

Formation of nutrient-poor soil patches in a semi-arid woodland by the European rabbit (*Oryctolagus cuniculus* L.)

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Abstract European rabbits (*Oryctolagus cuniculus* L.) occur over large areas of eastern Australia, where they disturb significant quantities of soil while constructing warrens. Although the effects of rabbits on vegetation are generally well understood, little is known about their effects on soil physical or chemical properties. We studied the effect of rabbit warrens on soil chemistry in a semi-arid woodland supporting a high density of rabbit warrens. Within one large warren, we examined nutrient concentrations within three microsites (mound, inter-mound and an intermediate disturbed area) representing a gradient of increasing rabbit disturbance, and supported this with a study of soil nutrients with depth within 1-m-deep trenches through five warrens. Landscape-level changes in surface chemistry were also examined at an additional 23 warrens. At both patch and landscape scales, pH, electrical conductivity, soluble and exchangeable Ca²⁺ and K⁺, and total Al and Ca generally increased with increasing rabbit disturbance, while total C and S (LECO), total P and S (ICP), and soluble Na⁺ declined, and total N remained unchanged. Although chemical changes with depth were generally ill defined, surface soils tended to be more similar in their composition than deeper soils. Overall, our results reinforced the view that rabbits have a negative effect on surface soils in semi-arid woodlands, and suggested that restoration of the original woodland vegetation may be hampered by changes in soil biogeochemistry associated with the warrens.

Key words: biopedturbation, disturbance, ecosystem engineering, soil chemistry, woodland.

INTRODUCTION

Many organisms change their physical and chemical environment when they forage for food or create or modify habitat to suit their needs (Day *et al.* 2003). This niche construction, which has been described as ecosystem engineering (Jones *et al.* 1997), results in changes to the flow of resources within ecosystems, and may influence the stability and resilience of ecosystems (Jones *et al.* 1997; Day *et al.* 2003). The term 'physical ecosystem engineer' has been used to describe those organisms that create, modify or maintain habitat for a range of organisms by modulating the supply of resources such as habitat or space without actually consuming them (Wilby *et al.* 2001). By changing the way that resources such as sediment and soil are generated, transported or retained, these organisms can have major impacts on ecosystems, and alter feedback processes on themselves and other organisms (Jones *et al.* 1997). The effects of physical

ecosystem engineers are most obvious in dry lands and deserts, where essential resources, such as water, sediment, nutrients and organic matter, are spatially and temporally limiting.

The European rabbit (*Oryctolagus cuniculus* L.) is a physical ecosystem engineer that alters the distribution of resources, specifically soil. In its native habitat in Spain, the European rabbit lives predominantly above-ground, sheltering under bushes and small shrubs. In Australia, however, rabbits generally live in large underground communal burrow systems (warrens) with multiple surface entrances. Like burrow systems of other fossorial and semi-fossorial animals, warrens provide protection from environmental extremes (Hall & Myers 1978; Wilkinson *et al.* 1998; Kinlaw 1999), are essential for evading predators (Wood 1988), are refuges for raising young and therefore centres of population growth and stabilization (Myers & Parker 1975), and are often sites for socialization, particularly on the mounds around the entrances (Hansell 1993; Kinlaw 1999). The structure of rabbit warrens also makes them ideal refugia for a range of other organisms, such as reptiles and amphibians (Read & Owens 1999; Heard *et al.* 2005), echidnas (Wilkinson *et al.* 1998), small mammals (Noble 1993) and some birds.

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Warrens also provide refuge for residual rabbit populations during droughts (Myers & Parker 1975).

Rabbits and their warrens occur over large areas of southern Australia, where a combination of a Mediterranean climate with hot summers and mild winters, friable soils suitable for digging, and few natural predators make it an ideal environment (Parker *et al.* 1976). Rabbits have two significant environmental effects: a trophic-level effect through herbivory, and an ecosystem engineering or facilitatory effect resulting from the construction of their warrens. Grazing by rabbits has substantial detrimental effects on native plants, and browsing is implicated in the decline in recruitment of many long-lived trees, such as *Acacia* spp., in the semi-arid woodlands (Lange & Graham 1983). Rabbits also eat seedlings and young stems of grasses and shrubs, reducing the rate at which these plants recover after droughts (Lange & Graham 1983; Foran 1986; Myers *et al.* 1994; Denham & Auld 2004). Many studies have demonstrated that the effects of grazing by rabbits combined with extreme drought can have disastrous consequences for the health and diversity of the arid-zone vegetation (e.g. Wood 1988; Leigh *et al.* 1989; Eldridge *et al.* 2006).

Digging by animals creates patches of soil that differ markedly from the surrounding soil matrix (Whitford & Kay 1999), often producing substantial effects on plant community structure (e.g. Contreras & Gutierrez 1991; Chew & Whitford 1992; Boeken *et al.* 1995; Guo 1996). Disturbance by European rabbits preferentially benefits exotic plants at the expense of native plants, and results in substantial reductions in plant diversity and richness (Tiver & Andrew 1997; Eldridge *et al.* 2006). Less well known, however, is the effect of rabbits on the soil ecosystem (but see Eldridge & Myers 1999) and, consequently, their putative role as ecosystem engineers. During warren construction, rabbits excavate large volumes of subsoil, depositing it on the surface (Myers *et al.* 1994), smothering the extant vegetation. During warren construction and re-activation, clay-rich subsoil with adsorbed nutrients and cations is transported to the surface, resulting in changes in the vegetation community. Subsoils are generally poorly structured, being subject to physical crusting and surface sealing by raindrop action, and resulting in an increased risk of wind and water erosion (Eldridge & Greene 1994; Walker *et al.* 1995). Furthermore, warren excavation is an ongoing process, with rabbits regularly excavating new burrows and channels when the soil is damp, thereby increasing the size of the warrens (Myers *et al.* 1994).

While the generally accepted view is that rabbits adversely affect soil surfaces, for example by reducing roughness and vegetative cover (e.g. Voslamber & Veen 1985; Milton *et al.* 1997; Eldridge & Myers 1999, 2001; Eldridge & Simpson 2002), little is known about their effect on soil chemistry. As far as we are aware,

no studies have documented changes in soil nutrients with depth, or differences at the scale of individual warrens. As warrens are used by successive generations of rabbits, it is likely that any physical and biogeochemical effects would be reinforced.

The objective of our study was to document the changes in soil chemistry associated with rabbit warrens. Our aims were to examine changes in soil chemistry across a gradient in disturbance from an undisturbed soil surface to a heavily disturbed rabbit warren. In doing this, we examined changes in soil chemistry at two different scales: (i) at the scale of individual warrens (patch scale) both across the surface of one large warren, and at depth on five warrens that have each been paired with an adjacent inter-mound, non-warren area; and (ii) at the community (landscape) scale, where differences were examined between warrens located over an area of about 100 ha.

METHODOLOGY

The study area

The study was carried out at Yathong Nature Reserve (32°35'S, 145°35'E, altitude 200–425 m), located approximately 130 km south of Cobar, in western New South Wales, Australia. The reserve is a UNESCO Man in the Biosphere Reserve and was formerly managed as a pastoral (grazing) station. Sheep and cattle were removed from the reserve in 1977, but eastern grey kangaroos (*Macropus giganteus*) and western grey kangaroos (*M. fuliginosus*) are present in high numbers up to 40 per square kilometre (McCullough & McCullough 2000). Rabbit grazing was once extensive over large areas of the reserve, but a combination of rabbit haemorrhagic disease, regular ripping of warrens and drought has drastically reduced their numbers.

Annual rainfall for the study site is highly variable from year to year, averaging 350 mm (Leigh *et al.* 1989). Evaporation is high, particularly in the non-winter months, with an annual mean of 1952 mm (Leigh *et al.* 1989). Maximum and minimum diurnal temperatures range from 35.0°C and 19.6°C in summer to 16.0°C and 3.6°C in winter (Eldridge & Greene 1994). The soils are classified (Soil Survey Staff 1975) as Typic Haplargids. Typical soil profiles consist of a clay loam to loamy clay surface horizon up to 60 cm deep overlying a light-medium clay B-horizon. Detailed profile descriptions are given in Eldridge and Greene (1994). The study area was located within a large colluvial fan about 800 m from the base of the Merriwagga Ranges.

Vegetation in the study area is predominantly semi-arid woodland dominated by western red box

(*Eucalyptus intertexta* R.T. Baker), bumble box (*E. populnea* F. Muell.) and white cypress pine (*Callitris glaucophylla* J. Thomps. & L.A.S. Johnson). The midstorey component consisted of shrubs of the genera *Dodonaea*, *Senna* and *Acacia*, and the understorey was dominated by perennial grasses, such as speargrass (*Austrostipa scabra* (Lindl.) S.W.L. Jacobs & Everett), white-top grass (*Austrodanthonia caespitosa* (Gaudich.) H.P. Linder) and number nine wiregrass (*Aristida jerichoensis* (Domin.) Henrard). The herbaceous vegetation occupies approximately 30–40% of the soil surface with a similar proportion of the surface occupied by biological soil crusts (Eldridge & Greene 1994).

Study design

Warrens are easily recognized by their slightly elevated, concave surface profile, and their often distinct assemblage of exotic vegetation. A previous study (Eldridge & Myers 1999) identified three microsites within a warren complex: the mound, the disturbed area and the inter-mound (control) area. The mound is the elevated section of the warren system, where the soil surface is generally extensively disturbed because the rabbits tend to congregate. The area away from the influence of the warren, where no soil disturbance is evident, is referred to as the inter-mound (control). An intermediate area with elements of both inter-mound and mound microsites is termed the 'disturbed' area and is characterized by scratchings, dung piles, small mounds of disturbed soil and undisturbed biological soil crust (Wood 1988; Eldridge & Myers 1999).

Our study examined differences both within and among warrens at the surface and at depth. The patch-level studies were carried out on five warrens used previously for a study of rabbit effects on vegetation (Eldridge & Myers 1999). Warrens were selected on the basis of three criteria. First, they had to be more than 150 m from the nearest adjacent warren in order to ensure that warren-free surfaces were not unduly influenced by nearby warrens. Second, warrens under or near trees were avoided, as *Eucalyptus* trees are known to influence soil physical and chemical properties (Tongway & Smith 1989; Eldridge & Rath 2002). Third, only warrens of comparable size were selected in order to avoid possible confounding effects of warren size (and therefore rabbit activity) on soil chemistry.

One of the five warrens was selected for the first patch-level study of spatial variation in nutrients, because it was large with a regular shape and would therefore provide a large number of 'independent' locations for sampling of surface soils. For this study, we established a grid of 196 1-m² quadrats (14 m by 14 m) centred on the highest point of the warren. These quadrats formed the basis for the collection of

soil samples. Each 1-m² quadrat was characterized as either mound, disturbed or inter-mound, depending on the dominant type in that quadrat. We then randomly selected 45 quadrats, comprising 27 inter-mound, 9 mound and 9 disturbed quadrats, in proportion to the relative cover of the three microsites over the 196 quadrats. Soil samples were taken from the surface 2 cm of the soil at a predetermined location within each quadrat.

The second patch-scale study examined nutrient change with depth. A trench was dug approximately 1 m deep, about 10 m long and 0.5 m wide from the centre of each of the five warrens described previously. This trench traversed both the mound and inter-mound microsites within each warren. For this study we sampled only mound and inter-mound microsites, as we were interested in the extremes of the warren complex gradient. Soil samples were collected from the exposed face at two locations for each of mound and inter-mound microsites from five depths (0–2, 5–10, 15–20, 40–50 and 70–80 cm). Samples were collected from either side of the centre of the warren (for mound microsites) and at either end of the trench (for the inter-mound microsites).

The landscape-scale study focused on the mound, disturbed and inter-mound microsites sampled at an additional 23 warrens located within an area of about 1 km² in the study area. Warrens were selected by walking along a transect in a predetermined direction, and selecting all warrens within 20 m of both sides of the transect. At each warren, we collected three soil samples from the top 2 cm of each microsite, bulked them, and used a 500-g subsample for chemical analyses.

Soil analyses

Except where indicated, duplicate soil samples ($n = 2$) were used for all analyses according to the following methods:

- pH (1:5 soil : water and 0.01 M CaCl₂ extract) and electrical conductivity (EC) using a 1:5 soil–water suspension shaken for 1 h;
- total carbon, nitrogen and sulphur using a high combustion LECO CNS-2000 analyser;
- Soluble and exchangeable cations (Ca²⁺, K⁺, Mg²⁺ and Na⁺) were determined using a Unicam 929 Atomic Absorption Spectrometer (AAS) in 1:5 soil : water and 1:5 soil : NH₄Cl extracts, respectively;
- total Ca, Al, P and S using inductively coupled plasma spectroscopy (Perkin Elmer Optima 3000 DV ICP-OES) for the depth study only; and
- particle size analysis of the <2.0-mm fraction using dispersed samples (Loveday 1974) for the depth study only.

To aid interpretation of the results of the depth study, various indices were derived: the proportion of fine material in the sediments (<20- μm fraction divided by the fraction >20 μm), C : N ratio, and total soluble and total exchangeable cations.

Statistical analyses

For the patch-level study at the detailed warren, we used one-way ANOVA to test for differences in soil physical and chemical properties, as locations in which the three microsites were sampled were randomly selected from across the warren; that is, there was no need for a blocking factor. For the depth study, given the extreme variability in the concentration of most soil nutrients between treatments and depths, we were unable to use ANOVA because transformation failed to stabilize the variances. Consequently, we used multivariate analyses and present the data graphically. A matrix comprising the values for each of 17 soil properties for the five warrens by two microsites by five depths ($n = 50$) was subjected to principal components analysis (PCA) using the PRIMER (version 4) statistical package (Clarke & Warwick 1994). Each variable was first normalized by subtracting the mean and dividing by the standard deviation in order to bring the data with mixed measurement scales to a common dimensionless scale. Derived variables, such as total soluble cations, were not included in the PCA because they were already known to be correlated with

the original variables. For the landscape-level study of the 23 warrens, we used a two-way ANOVA with warrens as Blocks, and tested for significance between microsites by using the Block (Warrens)-by-Microsite interaction as the residual mean square (d.f. = 44). Data subjected to ANOVA were first checked for homogeneity of variance using Levene's test (Minitab 1997) and diagnostic tools within the Minitab (1997) statistical program and transformed, where necessary, to stabilize the variance before undertaking ANOVA.

RESULTS

Patch-level variation in surface soil chemistry

There were clear differences between the mound, disturbed and inter-mound microsites within the large warren complex (Table 1). Soil pH and EC levels increased significantly with increasing disturbance, that is, from inter-mound, through disturbed to mound microsites ($P < 0.01$). Soluble and exchangeable Ca^{2+} and K^+ increased significantly with increased levels of disturbance, while soluble Na^+ decreased and exchangeable Na^+ remained unchanged. There were also significant increases in total Al and Ca with disturbance, a decline in total P, but no change in total S (ICP) with disturbance.

Concentrations of total C, N and S (LECO) decreased with increasing disturbance, but only differences in S were significant ($P < 0.001$; Table 1).

Table 1. Soil (0–2 cm) chemical data for mound, disturbed and inter-mound microsites from a single warren at Yathong Nature Reserve ($n = 45$ locations)

| Attribute | Inter-mound ($n = 27$) | Microsite disturbed ($n = 9$) | Mound ($n = 9$) | <i>P</i> -value | Trend with increasing disturbance† |
|---|-----------------------------|---------------------------------------|----------------------|-----------------|--|
| pH (1:5 water) | 6.25 ^a | 6.60 ^b | 6.87 ^c | <0.001 | Increase |
| pH (CaCl_2) | 5.28 ^a | 5.98 ^b | 6.75 ^c | <0.001 | Increase |
| EC (dS m^{-1}) | 0.071 ^a | 0.089 ^{ab} | 0.120 ^b | 0.01 | Increase |
| Total C (%) | 1.89 ^a | 1.75 ^a | 1.48 ^a | NS | – |
| Total N (%) | 0.16 ^a | 0.14 ^a | 0.11 ^a | NS | – |
| Total S (%) | 0.007 ^a | 0.006 ^{ab} | 0.004 ^b | <0.001 | Decrease |
| Total Ca (mg kg^{-1}) | 1738.6 ^a | 2498.5 ^b | 3634.9 ^c | <0.001 | Increase |
| Total Al (mg kg^{-1}) | 42380 ^a | 39432 ^b | 44333 ^a | 0.028 | * |
| Total P (mg kg^{-1}) | 171.5 ^a | 160.7 ^{ab} | 137.5 ^b | 0.023 | Decrease |
| Total S (mg kg^{-1}) | 184.3 ^a | 200.5 ^a | 177.0 ^a | NS | – |
| Soluble Ca (cmol (+) kg^{-1}) | 0.107 ^a | 0.194 ^a | 0.370 ^b | <0.001 | Increase |
| Soluble Mg (cmol (+) kg^{-1}) | 0.062 ^a | 0.060 ^a | 0.077 ^a | NS | – |
| Soluble Na (cmol (+) kg^{-1}) | 0.026 ^a | 0.020 ^b | 0.019 ^b | 0.002 | Decrease |
| Soluble K (cmol (+) kg^{-1}) | 0.147 ^a | 0.224 ^b | 0.231 ^b | 0.045 | Increase |
| Exchangeable Ca (cmol (+) kg^{-1}) | 5.780 ^a | 8.136 ^b | 10.347 ^c | <0.001 | Increase |
| Exchangeable Mg (cmol (+) kg^{-1}) | 2.130 ^a | 1.860 ^b | 1.841 ^b | 0.007 | Decrease |
| Exchangeable Na (cmol (+) kg^{-1}) | 0.024 ^a | 0.025 ^a | 0.027 ^a | NS | – |
| Exchangeable K (cmol (+) kg^{-1}) | 1.301 ^a | 1.714 ^b | 1.767 ^b | <0.001 | Increase |

Different superscripts within an attribute across microsites indicate a significant difference at $P < 0.05$. *Significant effect, but no meaningful disturbance effect. †From 'inter-mound' to 'disturbed' to 'mound'; –, NS, no significant change.

Patch-level variation in soil chemistry with depth

Changes in soil properties with depth were generally ill defined due to substantial differences between individual mounds and their associated inter-mound surfaces (Table 2, Fig. 1). Overall, mound soils were more variable in their chemical composition than the inter-mound soils (Fig. 1).

Principal components analyses indicated a gradient in soil chemistry from samples closer to the surface (high PC1 scores) to deeper soils (lower PC1 scores; Fig. 2b). Fifty-eight per cent of the variability in the 17 soil characteristics was captured in the first two dimensions. Surface soils tended to be more similar in their chemical composition than soils deeper within the profile, which had widely varying scores along the first axis (Fig. 2b).

The first principal component axis (PC1) represented mainly decreasing values of silt and clay, and soluble and exchangeable cations, particularly Mg^{2+} and Na^+ from the left- to right-hand side of Figure 2a. There was a significant depth effect on the first axis

($F_{4,45} = 17.15$, $P < 0.001$). The four depths less than 50 cm were not significantly different in their general chemical composition from each other, but were significantly different from samples at the greatest depth (70–80 cm; Fig. 2b). Increasing component 2 (PC2) scores were associated with increasing EC, soluble and exchangeable Ca^{2+} , soluble K^+ , and total N and C (Fig. 2a). The PCA biplot also indicated a moderate separation along the second axis between mound soils with high second component scores and non-mound soils with low scores ($t_{0.05} = 5.31$, d.f. = 38, $P < 0.001$, Fig. 2c).

Landscape-level variation in surface soil chemistry

Substantial differences in surface soil properties were apparent between the 23 individual warrens (Table 3). Both pH and EC increased, and total C and S (LECO) declined significantly with increases in disturbance ($P \leq 0.004$). Soluble and exchangeable Ca^{2+} and K^+ , and soluble Na^+ increased with increasing disturbance

Table 2. Chemical characteristics of mound and inter-mound soils at five depths on five warrens

| | 0–2 cm | | 5–10 cm | | 15–20 cm | | 40–50 cm | | 70–80 cm | |
|---|--------|---------|---------|---------|----------|---------|----------|---------|----------|---------|
| | Mound | I-mound | Mound | I-mound | Mound | I-mound | Mound | I-mound | Mound | I-mound |
| pH (1:5 water) | 8.04 | 6.81 | 8.08 | 6.65 | 8.03 | 6.70 | 7.86 | 7.26 | 8.20 | 8.12 |
| EC (dS m ⁻¹) | 0.080 | 0.032 | 0.088 | 0.016 | 0.157 | 0.016 | 0.282 | 0.034 | 0.158 | 0.088 |
| Total C (%) | 0.925 | 1.500 | 0.971 | 0.912 | 1.304 | 0.652 | 0.869 | 0.368 | 0.479 | 0.218 |
| Total N (%) | 0.062 | 0.110 | 0.066 | 0.057 | 0.085 | 0.041 | 0.064 | 0.027 | 0.044 | 0.022 |
| Total S (%) | 0.010 | 0.007 | 0.005 | 0.005 | 0.005 | 0.005 | 0.004 | 0.004 | 0.003 | 0.003 |
| C : N Ratio | 15.4 | 13.6 | 14.7 | 16.0 | 15.3 | 15.9 | 13.6 | 13.6 | 10.9 | 9.9 |
| % gravel | 3.0 | 1.9 | 3.0 | 2.0 | 2.5 | 2.5 | 2.7 | 4.1 | 1.9 | 3.5 |
| % clay | 23.4 | 21.8 | 24.7 | 24.3 | 21.0 | 26.7 | 25.5 | 31.7 | 38.7 | 40.1 |
| % sand | 64.5 | 67.7 | 64.7 | 65.9 | 68.2 | 63.9 | 63.6 | 61.0 | 48.3 | 43.7 |
| % silt | 12.1 | 10.5 | 10.6 | 9.8 | 10.8 | 9.5 | 11.0 | 7.3 | 12.9 | 16.2 |
| Ratio of fine : coarse material† | 0.55 | 0.48 | 0.55 | 0.52 | 0.47 | 0.56 | 0.58 | 0.64 | 1.20 | 1.38 |
| Soluble Na (cmol (+) kg ⁻¹) | 0.029 | 0.020 | 0.043 | 0.012 | 0.070 | 0.022 | 0.112 | 0.115 | 0.299 | 0.513 |
| Soluble K (cmol (+) kg ⁻¹) | 0.467 | 0.284 | 0.542 | 0.189 | 0.660 | 0.173 | 0.587 | 0.276 | 0.571 | 0.341 |
| Soluble Ca (cmol (+) kg ⁻¹) | 0.421 | 0.094 | 0.458 | 0.144 | 0.687 | 0.152 | 1.030 | 0.258 | 0.452 | 0.277 |
| Soluble Mg (cmol (+) kg ⁻¹) | 0.086 | 0.055 | 0.099 | 0.062 | 0.135 | 0.062 | 0.230 | 0.162 | 0.223 | 0.213 |
| Exchangeable Na (cmol (+) kg ⁻¹) | 0.096 | 0.066 | 0.045 | 0.067 | 0.090 | 0.075 | 0.104 | 0.171 | 0.735 | 0.927 |
| Exchangeable K (cmol (+) kg ⁻¹) | 3.806 | 3.197 | 3.281 | 2.830 | 3.992 | 2.912 | 3.280 | 3.098 | 5.254 | 4.737 |
| Exchangeable Ca (cmol (+) kg ⁻¹) | 11.167 | 5.524 | 8.934 | 5.489 | 11.478 | 5.726 | 10.923 | 6.012 | 10.766 | 10.107 |
| Exchangeable Mg (cmol (+) kg ⁻¹) | 1.995 | 2.423 | 1.813 | 1.912 | 1.924 | 1.957 | 2.254 | 3.078 | 5.736 | 6.720 |
| Total exchangeable cations (cmol (+) kg ⁻¹) | 17.07 | 11.21 | 14.07 | 10.30 | 17.48 | 10.67 | 16.56 | 12.36 | 22.49 | 22.49 |
| Total soluble cations (cmol (+) kg ⁻¹) | 1.00 | 0.45 | 1.14 | 0.41 | 1.53 | 0.41 | 1.96 | 0.81 | 1.55 | 1.34 |

Values are the means of five warrens (0–2, 5–10, 15–20, 40–50 and 70–80 cm). †Ratio of finer (<20 µm) to coarser (>20 µm) fractions. I-mound, inter-mound.

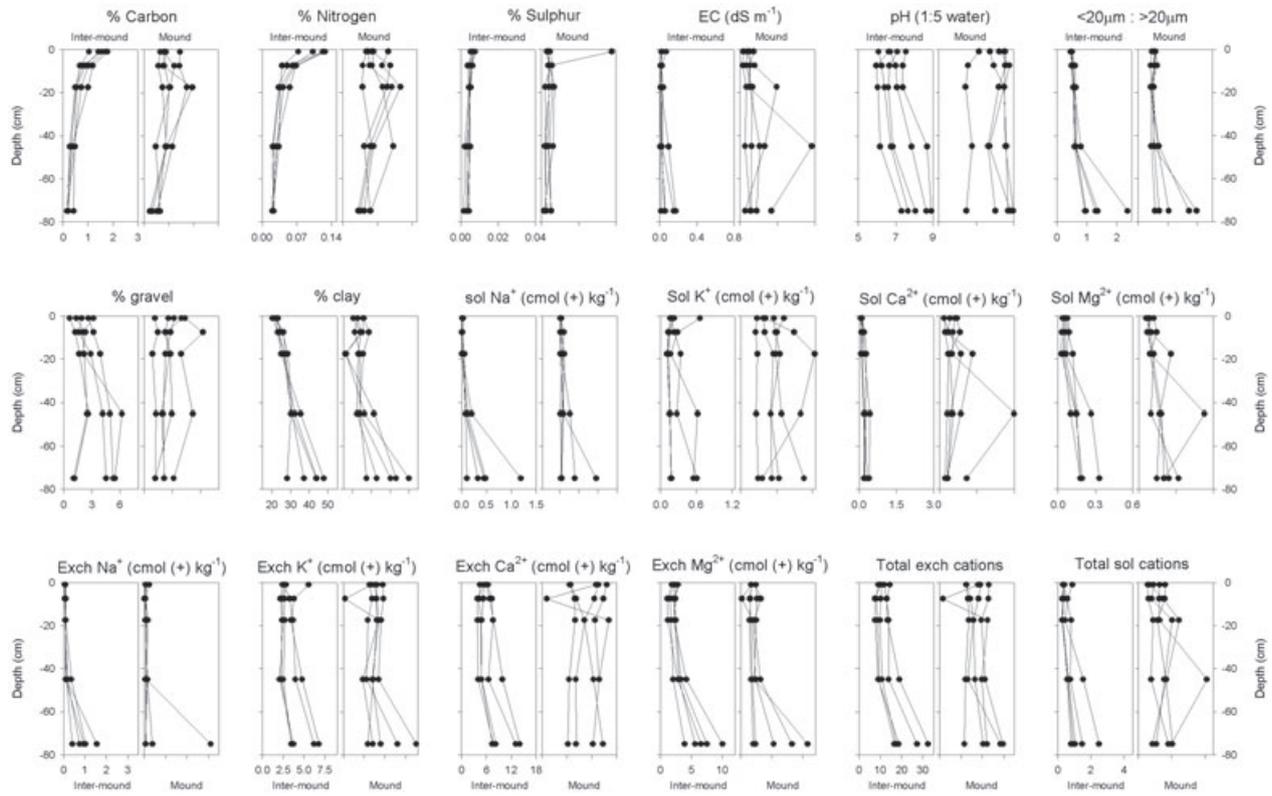


Fig. 1. Chemical characteristics of inter-mound and mound soils showing variation across five depths for five warrens. Scales are equivalent for each inter-mound and mound pair. Labelling has been omitted from the graphic where appropriate to reduce unnecessary detail.

($P < 0.043$, Table 3). Consistent with the patch-level study, concentrations of Al and Ca increased, but total P and S (ICP) declined, with increasing disturbance from inter-mound through disturbed to mound.

DISCUSSION

Warren construction, soil excavation and profile inversion by rabbits produced patches of disturbed soil differing markedly in chemical and physical properties from the surrounding soil matrix. Strong gradients in soil chemistry were apparent across the warrens from mounds to inter-mounds, but differences with depth through the soil profile were less well defined.

Rabbit-constructed mounds were biogeochemically distinct, and more variable, than inter-mound soils (Tables 1 and 3). Soil pH, EC and exchangeable Ca^{2+} and Mg^{2+} concentrations were greater on the mounds compared with the inter-mounds, accounting for 75% of the difference in chemistry between mounds and inter-mound soils. The concentrations of some nutrients and cations were clearly and consistently associated with the animal-disturbed mound soils, and changed with increasing levels of disturbance. Soluble

and exchangeable K^+ , and total Al and Ca increased with increasing disturbance, while total S (ICP) and P, soluble Na^+ and exchangeable Mg^{2+} declined (Tables 1 and 2).

Differences in warren chemistry are a direct consequence of soil removal and inversion brought about by burrowing and mound construction, which at Yathong is estimated to be in the order of 1.67 ± 0.11 tonnes of soil per hectare (Kwok 2005). Changes in the distribution of some cations (e.g. Ca^{2+} , Mg^{2+} , Na^+) are likely due to their redistribution, by wind and water (Schlesinger *et al.* 1996), from beneath the canopies of large eucalypts. Our data indicated a gradual increase in clay content on the non-mound soils from 21% at the surface to 40% at depth (Table 2). Concentrations of Ca and Al increased with rabbit disturbance, while S and P declined. Aluminium, for example, is relatively insoluble across a wide range of pH levels, and generally remains close to the site of weathering, where it is incorporated into clay minerals or hydrous oxides (Birkland 1974). Aluminium and Ca concentrations are, therefore, higher in the subsoil, where they are derived largely from parent material. Calcium carbonate, in the form of carbonate nodules or fine earth fraction, increases with depth in the Yathong soils.

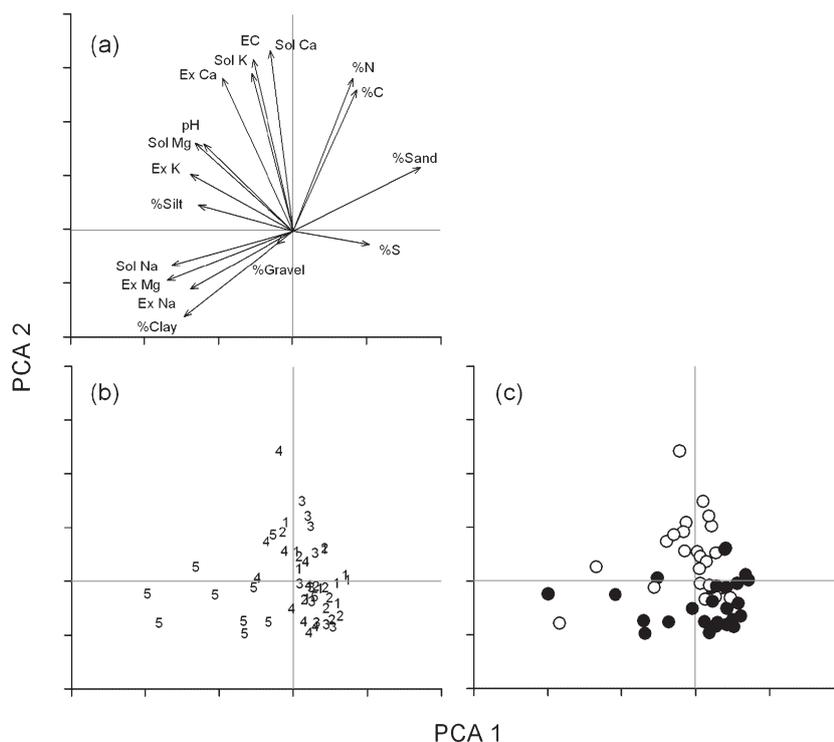


Fig. 2. Principal components analysis (PCA) biplot displaying the first two component axes for the depth study. Inter-relationships between soil variables are presented in graphic (a). Sites are coded for: depth using 1 (0–2), 2 (5–10), 3 (10–15), 4 (30–40) and 5 cm (70–80) in graphic (b); and for microsite using hollow circle (mound) and solid circle (non-mound) in graphic (c).

Table 3. Soil (0–2 cm) chemical data for inter-mound, disturbed and mound microsites averaged across 23 individual warrens at Yathong Nature Reserve

| Attribute | Inter-mound (<i>n</i> = 23) | Microsite disturbed (<i>n</i> = 23) | Mound (<i>n</i> = 23) | <i>P</i> -value | Trend with increasing disturbance† |
|--|---------------------------------|--|---------------------------|-----------------|--|
| pH (1:5 water) | 6.34 ^a | 6.71 ^b | 6.97 ^c | <0.001 | Increase |
| EC (dS m ⁻¹) | 0.098 ^a | 0.119 ^{ab} | 0.143 ^b | 0.004 | Increase |
| Total C (%) | 1.90 ^a | 1.77 ^a | 1.03 ^b | <0.001 | Decrease |
| Total N (%) | 0.146 ^a | 0.131 ^a | 0.142 ^a | NS | – |
| Total S (%) | 0.007 ^a | 0.006 ^a | 0.004 ^b | <0.001 | Decrease |
| Total Ca (mg kg ⁻¹) | 1647 ^a | 2325 ^b | 3247 ^c | <0.001 | Increase |
| Total Al (mg kg ⁻¹) | 44582 ^a | 45546 ^a | 49941 ^b | <0.001 | Increase |
| Total P (mg kg ⁻¹) | 181.0 ^a | 179.4 ^b | 128.2 ^c | <0.001 | Decrease |
| Total S (mg kg ⁻¹) | 184.0 ^a | 184.7 ^b | 146.2 ^c | <0.001 | Decrease |
| Soluble Ca (cmol (+) kg ⁻¹) | 0.169 ^a | 0.234 ^a | 0.343 ^b | 0.011 | Increase |
| Soluble Mg (cmol (+) kg ⁻¹) | 0.100 ^a | 0.089 ^a | 0.089 ^a | NS | – |
| Soluble Na (cmol (+) kg ⁻¹) | 0.260 ^{ab} | 0.230 ^a | 0.270 ^b | 0.043 | * |
| Soluble K (cmol (+) kg ⁻¹) | 0.210 ^a | 0.260 ^b | 0.300 ^c | 0.004 | Increase |
| Exchangeable Ca (cmol (+) kg ⁻¹) | 5.780 ^a | 7.260 ^b | 9.380 ^c | <0.001 | Increase |
| Exchangeable Mg (cmol (+) kg ⁻¹) | 2.180 ^a | 2.030 ^a | 1.890 ^a | NS | – |
| Exchangeable Na (cmol (+) kg ⁻¹) | 0.390 ^a | 0.380 ^a | 0.370 ^a | NS | – |
| Exchangeable K (cmol (+) kg ⁻¹) | 1.310 ^a | 1.620 ^b | 1.920 ^c | <0.001 | Increase |

Different superscripts among microsites within an attribute indicate a significant difference at *P* = 0.05. *Significant effect, but no meaningful disturbance effect. †Increasing disturbance from inter-mound to mound. –, NS, no significant change.

Consequently, higher concentrations of Al and Ca in mound soils compared with non-mound controls are indicative of the translocation of clay-rich sediment to the surface by rabbits.

Phosphorus, which does not have a biological input, is also largely derived from parent material, taken up by plants and recycled through litter fall. Decomposition of plant material by termites and microarthropods results in the recycling of P (Schaefer & Whitford 1981), and may account for the higher concentrations at the surface, corresponding with zones of greater biological activity. Plant-available P and S are frequently concentrated in the uppermost layers, particularly below the canopies of trees and shrubs (e.g. Ludwig *et al.* 2004), where they are redistributed to open areas by biotic and abiotic processes. Disturbance by rabbits therefore would have truncated their normal distributions, consistent with profiles for C and N, resulting in declining surface concentrations and reducing any concentrated patches. Lower P concentrations would likely have been exacerbated by the high pH of the warren soils (~8.0; Table 3), where binding to calcium minerals is common (Lajtha & Bloomer 1988). Analogous to the rabbit digging effect, concentrations of S (ICP) and P have been shown to be lower in the foraging pits of echidnas (Eldridge & Mensinga 2007).

Higher pH levels on mound compared with inter-mound soils could be due to various processes. Excavation of calcareous subsoil would expose lenses of calcrite (cemented calcium carbonate), and hardpans of cemented alumino-silicates, which are common below 30–40 cm (Isbell 2002). Unlike the locally extinct burrowing bettong (*Bettongia lesseur*) and the greater bilby (*Macrotis lagotis*) that occupied this landscape prior to European settlement (Noble 1999), rabbits would not have been able to penetrate the heavily indurated calcrite. Nonetheless, they would have been able to transport already detached material to the surface, elevating pH levels and increasing the concentrations of Ca²⁺ ions. Higher base saturation, that is, a greater concentration of exchangeable cations within the mound soils, would also result in higher pH levels in these soils. Increasing surface pH could also result from the effects of digging on soil aeration, mixing of litter, and increased microbial activity (Malizia *et al.* 2000), although this could have been offset by higher respiration rates. Higher pH is likely to influence soil mineralization processes and plant composition on the warrens, favouring some calcicolous plant species, particularly grasses.

Unlike other biogenic mounds constructed by semi-fossorial animals worldwide (e.g. Inouye *et al.* 1987; Midgley & Musil 1990; Mun & Whitford 1990; Aho *et al.* 1998; Whitford & Kay 1999; Ayarbe & Kieft 2000; Kerley *et al.* 2004; and references therein), the mounds in our study did not have sig-

nificantly elevated levels of the biologically derived C and N. Total mound C on the 23 warrens was 81% lower than levels on the inter-mounds (Table 3), and C and N concentrations were generally lower on the mounds, although not always significantly, because of the high spatial variability within and between warrens. Low C and N concentrations could have resulted from changes in physical processes on the mounds. Many warrens are in the open; therefore, litter fall from trees is low on the mounds (Eldridge & Myers 2001). Destruction and/or removal of the biological soil crust increases the tendency of these soils to form physical crusts, increasing levels of surface insolation (Mills & Fey 2004) and reducing the likelihood of organic material incorporation into the soil. Photo-oxidation of surface-resident organic material would dominate on the mounds, restricting decomposition by soil biota and, therefore, contributions to soil nutrient pools. Loss of organic-rich topsoil by erosion, exacerbated by rabbit activity, could also account for reduced mound C and N concentrations. Sparse plant cover and higher surface evaporation rates likely lead to shorter periods of time over which the decomposition of organic matter can occur (however, see Ayarbe & Kieft 2000), further depleting mound nutrient levels (Mohr *et al.* 2005). Low levels of soil N are likely to be reflected in lower content of tissue N in plants growing on the mounds (*sensu* Midgley & Musil 1990), depressed mound productivity, and further reducing decomposition rates and digestibility of plant material.

Rabbits do not cache food, and in contrast to semi-fossorial animals such as banner-tailed kangaroo rats (*Dipodomys spectabilis spectabilis*), do not carry plant material back to the warrens (see Kinlaw 1999; Whitford & Kay 1999). The soils of banner-tailed kangaroo rat mounds are constantly re-enriched by successive generations of rats, reinforcing existing nutrient concentrations. These nutrients eventually find their way to the surface through excavation and burrow reconstruction. Rabbits, however, both urinate and defecate off-mound on dung hills, intensifying the net export of resources away from the warrens. Unlike other burrow systems, where there is often a breakdown of material foraged from around the warrens and supplemented by the addition and breakdown of animal faeces (Inouye *et al.* 1987; Desmet & Cowling 1999; Brock & Kelt 2004), rabbit warrens ultimately become patches of lower C and N compared with inter-mound patches (Eldridge & Myers 1999).

Changes in soil chemistry with depth

The impact of rabbits on soil chemistry was greatest at the surface and declined with depth (Fig. 1), so that at about 80 cm, the limit of excavation by rabbits at

Yathong (Parer *et al.* 1987), there were few differences between mound and inter-mound soils (Fig. 2). Predictably, some elements increased and some declined with increasing depth, and we detected clear gradients in pH, EC, total C and N, clay and gravel content, and some soluble cations (Table 2, Fig. 1). In our study, EC declined naturally with depth, and although it was higher on the mounds at the surface, there was no difference between mounds and inter-mounds at depth (Fig. 1). We attribute the greater EC at the surface to increased movement of finer material (more clay) to the surface, although when the biopedturbated material is high in CaCO₃, then EC levels are likely to be lower (Abaturon 1972). High levels of soluble ions such as HCO⁻ and NO₃⁻ may result from some deposition of urine and faeces on the surface by rabbits, as has been observed in banner-tailed kangaroo rat, pack rat (*Neotoma albigula albigula*), and woodrat (*Neotoma* sp.) mounds and middens (Green & Reynard 1932; Finley 1990). Rabbits, however, tend to defecate on latrines or dung hills at some distance from their warrens (Campbell 1978; Sneddon 1991), so faecal additions to the warren are expected to be low.

Although we found no significant difference in particle size distribution between mound and inter-mound soils, there was a 75% greater concentration of clay at 80 cm (39.4%) compared with the surface (22.6%), corresponding with an increased sand concentration at the surface compared with depth. Increases in Na⁺ with depth (Table 2) are typical of soils disturbed by fossorial animals such as the plains vizcacha (*Lagostomus maximus*; Arias *et al.* 2005), which is of a similar body mass to *Oryctolagus*. We do not believe, however, that changes in Na⁺ in our study were ecologically significant despite the fact that soluble Na⁺ was greater on undisturbed soils compared with engineered patches (Table 3). Similarly, the twofold concentration of exchangeable cations and threefold concentration of soluble cations in the mounds persisted to about 40–50 cm, but by 70–80 cm, this had all but disappeared, except for soluble and exchangeable Na⁺, which was still substantially lower on the mounds. This suggests to us that the majority of digging by rabbits is confined to the top 50–70 cm of the soil, although depths penetrated depend on soil characteristics, and the depths to hardpans or caliche layers (Parer *et al.* 1987; Noble 1999).

Rabbit digging alters physical and biological, as well as chemical, processes within woodland soils, although the three processes are difficult to separate. Rabbit activity has a marked effect on soil surface morphology. For example, rabbit digging converts a stable cryptogamic crust with a roughened microtopography to a smooth, physically crusted surface, with marked impacts on soil surface health, water infiltration, plant germination and establishment (Eldridge & Simpson 2002). Rabbit activity also influences soil

seedbanks. Seedbanks on mounds at Yathong Nature Reserve had the lowest vascular plant diversity, and weedy species dominated the mounds, while perennial native grasses and forbs dominated the non-mound surfaces (Eldridge *et al.* 2006).

Rabbits also create smaller-scale disturbances as they excavate the below-ground structures of woody plants (Wood 1988; Myers *et al.* 1994). The foraging digs are functionally and morphologically similar to those of reptiles, such as goannas (*Varanus* spp.), bettongs (*Bettongia leuseur*) and the greater bilby. Although rabbit-constructed pits are important resource traps, preliminary data suggest that rabbits have not assumed the functional role of the locally extinct animals in terms of either the per-capita density of pits, the mass of soil they excavate, or the mass of litter trapped in the pits (James & Eldridge 2007). Although rabbits dig pits, it is doubtful whether they mimic the patchwork of pits and scraping on the soil surface created by native animals prior to their spread across the continent.

Taken together, our results reinforce the view that rabbits have a detrimental impact on semi-arid woodland soils. Given the pronounced changes in soil physical and chemical properties induced by rabbit digging at our site, we believe that altered soil chemistry may be an impediment to the restoration of native plant communities in rabbit-affected woodlands. This and other recent work on changes in soil seedbanks after warren destruction (Eldridge *et al.* 2006) indicates that restoration of the original woodland vegetation, even after the destruction of warrens by mechanical ripping, is likely to be a slow process.

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REFERENCES

- Abaturon B. D. (1972) The role of burrowing animals in the transport of mineral substances in the soil. *Pedobiologia* **12**, 261–6.
- Aho K., Huntly N., Moen J. & Oksanen T. (1998) Pikas (*Ochotona principis*: Lagomorpha) as allogenic engineers in an alpine ecosystem. *Oecologia* **114**, 405–9.

- Arias S. M., Quintana R. D. & Cagnoni M. (2005) Vizcacha's influence on vegetation and soil in a wetland of Argentina. *Rangel. Ecol. Manage.* **58**, 51–7.
- Ayarbe J. P. & Kieft T. L. (2000) Mammal mounds stimulate microbial activity in a semiarid shrubland. *Ecology* **81**, 1150–4.
- Birkland P. W. (1974) *Pedology, Weathering, and Geomorphological Research*. Oxford University Press, New York.
- Boeken B., Shachak M., Gutterman Y. & Brand S. (1995) Patchiness and disturbance in plant community responses to porcupine diggings in the central Negev. *Ecography* **18**, 410–22.
- Brock R. E. & Kelt D. A. (2004) Keystone effects of the endangered Stephens' kangaroo rat (*Dipodomys stephens*). *Biol. Conserv.* **116**, 131–9.
- Campbell D. A. (1978) Pasture species zonation associated with rabbit dunghills on the northern tablelands of NSW. Unpub BSc. Hons thesis, University of New England, Armidale.
- Chew R. M. & Whitford W. G. (1992) A long-term positive effect of kangaroo rats (*Dipodomys spectabilis*) on creosotebushes (*Larrea tridentata*). *J. Arid Environ.* **21**, 375–86.
- Clarke K. R. & Warwick R. M. (1994) *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*. Natural Environment Research Council, Plymouth.
- Contreras L. C. & Gutierrez J. R. (1991) Effects of the subterranean herbivorous rodent *Spalacopus cyanus* on herbaceous vegetation in arid coastal Chile. *Oecologia* **87**, 106–9.
- Day R. L., Laland K. N. & Odling-Smee J. (2003) Rethinking adaptation: the niche construction perspective. *Perspect. Biol. Med.* **46**, 80–95.
- Denham A. J. & Auld T. D. (2004) Survival and recruitment of seedlings and suckers of trees and shrubs of the Australian arid zone following habitat management and the outbreak of rabbit calicivirus disease (RCD). *Austral Ecol.* **29**, 585–99.
- Desmet P. G. & Cowling R. M. (1999) Patch creation by fossorial rodents: a key process in the revegetation of phytotoxic arid soils. *J. Arid Environ.* **43**, 35–45.
- Eldridge D. J. & Greene R. S. B. (1994) Assessment of sediment yield from a semi-arid red earth with varying cover of cryptogams. *J. Arid Environ.* **26**, 221–32.
- Eldridge D. J. & Mensinga A. (2007) Foraging pits of the short-beaked echidna (*Tachyglossus aculeatus*) as small-scale patches in a semi-arid Australian box woodland. *Soil Biol. Biochem.* **39**, 1055–65.
- Eldridge D. J. & Myers C. A. (1999) Rabbit warrens: nutrient-deprived mosaics in a semi-arid woodland. In: *People and Rangelands: Building the Future, Proceedings of the VIth International Rangelands Congress*, Vol. 1, (eds D. Eldridge & D. Freudenberger) pp. 133–5. International Rangelands Congress Inc, Townsville.
- Eldridge D. J. & 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. *J. Arid Environ.* **47**, 325–37.
- Eldridge D. J. & Rath D. (2002) Hip holes: kangaroo resting sites enhance the physical and chemical environment of woodland soils. *Austral Ecol.* **27**, 527–36.
- Eldridge D. J. & Simpson R. (2002) Rabbit *Oryctolagus cuniculus* L. impacts on vegetation and soils, and implications for management of wooded rangelands. *Basic Appl. Ecol.* **3**, 19–29.
- Eldridge D. J., Costantinides C. & Vine A. (2006) Short-term vegetation and soil responses to mechanical destruction of rabbit (*Oryctolagus cuniculus* L.) warrens in an Australian box woodland. *Restor. Ecol.* **14**, 50–9.
- Finley R. B. (1990) Woodrat ecology and behavior and the interpretation of paleomiddens. In: *Packrat Middens: The Last 40,000 Years of Biotic Change* (eds J. L. Betancourt, T. R. van Devender & P. S. Martin) pp. 28–42. University of Arizona Press, Tucson.
- Foran B. D. (1986) The impact of rabbits and cattle on an arid calcareous shrubby grassland in central Australia. *Vegetatio* **66**, 49–59.
- Green R. A. & Reynard C. (1932) The influence of two burrowing rodents *Dipodomys spectabilis spectabilis* (kangaroo rat) and *Neotoma albigula albigula* (pack rat) on desert soils in Arizona. *Ecology* **13**, 73–80.
- Guo Q. (1996) Effect of banner-tail kangaroo rat mounds on small-scale plant community structure. *Oecologia* **106**, 247–56.
- Hall L. S. & Myers K. (1978) Variations in the microclimate in rabbit warrens in semi-arid New South Wales. *Aust. J. Ecol.* **3**, 187–94.
- Hansell M. H. (1993) The ecological impact of animal nests and burrows. *Funct. Ecol.* **7**, 5–12.
- Heard G. W., Black D. & Robertson P. (2005) Habitat use by the inland carpet python (*Morelia spilota metcalfei*: Pythonidae): Seasonal relationships with habitat structure and prey distribution in a rural landscape. *Austral Ecol.* **29**, 446–60.
- Inouye R. S., Huntley N. J., Tilman D., Tester J. R., Zinnel K. C. & Stilwell M. (1987) Succession on a Minnesota sand plain. *Ecology* **68**, 12–26.
- Isbell R. F. (2002) *The Australian Soil Classification*. CSIRO, Collingwood.
- James A. I. & Eldridge D. J. (2007) Reintroduction of fossorial native mammals and potential impacts on ecosystem processes in an Australian desert landscape. *Biol. Conserv.* **138**, 351–59.
- Jones G. C., Lawton J. H. & Shachak M. (1997) Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* **78**, 1946–57.
- Kerley G. I. H., Whitford W. G. & Kay F. R. (2004) Effects of pocket gophers on desert soils and vegetation. *J. Arid Environ.* **58**, 155–66.
- Kinlaw A. (1999) A review of burrowing by semi-fossorial vertebrates in arid environments. *J. Arid Environ.* **41**, 127–45.
- Kwok A. (2005) *Biopedurbation in Relation to Vegetation and Spatial Scale in an Australian Semi-arid Woodland*. Unpublished BSc (Hons) Thesis, University of NSW, Australia.
- Lajtha K. & Bloomer S. H. (1988) Factors affecting phosphate sorption and phosphate retention in a desert ecosystem. *Soil Sci.* **146**, 160–7.
- Lange R. T. & Graham C. R. (1983) Rabbits and the failure of regeneration in Australian arid zone *Acacia*. *Aust. J. Ecol.* **8**, 377–81.
- Leigh J. H., Wood D. H., Holgate M. D., Slee A. & Stanger M. D. (1989) Effect of rabbit and kangaroo grazing on two semi-arid grassland communities in central-western New South Wales. *Aust. J. Bot.* **37**, 375–96.
- Loveday J. (1974) Methods for analysis of irrigated soils. *Technical Communication No. 54*, Bureau of Soils, Commonwealth Agricultural Bureau, Canberra.
- Ludwig F., de Kroon H., Berendse F. & Prins H. H. T. (2004) The influence of savanna trees on nutrient, water and light availability and the understorey vegetation. *Plant Ecology*. **170**, 93–105.
- McCullough D. R. & McCullough Y. (2000) *Kangaroos in Outback Australia: Comparative Ecology and Behaviour of Three Coexisting Species*. Columbia University Press, New York.

- Malizia A. I., Kittlein M. J. & Busch C. (2000) Influence of the subterranean herbivorous rodent *Ctenomys talarum* on vegetation and soil. *Zeitsch. Säuget.* **65**, 172–82.
- Midgley G. F. & Musil C. F. (1990) Substrate effects of zoogenic mounds on vegetation composition in the Worcester – Robertson Valley, Cape Province. *S Afr. J. Bot.* **56**, 158–66.
- Mills A. & Fey A. (2004) Transformation of thicket to savanna reduces soil quality in the Eastern Cape, South Africa. *Plant Soil* **265**, 153–63.
- Milton S. J., Dean W. R. J. & Klotz S. (1997) Effects of small-scale animal disturbances on plant assemblages of set-aside land in Central Germany. *J. Veg. Sci.* **8**, 45–54.
- Minitab. (1997) *References Manual, Release 10.1*. Minitab Inc. State College, University Park, PA.
- Mohr D., Cohnstaedt L. W. & Topp W. (2005) Wild boar and red deer affect soil nutrients and soil biota in steep oak stands of the Eifel. *Soil Biol. Biochem.* **37**, 693–700.
- Mun H. & Whitford W. G. (1990) Factors affecting annual plants assemblages on banner-tailed kangaroo rat mounds. *J. Arid Environ.* **18**, 165–73.
- Myers K. & Parker B. S. (1975) Effect of severe drought on rabbit numbers and distribution in a refuge area in semiarid north-western New South Wales. *Aust. Wildl. Res.* **2**, 103–20.
- Myers K., Parer I., Wood D. & Cooke B. D. (1994) The rabbit in Australia. In: *The European Rabbit: The History and Biology of a Successful Coloniser* (eds H. V. Thompson & C. M. King) pp. 108–57. Oxford Science Publications, London.
- Noble J. C. (1993) Relict surface-soil features in semi-arid mulga (*Acacia aneura*) woodlands. *Rangel. J.* **15**, 48–70.
- Noble J. C. (1999) Fossil features of mulga *Acacia aneura* landscapes: possible imprinting by extinct Pleistocene fauna. *Aust. Zool.* **31**, 396–402.
- Parer I., Fullagar P. J. & Malafant K. W. J. (1987) The history and structure of a large warren of the rabbit, *Oryctolagus cuniculus*, at Canberra, ACT. *Aust. Wildl. Res.* **14**, 505–13.
- Parker B. S., Hall L. S., Myers K. & Fullagar P. J. (1976) The distribution of rabbit warrens at Mitchell, Queensland, in relation to soil and vegetation characteristics. *Aust. Wildl. Res.* **3**, 129–48.
- Read J. L. & Owens H. M. (1999) Reptiles and amphibians of the Lake Eyre South region, 1, Part 3. In: *Lake Eyre South Monograph Series* (ed. W. J. H. Slaytor) pp. 111–214. Royal Geographical Society of South Australia, Adelaide.
- Schaefer D. A. & Whitford W. G. (1981) Nutrient cycling by the subterranean termite *Gnathamitermes tubiformans* in a Chihuahuan Desert ecosystem. *Oecologia* **48**, 277–83.
- Schlesinger W. H., Raikes J. E., Hartley A. E. & Cross A. F. (1996) On the spatial pattern of soil nutrients in desert ecosystems. *Ecology* **77**, 364–74.
- Sneddon I. (1991) Latrine use by the European rabbit (*Oryctolagus cuniculus*). *J. Mammal.* **72**, 769–75.
- Soil Survey Staff (1975) *Soil Taxonomy: A Basic System of Soil Classification for Making and Interpreting Soil Surveys*. U.S. D.A. Agric. Handbook No. 436. Government Printer, Washington, DC.
- Tiver F. & Andrew M. H. (1997) Relative effects of herbivory by sheep, rabbits, goats and kangaroos on recruitment and regeneration of shrubs and trees in eastern South Australia. *J. Appl. Ecol.* **34**, 903–14.
- Tongway D. J. & Smith E. L. (1989) Soil surface features as indicators of rangeland site productivity. *Aust. Rangel. J.* **11**, 15–20.
- Voslamber B. & Veen A. W. L. (1985) Digging by badgers and rabbits on some wooded slopes in Belgium. *Earth Surf. Process. Landf.* **10**, 79–82.
- Walker P. J., Koen T. B. & Gittins R. (1995) Natural regeneration of groundstorey vegetation in a semi-arid woodland following mechanical disturbance and burning. 2. Response of individual species. *Rangel. J.* **17**, 59–68.
- Whitford W. G. & Kay F. R. (1999) Biopedturbation by mammals in deserts: a review. *J. Arid Environ.* **41**, 203–30.
- Wilby A., Shachak M. & Boeken B. (2001) Integration of ecosystem engineering and trophic effects of herbivores. *Oikos* **92**, 436–44.
- Wilkinson D. A., Grigg G. C. & Beard L. A. (1998) Shelter selection and home range of echidnas, *Tachyglossus aculeatus*, in the highlands of south-east Queensland. *Wildl. Res.* **25**, 219–32.
- Wood D. H. (1988) The rabbit (*Oryctolagus cuniculus* L.) as an element in the arid biome of Australia. In: *Arid Australia* (eds H. G. Cogger & E. E. Cameron) pp. 273–87. Australian Museum, Sydney.