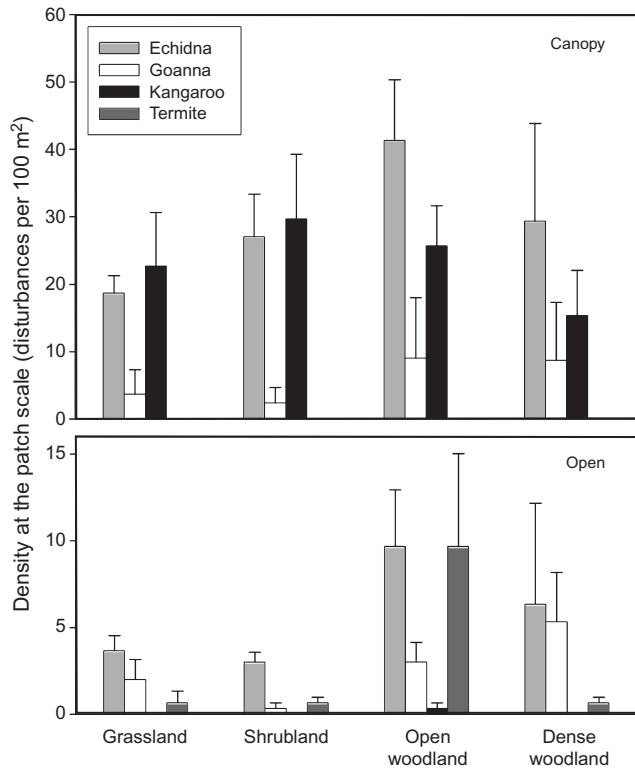
Fig. 2. Mean (+s.e.m.) density of animal disturbances within the 100 m^2

increasing density of trees at the landscape scale and density, cover or mass of soil disturbances ($P > 0.27$).

Micro-scale disturbances: ant nests and termite foraging galleries

There were no significant differences in the density of ant nests or termite foraging galleries among communities ($P = 0.361$), canopy or open patches ($P = 0.776$), or surface cover types (i.e. litter or bare soil; $P = 0.075$). Surprisingly, no spider burrows were found in any of the quadrats. Further, there were no significant two- or three-way interactions among community, patch type, and soil surface type ($P > 0.05$). However, a significantly greater area of soil surface was disturbed by ant and termite foraging in the open woodland compared with the other communities ($F_{3,8} = 4.28$, $P = 0.04$), and on litter-dominated surfaces (0.058%) compared with bare surfaces (0.008%;

$F_{1,3} = 24.67$, $P < 0.001$). There were no significant effects of bare or litter surface on cover, and no significant vegetation community, canopy nor surface cover effects.

Discussion

Our study demonstrated marked differences in the patterns of soil disturbance at the three spatial scales. For example, although the mass of soil excavated from individual rabbit warrens was similar across the vegetation communities, there were substantial landscape-level differences in total mass of soil excavated from all warrens in different vegetation communities. Similarly, the density of intermediate-sized disturbances and the mass of soil excavated from them differed markedly among vegetation communities, but only when viewed at the landscape scale when we took into account the relative proportion of canopy to open areas. This study reinforces our view that soil disturbance is strongly scale-dependent, and that both the foraging preferences in particular habitats and the cover of that habitat at the landscape-scale must be taken into account.

Trends in relation to different spatial scales

We found clear differences in the density of rabbit warrens among the four vegetation communities, with dense woodlands, the most heavily-wooded community (~21 trees/ha), supporting the fewest rabbit warrens, although grasslands, the least wooded community (~2 trees/ha), supported the greatest number of warrens. There are several possible reasons for this. The current distribution of warrens may reflect a preference by rabbits for open areas, which provides them greater access to more nutritious, shorter stature forbs and grasses, which are more prevalent in open grasslands (Leigh *et al*. 1989; Iason *et al*. 2002), as well as a more open environment where they can maintain vigilance against predators. More likely, however, is that rabbits now occupy warrens that were originally constructed by the burrowing bettong (*Bettongia lesueur*) which, apart from some sites where it has been re-introduced, is now extinct on the mainland (J. C. Noble, pers. comm.). In many of these warrens currently occupied by rabbits, the vestiges of the original bettong perimeter mound are still clearly visible from the air (Noble and Tongway 1986; Noble *et al*. 2001). Examination of warrens at some sites at Yathong indicates the presence of large amounts of indurated limestone mined from depth. We believe it highly unlikely that rabbits alone would have been able to penetrate the limestone hardpan and bring material to the surface, and, therefore, posit that many warrens were fossil bettong warrens. Although only three rabbit foraging pits were recorded during our study, the reserve has supported large rabbit populations in the past (Leigh *et al*. 1989). Both rabbit

Table 2. Mean (+s.e.m.) length (cm), width (cm), depth (cm) and mass of soil (kg) excavated in intermediate = scale disturbances by echidnas, goannas, kangaroos and termites

n.a., Not applicable

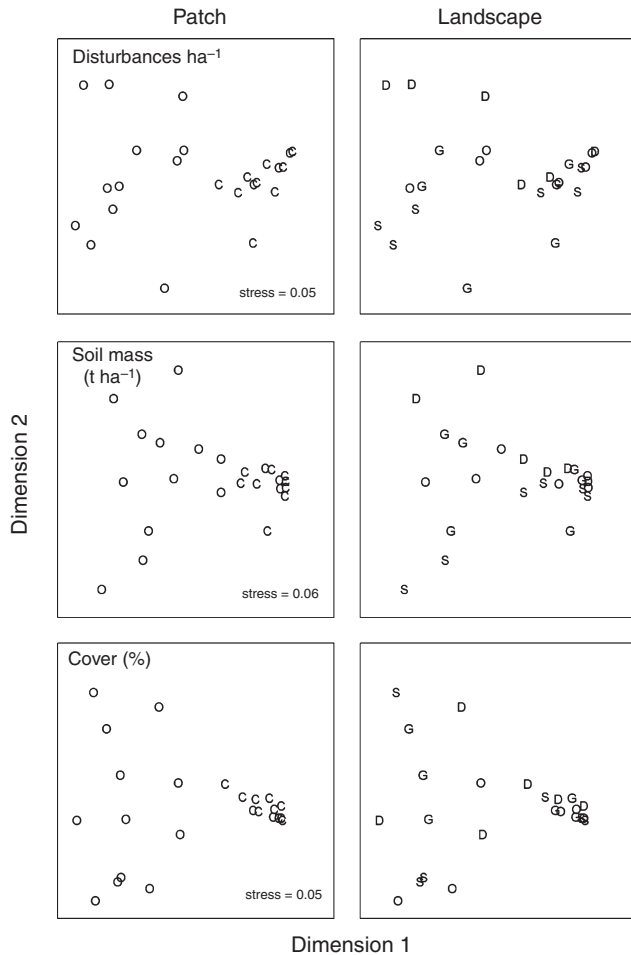| Attribute	Echidna		Goanna		Kangaroo		Termite	
	Mean	s.e.m.	Mean	s.e.m.	Mean	s.e.m.	Mean	s.e.m.
Length (cm)	26.6	0.09	21.5	1.09	69.3	1.35	50.4	4.76
Width (cm)	20.6	0.43	16.8	0.85	52.7	1.23	41.6	4.49
Depth (cm)	7.7	0.34	18.4	1.36	7.7	0.32	n.a.	n.a.
Soil excavated (kg)	2.2	0.19	3.4	0.04	6.3	0.40	n.a.	n.a.

Fig. 3. The first two dimensions of the non-metric multi-dimensional scaling (MDS) biplots for density, soil mass and cover of disturbances at the patch and landscape scales. Patch: C, canopy; O, open; Landscape: D, dense woodland; O, open woodland; S, shrubland; G, grassland. Note the large effect of canopy *v.* open but no general landscape (plant community) effect.

Fig. 4. Mean density per hectare of intermediate-sized disturbances (echidnas, kangaroos, goannas and termites) scaled up to the landscape scale for canopy and open patch types across the four vegetation communities. Different letters indicate a significant difference in density of total disturbances at $P < 0.05$.

Fig. 5. Mean ($\pm$s.e.m.) density of disturbances per hectare of echidna, goanna, kangaroo and termite disturbances in the four vegetation communities.

hemorrhagic disease and warren ripping across the reserve have reduced the population substantially over the past decade, and rabbits and their disturbance pits are now found only in isolated areas.

Despite the relatively sparse cover of warrens in all communities (<1.3% Table 1), rabbits (and presumably bettongs) have excavated a substantial mass of soil, ranging from 1 to 22 m³ soil/ha over the life of the warrens. Even when the relatively large number of intermediate-sized disturbances is scaled up to the landscape scale, rabbit warrens still accounted for 45–80% of total landscape-level soil excavation, depending on the vegetation community. We note, however, that this may not reflect the real level of soil movement by other animals such as echidnas because warrens are relatively long-lived, up to 300 years according to allometric relationships reported by Whitford and Kay (1999), whereas the other disturbances have substantially shorter half-lives. Pits of echidnas, for example, generally disintegrate rapidly, and although still recognisable as former foraging pits, have virtually no capacity for further resource capture after 3 years
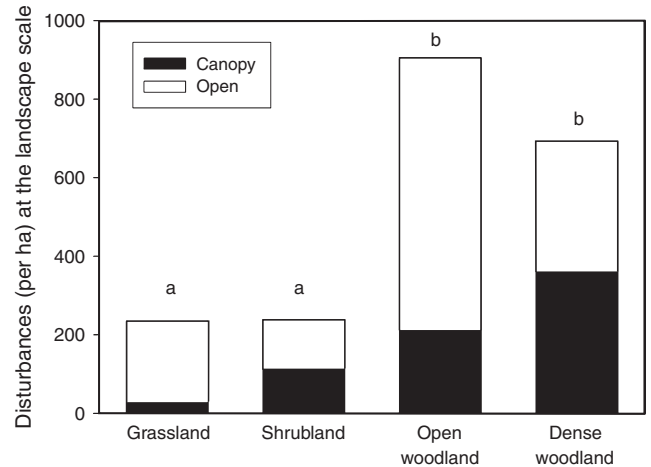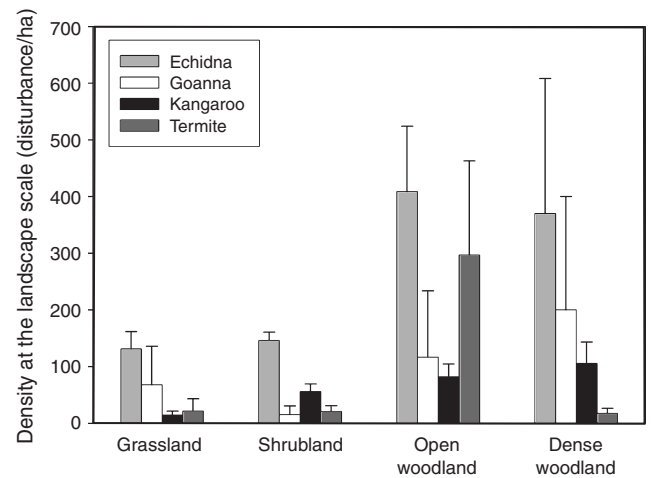
(D. J. Eldridge, unpubl. data). Rates of pit deformation will likely vary among communities and between patch types. Studies of infilling of artificially-created echidna pits from the same study area indicate an average rate of 84% for pits in the open compared with 69% for pits under the canopy over a period of 6 months (D. J. Eldridge, unpubl. data). Turnover rates for echidna pits monitored at Scotia Sanctuary in the West Darling region of NSW (D. J. Eldridge, unpubl. data) indicate that the volume of echidna pits totals ~1.3 m³/ha/year. On the assumption that rabbit warrens persist for 250–300 years (Whitford and Kay 1999), comparable soil turnover for echidnas over the same period would, therefore, be in the order of 325–390 m³/ha, far in excess of that of rabbit (or bettong) warrens. The point we emphasise here is that although warrens are substantial repositories of soil at any one point in time, over their lifetime they are likely to be exceeded by total turnover

of soil from smaller structures constructed by animals such as echidnas.

Very few mammals, apart from some fossorial rodents from China (Hongo *et al*. 1993), Chile (Contreras and Gutierrez 1991) and Argentina (Whitford and Kay 1999) construct such conspicuous structures on such a broad scale as the European rabbit (or burrowing bettong). Rates of total mass of soil for rabbit warrens are within the range reported for the hairy-nosed wombat (*Lasiorhinus latifrons*), which varied between 16 and 55 m^3 of soil per warren system (Steele and Temple-Smith 1998), though rabbit warrens tended to be closer in size to mounds of black-tailed prairie dogs (*Cynomys ludovicianus*), which excavate an average of ~1.4 m^3/ha (White and Carlson 1984). The volume of soil excavated in rabbit warrens from the grasslands is comparable to values reported for the American badger (*Taxidea taxus*; 20 m^3/ha; Eldridge 2004) and several North American gopher species (3.4–57.4 m^3/ha/year; Smallwood and Morrison 1999).

As predicted, there were four times more intermediate-sized disturbances (Fig. 2), nine times greater cover of disturbances, and 20 times greater mass of excavated soil beneath tree canopies than in sites in the open. When scaled up to the landscape scale, however, the results for intermediate-sized disturbances indicate that open areas are substantial contributors to landscape-scale soil disturbance, particularly in the grasslands and open woodlands, simply because open patches make up a considerable proportion of the landscape. However, this scaling also demonstrated that disturbances below the canopy contributed disproportionately to both total density and soil excavation at landscape scales. Thus, for example, although only 10% of dense woodlands were covered by the canopies of large trees, 63% of the total mass of soil excavated in the dense woodlands occurred beneath the canopy. We acknowledge that we may have underestimated the landscape-level extent of soil disturbance, since smaller shrubs and trees, not included in our measurements, will probably support some animal disturbance. Nevertheless, we believe that our results provide a reasonable estimate of landscape-scale soil disturbance by animals, though they are likely to be conservative.

Our observation that canopies are hotspots of animal activity is consistent with findings that woodland animals worldwide preferentially utilise canopies for both resting and foraging. For example, kori bustards (*Ardeotis kori*), springbok (*Antidorcas marsupialis*), emsbok (*Oryx gazelle*), blue wildebeest (*Connochaetes taurinus*) and bat-eared fox (*Otocyon megalotis*) actively seek shade underneath or in trees during the heat of the day (Dean and Milton 1991; Dean *et al*. 1999). In Australia, the foraging pits of the Tasmanian bettong (*Bettongia gaimardi*) and the brush-tailed bettong (*Bettongia penicillata*) tend to be clumped around tree trunks that provide the hypogeous fruits on which the animals feed (Johnson 1994). In our study, foraging pits by echidnas and diurnal resting sites of kangaroos dominated the subcanopy disturbances, but unlike echidna pits, hip holes were rarely found in the open (Fig. 2), consistent with evidence for the preferential use of tree canopies by kangaroos as diurnal resting sites (Eldridge and Rath 2002) when surface temperatures often exceed 60°C over summer. Our results accord with observations of preferential use of canopies by echidnas (Smith *et al*. 1989; Rismiller 1999; Eldridge and Mensinga 2007).

At the intermediate scale, the relative contribution of each animal to total disturbance varied, as predicted, among vegetation communities. Echidna foraging pits and kangaroo hip holes occurred across all vegetation communities, though termite pavements were most abundant in open woodland, and goanna foraging pits in dense and open woodland (Fig. 5). These trends may reflect relative differences in the abundance of each animal across communities. There are some species-specific differences in the way kangaroos use different vegetation communities at Yathong (McCullough and McCullough 2000), and it is conceivable that patterns of disturbance could reflect the differences in habitat use by red and grey kangaroos in different parts of the reserve. That neither density nor cover of fine-scale animal disturbances varied among vegetation communities, or tree and open patches, suggests that fine-scale disturbance is largely unresponsive to changes at larger spatial scales. Although bare soil surfaces supported a slightly greater cover of fine-scale disturbances, there was no significant difference in the density of disturbances between bare- and litter-covered surfaces. Results from the present study suggest that the links between fine-scale surface attributes (i.e. litter and bare soil) and animal disturbances were, at best, ambiguous.

Soil disturbance – a scale-dependent phenomenon

Although it is relatively apparent how large-scale animal structures (e.g. rabbit–bettong warrens) might affect landscape-level processes through moderation of water flow and changes in soil deposition, it is less clear how intermediate-sized disturbances might affect ecosystem processes. At intermediate spatial scales, animal disturbances affect water infiltration and nutrient pools in individual animal diggings (Eldridge and Mensinga 2007; James and Eldridge 2007). At larger spatial scales, disturbances such as the mounds of banner-tailed kangaroo rats (*Dipodomys* spp.), colonies of prairie dog (*Cynomys ludovicianus*) and warren systems of European rabbits affect the distribution and abundance of plants and animals dependent on these structures (Archer *et al*. 1987; Reichman *et al*. 1993; Ceballos *et al*. 1999; Schooley and Wiens 2001; Davidson and Lightfoot 2006), thereby altering landscape-level patterns of resources. Fine-scale forms of disturbance such as soil movement by ants and termites can have substantial effects at landscape scales including increased infiltration (through the creation of macropores; Eldridge 1993; Whitford 2002), redistribution of nutrients (Nkem *et al*. 2000), altered plant productivity (Gutierrez and Whitford 1987) and the development of substantial soil biomantles (Whitford and DiMarco 1995).

Many animals create several forms of disturbance at different spatial scales. As well as creating larger burrow structures, kangaroo rats and European rabbits also excavate small pits on the soil surface while foraging (Kay and Whitford 1978; Whitford and Kay 1999; James and Eldridge 2007). The extent to which these intermediate-level disturbances contribute to landscape-level differences in resources is obvious when one considers per-capita pit construction and estimates of pit longevity. Although we have no data on the persistence of intermediate-sized structures, empirical relationships for a range of fossorial mammals relating the area of animal disturbance to the longevity of their diggings suggest that pits will persist for up to 3–6 years, depending on their size (Whitford and Kay 1999).

This study has demonstrated that the drivers of soil disturbance i.e. the patterns of vegetation that influence the spatial distribution of soil-disturbing animals, are scale- and process-dependent. Landscape-level disturbances (rabbit warrens) varied among vegetation communities, while finer-scale disturbances were not influenced at this spatial scale. Similarly, intermediate-level patterns of vegetation distribution such as the canopy and open areas were only important for disturbances operating at intermediate scales (echidna, goanna, rabbit, termite pavement). The importance of vegetation as a driver of soil disturbances in this semi-arid woodland depends on both the scale at which the structure is observed, and the scale of the vegetation driver. Overall, animal disturbances in the semi-arid woodlands were scale-dependent, with clear preference for the canopy microsites at intermediate scales but not at landscape scales.

The results of this study also suggest to us that the extent and distribution of soil disturbances by animals, particularly native animals, may be a useful non-invasive method of assessing habitat quality and preference for foraging sites at different spatial scales. For example, Hone (1988) showed that the number of diggings by feral pigs (*Sus scrofa*) was indicative of pig densities. Similarly, our understanding of these preferences at the landscape scale could inform management decisions about which areas are of highest conservation priority. If, for example, each landscape (or vegetation community) shows the same trends of increased animal foraging under trees, then those landscapes with fewer scattered trees may be a greater management priority due to their important habitat significance compared with communities that have many trees. Research is currently underway to establish the nature of the links between foraging activity of woodland animals and resources.

Acknowledgements

References

Archer, S., Garrett, M. G., and Detling, J. K. (1987). Rates of vegetation change associated with prairie dog (*Cynomys ludovicianus*) grazing in North American mixed-grass prairie. *Vegetatio* **72**, 159–166.

Bochet, E., Rubio, J. L., and Poesen, J. (1999). Modified topsoil islands within patchy Mediterranean vegetation in SE Spain. *Catena* **38**, 23–44. doi: 10.1016/S0341-8162(99)00056-9

Boeken, B., Lipchin, C., Gutterman, Y., and van Rooyen, N. (1998). Annual plant community responses to density of small-scale soil disturbances in the Negev Desert of Israel. *Oecologia* **114**, 106–117. doi: 10.1007/s004420050426

Bossdorf, O., Schurr, F., and Schumacher, J. (2000). Spatial patterns of plant association in grazed and ungrazed shrublands in the semi-arid Karoo, South Africa. *Journal of Vegetation Science* **11**, 253–258. doi: 10.2307/3236804

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. doi: 10.1006/jare.1998.0479

Clarke, K. R., and Gorley, R. N. (2001). 'PRIMER v5: User manual/tutorial.' (PRIMER-E: Ivybridge, UK)

Contreras, L. C., and Gutierrez, J. R. (1991). Effects of the subterranean herbivorous rodent *Spalacopus cyanus* on herbaceous vegetation in arid coastal Chile. *Oecologia* **87**, 106–109. doi: 10.1007/BF00323787

Cooper, W. E. Jr., and Whiting, M. J. (2000). Islands in a sea of sand: use of *Acacia* trees by tree skinks in the Kalahari Desert. *Journal of Arid Environments* **44**, 373–381. doi: 10.1006/jare.1999.0616

Davidson, A. D., and Lightfoot, D. C. (2006). Keystone rodent interactions: prairie dogs and kangaroo rats structure the biotic composition of a desertified grassland. *Ecography* **29**, 755–765. doi: 10.1111/j.2006.0906-7590.04699.x

Dean, W. R. J., and Milton, S. J. (1991). Patch disturbances in arid grassy dunes: antelope, rodents and annual plants. *Journal of Arid Environments* **20**, 231–237.

Dean, W. R. J., Milton, S. J., and Jeltsch, F. (1999). Large trees, fertile islands, and birds in arid savanna. *Journal of Arid Environments* **41**, 61–78. doi: 10.1006/jare.1998.0455

Dunkerley, D. L., and Brown, K. J. (1995). Runoff and runon areas in a patterned chenopod shrubland, arid western New South Wales, Australia: characteristics and origin. *Journal of Arid Environments* **30**, 41–55. doi: 10.1016/S0140-1963(95)80037-9

Eldridge, D. J. (1993). Effects of ants on sandy soils in semi-arid eastern Australia: Local distribution of nest entrances and their effect on infiltration of water. *Australian Journal of Soil Research* **31**, 509–518. doi: 10.1071/SR9930509

Eldridge, D. J. (2004). Mounds of the American badger (*Taxidea taxus*): significant geomorphic features of North American shrub-steppe ecosystems. *Journal of Mammalogy* **85**, 1060–1067. doi: 10.1644/BEH-105.1

Eldridge, D. J., and Greene, R. S. B. (1994). Assessment of sediment yield from a semi-arid red earth with varying cover of cryptogams. *Journal of Arid Environments* **26**, 221–232. doi: 10.1006/jare.1994.1025

Eldridge, D. J., and Mensinga, A. (2007). Foraging pits of the short-beaked echidna (*Tachyglossus aculeatus*) as small-scale patches in a semi-arid Australian box woodland. *Soil Biology & Biochemistry* **39**, 1055–1065. doi: 10.1016/j.soilbio.2006.11.016

Eldridge, D. J., and Myers, C. A. (2001). 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. doi: 10.1006/jare.2000.0685

Eldridge, D. J., and Rath, D. (2002). Hip holes: kangaroo (*Macropus* spp.) resting sites modify the physical and chemical environments of woodlands. *Austral Ecology* **27**, 527–536. doi: 10.1046/j.1442-9993.2002.01212.x

Fischer, J., and Lindenmayer, D. B. (2002). The conservation value of paddock trees for birds in a variegated landscape in southern New South Wales. 1. Species composition and site occupancy patterns. *Biodiversity and Conservation* **11**, 807–832. doi: 10.1023/A:1015371511169

Garkaklis, M. J., Bradley, J. S., and Wooler, R. D. (2000). Digging by vertebrates as an activity promoting the development of water-repellent patches in sub-surface soil. *Journal of Arid Environments* **45**, 35–42. doi: 10.1006/jare.1999.0603

Garkaklis, M. J., Bradley, J. S., and Wooler, R. D. (2003). The relationship between animal foraging and nutrient patchiness in south-west Australian woodland soils. *Australian Journal of Soil Research* **41**, 665–673. doi: 10.1071/SR02109

Garner, W., and Steinberger, Y. (1989). A proposed mechanism for the formation of 'fertile islands' in the desert ecosystem. *Journal of Arid Environments* **16**, 257–262.

Gibb, K., Beard, J., O'Reagain, P., Christian, K., Torok, V., and Ophel-Keller, K. (2008). Assessing the relationship between patch type and soil mites: a molecular approach. *Pedobiologia* **51**, 445–461. doi: 10.1016/j.pedobi.2008.01.004

Greene, R. S. B. (1992). Soil physical properties of three geomorphic zones in a semi-arid mulga woodland. *Australian Journal of Soil Research* **30**, 55–69. doi: 10.1071/SR9920055

Gutierrez, R. J., and Whitford, W. G. (1987). Effects of eliminating subterranean termites on the growth of creosotebush *Larrea tridentata*. *The Southwestern Naturalist* **34**, 549–551. doi: 10.2307/3671517

Gutterman, Y. (1997). Ibex diggings in the Negev Desert highlands of Israel as microhabitats for annual plants. Soil salinity, location, and digging depth affecting variety and density of plant species. *Journal of Arid Environments* **37**, 665–681. doi: 10.1006/jare.1997.0305

Gutterman, Y., Golan, T., and Garsani, M. (1990). Porcupine diggings as a unique ecological system in a desert environment. *Oecologia* **51**, 332–334. doi: 10.1007/BF00540902

Hone, J. (1988). Feral pig rooting in a mountain forest and woodland: distribution, abundance and relationships with environmental variables. *Australian Journal of Ecology* **13**, 393–400. doi: 10.1111/j.1442-9993.1988.tb00987.x

Hongo, A., Matsumoto, S., Takahashi, H., Zou, H., and Cheng, J. (1993). Effects of mounds of the Cansu mole-rat (*Myospalax cansus* Lyon.) on shrub steppe vegetation on the Loess Plateau, north-west China. *Journal of the Japanese Society of Grassland Science* **39**, 306–316.

Iason, G. R., Manso, T., Sim, D. A., and Hartley, F. G. (2002). The functional response does not predict the local distribution of European rabbits (*Oryctolagus cuniculus*) on grass swards: experimental evidence. *Functional Ecology* **16**, 394–402. doi: 10.1046/j.1365-2435.2002.00640.x

Isbell, R. F. (1996). 'The Australian Soil Classification.' (CSIRO Publishing: Melbourne.)

Jackson, E. C., Krogh, S. N., and Whitford, W. G. (2003). Desertification and biopedturbation in the northern Chihuahuan Desert. *Journal of Arid Environments* **53**, 1–14. doi: 10.1006/jare.2002.1022

James, A. I., and Eldridge, D. J. (2007). Reintroduction of fossorial native mammals and potential impacts on ecosystem processes in an Australian desert landscape. *Biological Conservation* **138**, 351–359. doi: 10.1016/j.biocon.2007.04.029

Johnson, C. N. (1994). Distribution of feeding activity of the Tasmanian Bettong (*Bettongia gaimardi*) in relation to vegetation patterns. *Wildlife Research* **21**, 249–255. doi: 10.1071/WR9940249

Kay, F. R., and Whitford, W. G. (1978). Burrow environment of the banner-tailed kangaroo rat, *Dipodomys spectabilis*, in south-central New Mexico. *American Midland Naturalist* **99**, 270–279. doi: 10.2307/2424805

Leigh, J. H., Wood, D. H., Holgate, M. C., Slee, A., and Stanger, M. G. (1989). Effects of rabbit and kangaroo grazing on two semi-arid grassland communities in central-western New South Wales. *Australian Journal of Botany* **37**, 375–396. doi: 10.1071/BT9890375

Levin, S. A. (1992). The problem of pattern and scale in ecology. *Ecology* **73**, 1943–1967. doi: 10.2307/1941447

Lucero, M. E., Barrow, J. R., Osuna, P., and Reyes, I. (2006). Plant–fungal interactions in arid and semi-arid ecosystems: large-scale impacts from microscale processes. *Journal of Arid Environments* **65**, 276–284. doi: 10.1016/j.jaridenv.2005.08.014

Ludwig, J. A., Wilcox, B. P., Breshears, D. D., Tongway, D. J., and Imeson, A. C. (2005). Vegetation patches and runoff-erosion as interacting ecohydrological processes in semiarid landscapes. *Ecology* **86**, 288–297. doi: 10.1890/03-0569

McCullough, D. R., and McCullough, Y. (2000). 'Kangaroos in Outback Australia: Comparative Ecology and Behaviour of Three Coexisting Species.' (Columbia University Press: New York.)

Minitab (1997). 'Reference Manual, Release 14.' (Minitab Inc., State College: PA.)

Murray, J. V., Low Choy, S., McAlpine, C. A., Possingham, H. P., and Goldizen, A. W. (2008). The importance of ecological scale for wildlife conservation in naturally fragmented environments: a case study of the rush-tailed rock wallaby (*Petrogale penicillata*). *Biological Conservation* **141**, 7–22. doi: 10.1016/j.biocon.2007.07.020

Nkem, J. N., Lobry de Bruyn, L. A., Grant, C. D., and Hulugalle, N. R. (2000). The impact of ant bioturbation and foraging activities on surrounding soil properties. *Pedobiologia* **44**, 609–621. doi: 10.1078/S0031-4056(04)70075-X

Noble, J. C., Diggle, P. J., and Whitford, W. G. (1989). The spatial distributions of termite pavements and hummock feeding sites in a semi-arid woodland in eastern Australia. *Acta Oecologica* **10**, 355–376.

Noble, J. C., Gillen, J., Jacobson, G., Low, W. A., Miller, C., and Mutitjulu, Community (2001). The potential for degradation of landscape function and cultural values following the extinction of mitika (*Bettongia lesueur*) in Central Australia. *In*: 'Land Degradation in Australia'. (Ed. A. Conacher.) pp. 71–89. (Kluwer Scientific Publications: Dordrecht, The Netherlands.)

Noble, J. C., and Tongway, D. J. (1986). Herbivores in arid and semi-arid rangelands. *In*: 'Australian Soils: The Human Impact'. (Eds J. S. Russell and R. F. Isbell.) pp. 243–270. (University of Queensland Press: St Lucia, Qld.)

Okin, G. S., Gillette, D. A., and Herrick, J. E. (2006). Multi-scale controls on and consequences of aeolian processes in landscape change in arid and semi-arid environments. *Journal of Arid Environments* **65**, 253–275. doi: 10.1016/j.jaridenv.2005.06.029

Ongley, E. D. (1974). Fluvial morphometry on the Cobar Pediplain. *Annals of the Association of American Geographers* **64**, 281–292. doi: 10.1111/j.1467-8306.1974.tb00977.x

Pandolfi, J. M. (2002). Coral community dynamics at multiple scales. *Coral Reefs* **21**, 13–23.

Payne, R. W., Lane, P. W., Digby, P. G. N., Harding, S. A., Leech, P. K., *et al.* (1993). 'Genstat 5 Release 3 Reference Manual.' (Oxford University Press: New York.)

Peters, D. P. C., and Havstad, K. M. (2006). Nonlinear dynamics in arid and semi-arid systems: Interactions among drivers and processes across scales. *Journal of Arid Environments* **65**, 196–206. doi: 10.1016/j.jaridenv.2005.05.010

Reichman, O. J., Benedix, J. H., and Seastedt, T. R. (1993). Distinct animal-generated edge effects in a tallgrass prairie community. *Ecology* **74**, 1281–1285. doi: 10.2307/1940496

Rismiller, P. (1999). 'The Echidna: Australia's Enigma.' (Hugh Lauter Levin Associates: Westport, CT.)

Saab, V. (1999). Importance of scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. *Ecological Applications* **9**, 135–151. doi: 10.1890/1051-0761(1999)009[0135:IOSSTH]2.0.CO;2

Sapir, N., Abramsky, Z., Shochat, E., and Izhaki, I. (2004). Scale-dependent habitat selection in migratory frugivorous passerines. *Naturwissenschaften* **91**, 544–547. doi: 10.1007/s00114-004-0564-2

Schlesinger, W. H., Raikes, J. A., Hartley, A. E., and Cross, A. F. (1996). On the spatial pattern of soil nutrients in desert ecosystems. *Ecology* **77**, 364–374. doi: 10.2307/2265615

Schooley, R. L., and Wiens, J. A. (2001). Dispersion of kangaroo rat mounds at multiple scales in New Mexico, USA. *Landscape Ecology* **16**, 267–277. doi: 10.1023/A:1011122218548

Smallwood, K. S., and Morrison, M. L. (1999). Estimated burrow volume and excavation rate for pocket gophers (Geomyidae). *The Southwestern Naturalist* **44**, 173–183.

Smith, A. P., Wellham, G. S., and Green, S. W. (1989). Seasonal foraging activity and microhabitat selection by echidnas (*Trachyglossus aculeatus*) on the New England Tablelands. *Australian Journal of Ecology* **14**, 457–466. doi: 10.1111/j.1442-9993.1989.tb01455.x

Steele, V. R., and Temple-Smith, P. D. (1998). Physical structure of warrens of a small colony of southern hairy-nosed wombats *Lasiorhinus latifrons*. *In*: 'Wombats'. (Eds R. T. Wells and P. A. Pridmore.) pp. 113–124. (Surrey-Beatty and Sons: Chipping Norton.)

Tongway, D. J., Ludwig, J. A., and Whitford, W. G. (1989). Mulga log mounds: fertile patches in the semi-arid woodland of eastern Australia. *Australian Journal of Ecology* **14**, 263–268. doi: 10.1111/j.1442-9993.1989.tb01436.x

White, E. M., and Carlson, D. C. (1984). Estimating soil mixing by rodents. *Proceedings of the South Dakota Academy of Science* **63**, 34–37.

Whitford, W. G. (1998). Contribution of pits dug by goannas (*Varanus gouldii*) to the dynamics of banded mulga landscapes in eastern Australia. *Journal of Arid Environments* **40**, 453–457. doi: 10.1006/jare.1998.0464

Whitford, W. G. (2002). 'The Ecology of Desert Ecosystems.' (Academic Press: New York.)

Whitford, W. G., and DiMarco, R. (1995). Variability in soils and vegetation associated with harvester ant (*Pogonomyrmex rugosus*) nests on a Chihuahuan Desert watershed. *Biology and Fertility of Soils* **20**, 169–173. doi: 10.1007/BF00336554

Whitford, W. G., and Kay, F. R. (1999). Biopedturbation by mammals in deserts: a review. *Journal of Arid Environments* **41**, 203–230. doi: 10.1006/jare.1998.0482

Wiens, J. A. (1989). Spatial scaling in ecology. *Functional Ecology* **3**, 385–397. doi: 10.2307/2389612

Wiens, J. A., and Milne, B. T. (1989). Scaling of 'landscapes' in landscape ecology, or, landscape ecology from a beetle's perspective. *Landscape Ecology* **3**, 87–96. doi: 10.1007/BF00131172

Yair, A., and Rutin, J. (1981). Some aspects of the regional variation in the amount of available sediment produced by isopods and porcupines in northern Negev, Israel. *Earth Surface Processes and Landforms* **6**, 221–234. doi: 10.1002/esp.3290060304

York Main, B. (2001). Historical ecology, responses to current ecological changes and conservation of Australian spiders. *Journal of Insect Conservation* **5**, 9–25. doi: 10.1023/A:1011337914457