Short-Term Vegetation and Soil Responses to Mechanical Destruction of Rabbit (*Oryctolagus cuniculus* L.) Warrens in an Australian Box Woodland

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Abstract

We studied the impact of disturbance by rabbits on plants and soils along a gradient out from the center of ripped rabbit warrens in an Australian semiarid woodland. Five years after the warrens were ripped, the impact of rabbits was still apparent. The cover of bare soil declined, and the cryptogam cover increased with increasing distance from the warren mound. However, litter cover, plant cover, and plant diversity remained unchanged with increasing distance from the mounds. Differences in plant composition were apparent with increasing distance from the mounds, with three species, *Schismus barbatus*, *Salsola kali* var. *kali*, and *Chenopodium melanocarpum* dominating the mounds, whereas the perennial grass *Austrostipa scabra* dominated the nonwarren control surfaces. Two species, *Crassula sieberana* and *S. barbatus*, dominated the active soil seed bank on ripped warrens. The mounds had the lowest number of species in the soil seed bank, whereas the warren edge microsite had the greatest. Ripped and unripped warrens differed substantially in their complement of species, and ripped warrens contained an order of magnitude fewer active warren entrances compared with unripped warrens. Ripped warrens also had significantly more plant cover than unripped warrens. Taken together, our results reinforce the view that rabbits have a destructive effect on surface soils and vegetation in semiarid woodlands and suggest that restoration of the original woodland vegetation after warren ripping is likely to be a slow and ongoing process.

Key words: **bioturbation, ecosystem engineering, *Oryctolagus cuniculus*, rabbit warren, restoration, seed banks.**

Introduction

Grazing by domestic and feral animals can have substantial impacts on the structure and function of terrestrial ecosystems at a range of spatial scales (Milchunas et al. 1998). Grazing and browsing by feral herbivores can lead to changes in plant growth and form, reproduction, species composition, changes in soil litter layers, reductions in the quality of the soil surface, reductions in concentrations of biologically derived soil nutrients, increases in rates of fecal and nutrient contamination, and ultimately, flow-on effects to other biota within the ecosystem (Crooks 2002).

In the 150 years since European settlement of eastern Australia, arid and semiarid areas have experienced dramatic changes in ecosystem structure and function brought about by the widespread and unrestricted grazing of domestic and feral herbivores (Morton 1990; James et al. 1999). The European rabbit (*Oryctolagus cuniculus* L.) has established itself as the most ecologically damaging feral herbivore in the country. Originally released in 1788, rabbits quickly became Australia's number one vertebrate pest within a century of European colonization (Coman 1999). Today, the European rabbit is a significant pest over much of the arid and semiarid Australia and occupies about 30% of all the land used for agriculture or grazing (Coman 1999). Annual losses in agricultural production due to rabbit damage are estimated to be of the order of A$500 million (Wilson 1995).

Rabbits occupy large areas of the southern part of the continent where a combination of a Mediterranean climate, with its hot summers and mild winters, soils suitable for digging, and few predators make it an ideal habitat. Rabbits have a multitude of influences on the environment. In the semiarid regions, they consume plants which are more nutritious, have a higher water content, and are lower in fiber and sodium (Friedel 1985; Foran 1986). Consequently, small shrubs and plants, perennial grasses, and succulents such as forbs are eaten first (Lange & Graham 1983; Foran et al. 1985; Friedel 1985; Foran 1986; Leigh et al. 1989). Rabbits eat seedlings and young stems of grasses, shrubs, and trees, substantially reducing establishment and revegetation (Lange & Graham 1983; Foran 1986; Myers et al. 1994). In some arid areas, grazing and browsing by rabbits has completely eliminated the recruitment of arid zone woody plants (Lange & Graham 1983).

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Rabbits also have marked effects on the soil surface (Eldridge & Myers 2001; Eldridge & Simpson 2002). They live in large, communal, underground burrow systems (warrens). During warren construction, rabbits deposit large volumes of nutrient-poor subsoil on the surface (Myers et al. 1994; Eldridge & Myers 2001), smothering the existing vegetation and creating a hostile environment for germinating seeds. Warren excavation is an ongoing process, and rabbits regularly open up new burrows and channels when the soil is damp, thereby increasing the size of the warrens (Myers et al. 1994). This digging results in the deposition of clay-rich material on the surface, leading to wind and water erosion, surface sealing, and physical crusting under the action of raindrops (Eldridge & Greene 1994; Walker & Koen 1995). Warrens are used by successive generations for many years, maintaining a surface which is physically and biologically depauperate.

Many biological, chemical, and physical methods have been used to control rabbits, and control is costly and ongoing. Biological methods involve the use of viruses such as the myxoma virus which causes myxomatosis and calicivirus which produces Rabbit Calicivirus Disease (RCD) (Hall & Myers 1978; Cooke 1990; Williams et al. 1990; Myers et al. 1994). Chemical methods involve the use of baiting, gassing, or fumigating of rabbits while in their warrens (Myers et al. 1994). However, research has shown that the most effective form of rabbit control is the physical destruction of the warren, usually by ripping (Martin & Eveleigh 1979; Cooke & Hunt 1987; Mutze 1991; Parer & Milkovits 1994). Ripping is generally carried out using a tined ripper that reaches to a depth of at least 80 cm. The ripper is connected to a tractor or bulldozer and dragged across the top of warrens, often along two perpendicular axes, thereby collapsing and destroying the warrens (Martin & Eveleigh 1979; Parer & Parker 1986). Control is most effective in summer following long dry periods when rabbit populations are low, when the warrens are more likely to collapse because the soil is more friable, and because rabbits are more vulnerable due to water stress (Wood 1985; Cooke & Hunt 1987; Myers et al. 1994). The rabbits are also more likely to be in their warrens during summer in order to stay cool (Myers et al. 1994; Parer & Milkovits 1994) and are suffocated.

Since the early 1990s, there has been a concerted effort by officers of the Department of Environment and Conservation (previously New South Wales National Parks and Wildlife Service) to eradicate rabbits from National Parks in New South Wales (NSW). In September 1996, Yathong Nature Reserve, a large woodland UNESCO Man and the Biosphere reserve in semiarid NSW, was chosen as an official release point for RCD. Before the release of RCD, large numbers of warrens had been ripped, and it was hoped that this would increase the overall effectiveness of rabbit control in the reserve. Anecdotal evidence and field observations indicate that warrens are unfavorable sites for colonization by native plants, and abandoned warrens often support similar plant species to those that are occupied by rabbits. Despite the large amount of ripping carried out in NSW during the last decade, there are few empirical data on the recovery of vegetation or soils after ripping.

In this study, we describe four studies carried out at Yathong Nature Reserve to examine the effects of rabbits on vegetation and soils and the short-term recovery of vegetation after warren ripping. We examined differences in vascular plants in relation to soil surface morphology along a gradient from the center of a ripped warren to an unripped, rabbit-free (control) microsite (study 1) and combined this with an assessment of the germinable soil seed bank along this gradient (study 3). We compared vascular plant cover from a series of ripped warrens with adjacent unripped warrens (study 2) and assessed the effects of warren ripping on the degree of warren reinvasion by rabbits (study 4). Together, these studies provide insights into the usefulness of warren ripping for restoring native vegetation communities in rabbit-infested woodlands.

Methods

The Study Area

The study was undertaken at Yathong Nature Reserve, 130 km south of Cobar, in central-western NSW, Australia (32°35′S, 145°35′E; altitude 200–425 m). Yathong Nature Reserve consists of former grazing leases acquired by the Department of Environment and Conservation in the 1970s. The climate is semiarid with hot summers and cool winters, and average annual rainfall is between 325–350 mm. The 100-year mean rainfall for any month is between 23 and 35 mm (Leigh et al. 1989). The mean daily minimum temperature (from Cobar) is 4.1°C in July, and the mean daily maximum temperature is 34.6°C in January (Leigh et al. 1989). The study site is located on Quaternary-aged, massive, red earth soils (Gn2.13, Northcote 1979), often overlain with an extensive biological (cryptogamic) soil crust. Slopes are generally less than 1% (Eldridge & Myers 2001).

The red earth soils support an open woodland with an upperstorey of *Eucalyptus intertexta* (R.T. Baker), *E. populnea* (F. Muell.), *Casuarina cristata* (Miq.), and *Callitris glaucophylla* (J. Thomps. & L.A.S. Johnson). The shrub layer comprised scattered shrubs from the genera *Dodonaea* and *Acacia* in the open areas between trees or *Rhagodia spinescens* (F. Muell.) and *Einadia nutans* (R.Br.) A.J. Scott below tree canopies. The herbaceous vegetation was dominated by perennial grasses (*Austrostipa*, *Aristida*, *Austrodanthonia* spp.) and perennial and annual forbs.

Warren Ripping Treatments

Warrens in the study area are typically subcircular and up to 20 m in diameter. The central, elevated (to 0.8 m high) area, termed the “mound,” is highly modified and contains most of the burrows. An intermediate area between the mound and control (off-mound) sites termed the "disturbed" area has characteristics of both the mound and control areas and is characterized by rabbit scratchings, dung piles, and small mounds of disturbed soil among undisturbed biological soil crust (Eldridge & Myers 1999). A control (nonwarren) surface occurs around the perimeter of the mound.

Warrens were ripped between midsummer and late autumn (January–May) 1997 using a winged three-tined ripper pulled behind a crawler tractor. The warrens are generally ripped in one direction but are occasionally cross-ripped to increase the effectiveness of ripping (Richard Atkinson, NPWS 1999, personal communication). Ripping creates a series of parallel furrows 50 cm apart and about 25 cm deep and destroys the mound and intermediate disturbed microsites, as well as small areas of nonmound (control) sites adjacent to the mound.

Field Measurements

For study 1, we compared 10 ripped warrens with 10 adjacent unripped control surfaces. The ripped warrens were of similar size (17–20 m diameter) and separated by at least 150 m, the grazing range of rabbits (Leigh et al. 1989). We avoided warrens under trees to reduce the effects of trees on the species composition in the seed bank. A 60-m transect was placed through the longest axis of each warren, so that the middle of the transect aligned with the center of the warren. The vegetation was sampled at 10 positions, 5 on either side of the warren center. These positions were (1) 1 m either away from the center of the warren (termed "center" $n = 2$); (2) halfway between the warren center and the warren edge (approximately 5 m from the warren center, termed "midwarren," $n = 2$); (3) at the edge of the warren (approximately 10 m, termed "warren edge," $n = 2$); (4) twice the warren radius (approximately 20 m) away from the center of the warren (termed "near control," $n = 2$); and (5) three times the radius of the warren (approximately 30 m, termed "far control," $n = 2$). This resulted in 10 positions per warren. At each of the 10 positions, we recorded the cover of bare soil, litter, cryptogamic crusts, and vascular plants by species within a 0.5- by 0.5-m quadrat. For the analyses, data for the same position on each warren were pooled because the positions either side of the same warren could not be regarded as true replicates. Soil samples were collected from the same 10 positions at each warren to assess the germinable soil seed bank (study 3). About 600 g of soil was taken from a fixed area of 0.03 m^2 to a depth of 25 mm.

We measured the proportion of the soil surface made up of various microtopographical and cover types with a line-intercept method at two random locations on a mound and adjacent control on all 10 warrens. Each transect was 1 m long. Microtopography was classified as microscarps, depressions, or flats. Flats are level surfaces with less than 1 mm microtopography; scarps are small microcrags where the soil has been eroded exposing a cliff-like soil face; and depressions are small indentations in the surface. Scarps and flats were each further subdivided into bare soil, litter, cryptogamic crust, gravel, and dung. Together, these features are a useful indicator of the degree to which the soil surface has resisted or undergone change through erosion processes (Eldridge & Greene 1994).

We compared vegetation data collected from a previous study of 10 unripped warrens (see Eldridge & Simpson 2002 for study details) with data from study 1 (with certain caveats; see Statistical analyses below) to determine if there were differences in plant composition between ripped and unripped warrens (study 2).

Soil Seed Bank Study

A pilot trial was carried out to examine the feasibility of identifying the seeds found in soil under a 10× dissecting microscope from a sieved slurry of soil, dispersal agent (10% calgon), and water (Meissner & Facelli 1999). This approach proved to be difficult, time consuming, and failed to detect the large number of smaller seeds (e.g., *Crassula* spp.) which we knew were in the soil seed bank. Accordingly, we germinated seeds in the glasshouse (study 3) and used the number of germinable seeds as an estimate of the soil seed bank. Approximately 300 g of each soil sample was scattered over a layer of approximately 2 kg of propagation sand in shallow trays measuring 345 × 285 × 55 mm. Control trays were also set up containing propagation sand only to control for the presence of any glasshouse weeds. Trays were placed in the glasshouse at average temperatures ranging from 17.3 to 24.2°C and allowed to germinate under natural light conditions. An automatic sprinkler system delivered water to the trays for 1 min twice daily (08:00 hr and 15:00 hr). The trial was run from 19 April to 2 August 2002. Seedlings were counted and removed from the trays once they could be identified. Unidentified seedlings were transplanted to larger pots and grown on until they could be identified.

Warren Reinvasion Study

For study 4, we compared reoccupation of ripped and unripped warrens by rabbits coincident with the local release of RCD. A warren survey was carried out about 5 km east of the location of study 1 in areas with similar vegetation and soils. Within an area of about 25 ha, we selected the first 100 ripped and 100 unripped warrens we encountered along a series of wandering random transects. All warrens were of similar size, and warrens under trees were rejected. At each warren, we estimated plant cover and recorded the number of active and inactive burrow entrances. The diameter of the longest axis through the center and the secondary axis perpendicular to the first axis was also measured in order to derive a measure of warren area using the following equation: warren area = $(\frac{1}{2}(b)\prod)^2 + ((a-b)b)$, where a is the diameter of the largest axis, and b is the diameter of the second axis perpendicular to axis a. Active burrow entrances showed recent evidence of rabbit activity including fresh rabbit tracks or scratch marks, feces near the entrance, or an entrance which had been recently reworked and was devoid of debris (leaf litter, sticks, or weeds).

Statistical Analyses

We used the Kruskal–Wallis test to determine differences in soil microtopography between mound and nonmound sites and differences in ground cover (study 1; bare ground, litter, cryptogam), plant diversity (number of species, number of individuals, Margalef's richness, Pielou's evenness), and the number of germinants (study 3) between the five warren locations (using the mean of the two transects per warren; Minitab 1997). Differences in the median values were determined using multiple-comparison tests described in Siegel and Castellan (1988). Bonferroni adjustments were applied when comparing median values across the five warren locations because of the large number of multiple comparisons. For the study of warren reinvasion by rabbits, one-way analysis of variance was used to examine differences in plant cover and the number of active and inactive burrow entrances between ripped and unripped sites after checking for normality and homogeneity of variance (Levene's test, Minitab 1997). Simple linear regression was used to examine relationships between the number of burrow entrances and warren size.

For study 1, we pooled the data for each warren to look at gross changes at three locations (microsites) across the warren: (1) "mound" (average of warren center and mid-warren); (2) "control" (average of near and far controls); and (3) "intermediate" (intermediate between mound and control). For each of the 10 warrens, we derived two matrixes, one of 30 quadrats (3 microsites $\times$ 10 warrens) by 21 attributes (18 plant species, plus bare soil, litter, and cryptogam cover) and a second matrix of plant species (i.e., 30 quadrats by 18 plant species).

We explored possible differences in plant community structure between ripped and unripped warrens (study 2) using a matrix of 20 locations (10 ripped warrens—present study; 10 unripped warrens—Eldridge & Simpson 2002 study) by 52 species. Data were converted to presence-absence before analysis because of differences in the way the data were collected between the two studies. We have been monitoring vegetation in the reserve for more than 15 years and do not believe that differences between ripped and unripped are confounded by seasonal conditions, given that both studies were 2 years apart. Rainfall in the 6 months preceding both studies was below average giving us confidence that differences between the studies reflect the treatment rather than seasonal effects.

The data matrixes were converted to a similarity matrix using the Bray Curtis similarity coefficients contained within the PRIMER (Version 5) statistical package (Clarke & Gorley 2001) and subjected to nonmetric multidimensional scaling (MDS). Data from study 1 were log (x + 1), transformed prior to analyses. Hypothesis tests of differences in the pattern of species cover between the three warren microsites (studies 1 and 3; mound, control, intermediate) or ripping status (study 2; ripped, unripped) defined a priori were performed using analysis of similarities (ANOSIM) which derives a test statistic (Global R) and a significance level. The degree of association of individual plant species with the three microsites or ripped versus unripped sites was measured using indicator species analysis (Dufrene & Legendre 1997). Indicator values combine information on relative abundance and frequency of species. The indicator value is maximal (IV = 100) when all individuals of a given species are restricted to a particular microsite, and all samples from the particular microsite contain an occurrence of that species. Species data were randomized among the microsites and ripping status and a Monte Carlo randomization procedure performed with 1,000 iterations in order to determine the statistical significance of the indicator values. Indicator value analysis was performed using PC-ORD (McCune & Mefford 1999). The community structure of the germinable soil seed bank (10 warrens by five locations by 44 species) was also analyzed using MDS, ANOSIM, and indicator species analysis as described above, using seed germination data (seeds/m^2). This process was repeated with the exclusion of species with less than 335 germinants (i.e., the uncommon species).

Results

Surface Cover and Morphology

Bare soil declined significantly ($H = 57.54$, $p < 0.001$), and cryptogam cover increased significantly ($H = 74.23$, $p < 0.001$) with distance away from the center of the warren (Fig. 1). Plant cover (mean = 19.5%), litter cover (18.3%), and the number of species (5.2) did not change significantly with distance from the warren center ($p > 0.31$).

The surface of the ripped warrens differed significantly from the adjacent undisturbed control areas. Ripped warrens had a significantly greater proportion of scarps (12.4% vs. 0.2%, $H = 9.42$, $p = 0.002$), bare soil in the depressions (16.9% vs. 0.5%, $H = 10.41$, $p = 0.001$) and flats (37.0% vs. 15.6%, $H = 4.64$, $p = 0.031$), more gravel in the depressions (4.6% vs. 0%, $H = 7.82$, $p = 0.005$) and flats (10.8% vs. 0.8%, $H = 8.15$, $p = 0.004$), and significantly less cryptogam cover (0.8% vs. 42.7%, $H = 15.25$, $p < 0.001$) and dung in the flats (0.4% vs. 2.8%, $H = 0.90$, $p = 0.026$) compared with the undisturbed control surfaces.

Plants Growing on the Warrens

Multivariate analyses indicated substantial difference in the plant species composition (n = 18 plant species) between the three warren microsites averaged over the

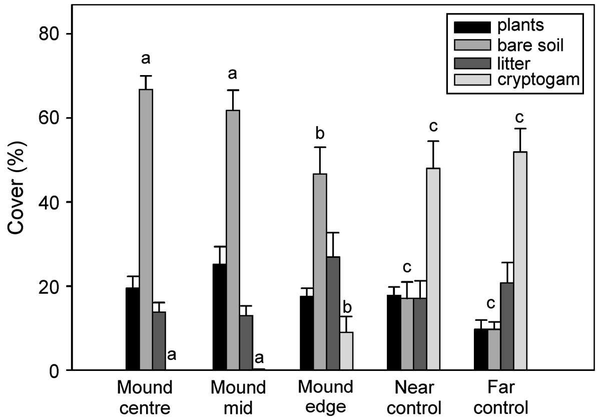

Figure 1. Mean cover (±SE) of plants, bare soil, litter, and cryptogams on the five warren microsites. Different letters between different microsites within a cover type indicate significant differences at $p < 0.05$.

five positions, that is, ripped mound, intermediate (disturbed) area, and control (Global $R = 0.466$, $p = 0.019$), and all microsites were significantly different from each other ($p < 0.019$). There was a strong positive association between the plant species matrix and a larger matrix that included bare soil, cryptogams, and litter ($n = 21$, standardized Mantel statistic $r = 0.656$, $p = 0.001$) indicating that plants alone were just as useful indicators of warren microsite as plants and surface cover attributes combined. Indicator species analysis showed that there were six species associated with the mound or control microsites. Mound indicators were *Schismus barbatus* (IV = 71.9, $p =$ 0.001), *Salsola kali* var. *kali* (IV = 57.7, $p = 0.006$), and *Chenopodium melanocarpum* (IV = 56.3, $p = 0.007$), whereas the only significant control indicator was *Austrostipa scabra* (IV = 62.8, = 0.008).

The first dimension of the MDS biplot corresponded with a clearly defined gradient from mound microsites to control microsites. This gradient was also significantly correlated with both the cover of bare soil ($F_{[1,28]} = 39.42$, $r^2 = 0.57$, $p < 0.001$) and the cryptogam cover ($F_{[2,27]} =$ 27.09, $r^2 = 0.62$, $p < 0.001$; Fig. 2). This first dimension was highly positively correlated with the abundance of *A. scabra* ($r^2 = 0.76$) and negatively correlated with the abundance of *S. kali* ($r^2 = 0.76$). There was a significant, though weak, relationship between the second MDS dimension and the total number of plant species at a site ($F_{[1,28]} = 7.5$, $r^2 = 0.18$, $p < 0.011$; Fig. 2).

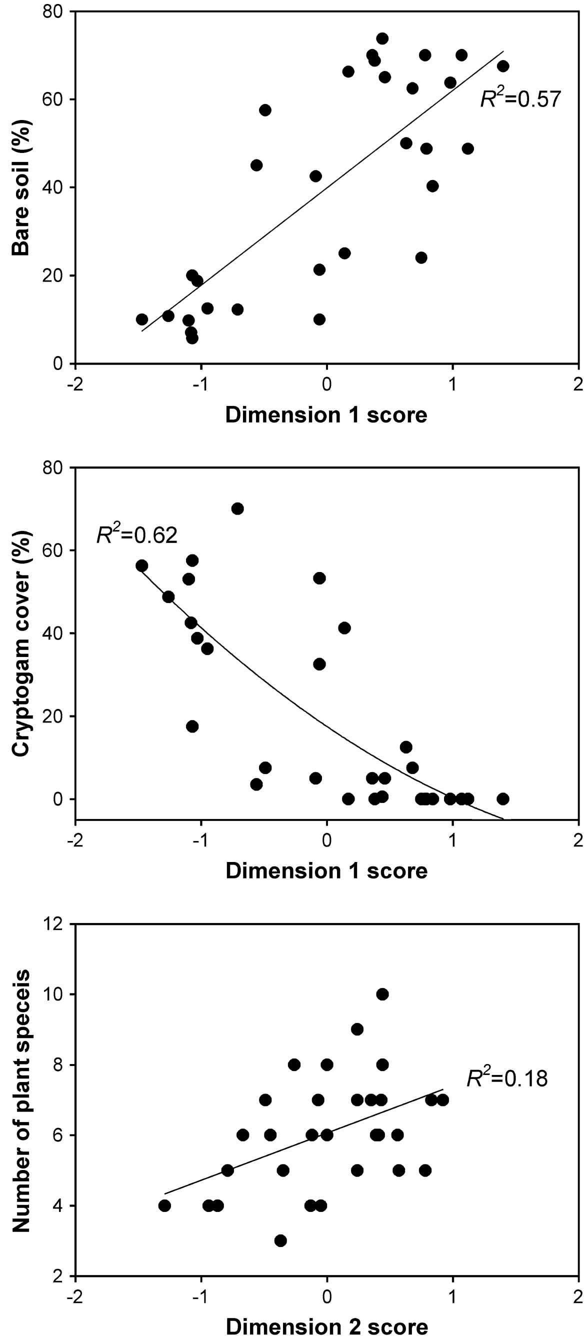

Figure 2. Cover of bare soil, cryptogams, and diversity of plant species in relation to selected dimension 1 and 2 scores of the MDS biplot.

Comparison of Plants on Ripped and Unripped Warrens

Ripped and unripped warrens differed significantly in their complement of plant species (Global $R = 0.815$, $p =$ 0.001). Most of the differences between ripped and unripped warrens were due to a greater proportion of *Erodium crinitum* (IV = 90, $p = 0.001$), *Tetragonia tetragoniodes* (IV = 90, $p = 0.001$), *Centaurea mellitensis* (IV = 83.3, $p = 0.001$), *Sclerolaena diacantha* (IV = 67.5, $p = 0.019$), and *Convolvulus erebescens* (IV = 60, $p = 0.006$) on the ripped compared with the unripped warrens.

Structure of the Germinable Soil Seed Bank

We recorded 30,188 germinants from 44 species in the germination study (Table 1). Only 323 germinants (1%) could not be identified. Eight species (*Vittadinia cuneata*

Table 1. Density of seeds (m^{-2}) emerging from the seed bank in relation to warren location for species with a total of more than 20 seeds/m^2 across the five locations.

	Location within the Warren Complex					
Plant Species	*Warren Center*	*Midwarren*	*Warren Edge*	*Near Control*	*Far Control*	*p Value*
*Schismus barbatus**	6,160.0[a]	5,740.0[a]	3,298.3[a]	536.7[b]	1,275.0[b]	0.001
Crassula sieberana	258.4[a]	538.3[a]	3,748.3[b]	6,796.7[b]	5,178.3[b]	0.001
*Medicago laciniata**	100.0[a]	133.3[a]	250.0[b]	716.7[b]	720.0[b]	0.001
Calandrinia ptychosperma	28.3[a]	31.7[a]	203.3[b]	605.0[b]	221.7[b]	0.001
Cuphonotus humistratus	3.3[a]	3.3[a]	111.8[b]	238.3[b]	221.7[b]	0.001
Aristida jerichoensis	450.0	313.3	1,891.7	713.3	1,358.3	0.01
Chenopodium melanocarpum	631.7	898.3	646.7	140.0	215.0	0.17
*Cirsium vulgare**	828.3	365.0	148.3	63.3	98.3	0.04
Vittadinia cuneata complex	175.0	163.3	220.0	218.3	186.7	0.50
Medicago polymorpha var. *vulgaris**	105.0	51.7	175.0	163.3	128.3	0.32
Tetragonia eremaea	153.3	223.3	23.3	60.0	70.0	0.32
*Sisymbrium erysimoides**	243.3	148.3	98.3	16.7	6.7	0.03
Wahlenbergia gracilis	30.0	40.0	56.7	66.7	78.3	0.23
Sclerolaena diacantha	0	0	43.3	38.3	190.0	0.01
Chthonocephalus pseudevax	26.7	15.0	56.7	80.0	90.0	0.08
*Echium plantagineum**	71.7	28.3	8.4	10.0	33.3	0.54
*Erodium malacoides**	18.3	11.7	16.7	38.3	45.0	0.61
Goodenia pinnatifida	5	6.7	25.0	23.3	58.3	0.96
*Eleusine indica**	33.3	28.3	18.3	8.3	26.7	0.70
Geococcus pusillus	23.3	0	28.3	16.7	0	0.45
Phyllanthus involutus	1.7	0	55.0	0	0	0.22
Pterostylis nana	1.7	11.7	3.3	11.7	18.3	0.56
*Hypochoeris radicata**	1.7	0	10.0	1.7	21.7	0.36
Acacia sp.	8.3	6.7	3.3	6.7	10.0	0.76
Calotis lappulacea	0	0	0	15.0	18.3	0.25
*Chenopodium murale**	13.3	11.7	0	0	0	0.25
*Oxalis pes-caprae**	5.0	3.3	6.7	8.3	1.7	0.67
Myoporum platycarpum	5.0	0	0	3.3	11.7	0.37
Pycnosorus sp.	0	0	21.7	0	0	0.41

For a given species, different letters indicate a significant difference in seed density between warren location at $p = 0.005$. Nomenclature follows Harden (1990–1993).
*Exotic species.

complex, *Calandrinia ptychosperma*, *Cirsium vulgare*, *Medicago laciniata*, *C. melanocarpum*, *Aristida jerichoensis*, *Crassula sieberana*, and *S. barbatus*) contributed 90% of the total germinants. Two species, *C. sieberana* and *S. barbatus*, accounted for 66% of all germinants emerging from the seed bank. Significantly more species were recorded at the warren edge followed by the control sites. The least number was recorded on the ripped mounds ($H = 12.06$, $df = 4$, $p = 0.017$; Table 2). Richness was significantly lower on the mounds compared with the other locations ($H = 10.44$, $df = 4$, $p = 0.034$), but there were no significant differences in the number of individuals or evenness in relation to warren location ($p > 0.66$).

ANOSIM tests indicated significant differences in the composition of the soil seed bank between the mound (warren center and midwarren) and control (near- and far-control) microsites (Global $R = 0.713$, $p = 0.001$ for $\log_{(x+1)}$ transformation). Restricting analyses to the dominant 28 species (i.e., >334 germinants/m^2) produced the same result (Mantel statistic $r = 0.99$, $p < 0.0001$). Six species were associated with the mound or control microsites. Mound indicators were *C. vulgare* (IV = 65, $p = 0.025$) and *S. barbatus* (IV = 58.6, $p = 0.008$), whereas control species were *M. laciniata* (IV = 62.9, $p = 0.001$), *C. ptychosperma* (IV = 60.7, $p = 0.001$), *C. sieberana* (IV = 59.1, $p = 0.007$), and *Cuphonotus humistratus* (IV = 53.3, $p = 0.007$). The structure of the soil seed bank community was weakly similar to the structure of the plant community recorded in the field survey (standardized Mantel statistic $r = 0.40$, $p = 0.001$).

Warren Reinvasion by Rabbits

Unripped warrens had about 10 times more active warren entrances (4.01) compared with ripped warrens (0.43, $F_{[1,98]} = 328.18$, $p < 0.001$), and larger warrens had more entrances, both active and inactive ($F_{[1,198]} = 73.21$, $p < 0.001$, $r^2 = 0.26$). When separate analyses were performed for both ripped and unripped sites, the total number of entrances increased significantly with warren size at both the unripped ($F_{[1,98]} = 328.18$, $p < 0.001$, $r^2 = 0.77$) and ripped sites ($F_{[1,98]} = 14.23$, $p < 0.001$, $r^2 = 0.11$), respectively. Ripped warrens had significantly more plant cover (mean = 87%) compared with unripped warrens (73.5%; $F_{[1,198]} = 63.58$, $p < 0.001$).

Table 2. Diversity of seeds germinating from the seedbed in relation to warren microsite.

	Warren						Control			
	Center		Mid		Edge		Near		Far	
Component	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
No. of species	12.8[a]	0.84	12.7[a]	0.47	17.1[b]	0.86	15.7[c]	1.7	15.8[c]	1.3
No. of individuals	288.0[a]	53.0	268.0[a]	65.0	339.0[a]	50.0	321.0[a]	75.0	311.0[a]	57.0
Richness	2.17[a]	0.14	2.22[b]	0.16	2.84[b]	0.13	2.59[b]	0.26	2.64[b]	0.14
Evenness	0.49[a]	0.06	0.50[a]	0.06	0.58[a]	0.03	0.53[a]	0.04	0.53[a]	0.03

Different subscripts within a row indicate a significant difference in that attribute at $p = 0.05$.

Discussion

Our results reveal striking differences in vegetation and soils between rabbit warrens and adjacent soil surfaces in a semiarid woodland. Firstly, compared with the adjacent control surfaces, ripped warrens had more bare soil, less cryptogam cover, and a markedly different plant composition even 5 years after ripping. The differences in plant community composition were also reflected in the germinable soil seed bank, which was markedly different between the warren mounds and the control surfaces. Compared with the control surfaces, which were dominated by perennial native plants such as the grass *Austrostipa scabra*, mounds tended to be dominated by a different suite of mainly exotic annual species. The low numbers of viable seeds of the dominant perennial grasses (*Austrodanthonia*, *Aristida*, and *Austrostipa* spp.) in the soil seed bank mitigate against a recovery of vegetation from the soil seed bank. Secondly, our study showed that in comparison with unripped warrens, ripped warrens supported some native forbs but were mostly dominated by weedy or annual species. Thirdly, the soil surface measurements show that mounds have a degraded surface morphology dominated by microscarps and features typical of erosional surfaces (Eldridge & Myers 1999). Our data are supported by unpublished data from Central Australia which show very little recovery of vegetation on warrens 10 years after ripping (W. Low, 2004 personal communication). Taken together, our results reinforce the view that rabbits have a damaging and prolonged effect on surface soils and vegetation in semiarid woodlands and suggest that restoration of the original woodland vegetation is likely to be a slow and difficult process.

Unlike native rodents and fossorial mammals that are considered to play positive roles in soil and ecological processes in semiarid environments (e.g., Steinberger & Whitford 1983; Laundré 1998; Garkaklis et al. 2000; Kerley et al. 2004), rabbits have substantial detrimental impacts on soil and vegetation. Indicator species analyses of our data from Yathong Nature Reserve demonstrated that the elevated mounds on the warrens were dominated by annual exotic forbs and grasses such as *Schismus barbatus*, *Salsola kali* var. *kali*, and *Chenopodium melanocarpum*, whereas control soils supported a mixed community of perennial grasses such as *A. scabra*. We expected a greater cover of exotic, annual nitrophilous plants on the mounds because of the putative higher levels of available nitrogen associated with animal-engineered structures. For example, nitrogen is known to accumulate within animal bedding sites of many animals due to increased rates of excretion, as well as accumulation of detritus and organic material (Whitford & Kay 1999). However, total nitrogen and carbon levels on rabbit mound soils are substantially lower than levels on nonmound soils (Eldridge & Myers 1999). We attribute the depleted nutrient concentrations on warrens to the transfer of nutrient-poor subsoils to the surface by the rabbits during construction of the mounds (Eldridge, unpublished data). Low nutrient levels are further reinforced by the grazing habit of rabbits which is to defecate off the mounds on dunghills or latrines (Campbell 1978), resulting in a net export of resources from mound to nonmound microsites. Eventually, the mounds become markedly nutrient depleted (Eldridge & Myers 1999).

Prolonged disturbance by rabbits leads to the persistence of weedy plant species (Tiver & Andrew 1997). Disturbance changes the morphology of the soil seedbed, altering the levels of soil seed contact, soil moisture, and access to safe sites for germination. The scratching and digging activities of rabbits create a mosaic of small digs interspersed with patches of cryptogamic crust and microdeposits of subsoil at small (<20 cm) spatial scales. This patchwork of microniches is likely to favor species with a wide range of regenerative strategies (Grubb 1977) and may explain why many species were found on both mound and nonmound surfaces. Shallow diggings are known to favor wind- and mammal-dispersed seeds, whereas more substantial disturbances, which expose the soil to sunlight, favor self-dispersed small therophytes and agricultural weeds (Milton et al. 1997). *Medicago laciniata*, a naturalized annual forb which was common on both mounds and nonmounds, has a burr that captures wind- and waterborne sediments, giving it a competitive advantage on an erodible surface where the material is constantly moving.

The pattern of rabbit foraging also reinforces differences in vegetation on the mounds. Rabbits rarely forage more than 150 m from their warrens, and this leads to the development of clearly defined grazing gradients out from the warrens (Leigh et al. 1989). Rabbits prefer herbaceous plants and native grasses which are quickly removed from the mounds. Some Mediterranean weedy species such as Horehound (*Marrubium vulgare*) and Wild sage (*Salvia verbenaceae*) contain aromatic substances which discourage rabbit grazing. The combination of release from grazing and the maintenance of a disturbed environment means that in dry periods these plants often dominate the mounds, outcompeting (generally native) species which have only a small transient seed bank (Odgers 1999). Persistence of weedy vegetation on the mounds is reinforced by the removal of more palatable species by the rabbits.

Management of Rabbit-Infested Woodlands

To what extent will woodlands revert to their original plant community after the removal of rabbits? This is the question often posed by land managers in woodlands infested with rabbits. Our results indicate that there are likely to be large differences between ripped and unripped warrens in terms of plant species composition, though our results are based on only 5 years of recovery after ripping. Restoring the vegetation community to that of the adjacent nonrabbit surfaces is highly depended on the recovery of soil surface morphology, in particular, reinstatement of the biological crust, which is a dominant feature of woodlands soils in eastern Australia (Eldridge & Greene 1994). Laboratory-based germination studies indicate that weedy species fail to germinate on nonmound soils dominated by cryptogamic crusts (Eldridge & Simpson 2002). In their study, Eldridge and Simpson (2002) showed that the germination of the perennial native grass *A. caespitosa* was very low, whereas germination of the weeds *M. vulgare* and *Brassica tornefortii* was enhanced on degraded mound soils. Differences in germination rates are attributed to major differences in the degree of soil seed contact, in particular, the ability of the seeds to retain water during imbibition.

In the present study the total germinable seed density on the mounds (9,200 ± 1,359 seeds/m^2) was very similar to that on the control soils (10,400 ± 1,510 seeds/m^2), and was of a similar density to grassland soils in northern Victoria (18,660 seeds/m^2; Morgan 1998) and semiarid *Eucalyptus populnea* woodlands in western Queensland (13,200 seeds/m^2; Navie and Rogers 1997). However, the germinable seed bank on the mounds was dominated by weedy exotic species such as *S. barbatus* or natives which do not dominate the aboveground vegetation in either cover or biomass. Our results indicate that rabbit mounds are unlikely to regenerate in the short term, given the paucity of desirable plant species in the active soil seed bank. We know very little about the postdisturbance plant recovery on ripped or abandoned intact warrens, though anecdotal evidence suggests that it is at the scale of many tens of years. Empirical data relating the size of animal-created mounds and pits to their longevity (in terms of their structural integrity) indicate that rabbit warrens will persist for periods ranging from 250 to more than 1,200 years (for warrens with diameters ranging from 10 to 40 m; Whitford & Kay 1999). Intact, abandoned warrens are still obvious in many parts of arid Australia due of their failure to regenerate (Myers et al. 1994).

As indicated above, current control is based on a range of techniques including biological and chemical control used in conjunction with warren destruction, generally by ripping (Cooke & Hunt 1987; Mutze 1991). Irrespective of vegetation succession on the mounds, removal of rabbits should be the primary land-management objective of any control program, and destruction of the warrens should be the first step in the restoration process. Rabbits developing resistance to biological control methods are likely to form the nucleus of new populations which will readily reinvade intact, abandoned warrens. Intact warrens often become refugia for new generations of rabbits and probably represent previous colonial sites of threatened native animals such as the Bilby (Noble 1999). The necessity to destroy warrens is supported by our work on warren reinvasion, which clearly demonstrates that unless warrens are physically destroyed, they will continue to act as harbor for rabbits. Mutze (1991) found that 10 years after ripping, only 2% of the original ripped warrens showed signs of reactivation compared with 82% of unripped warrens. Similar results have been found in other areas (e.g., Parker et al. 1976; Foran et al. 1985; Parer & Milkovits 1994).

Rainfall in semiarid landscapes is highly variable and likely to influence the success of restoration techniques which involve reseeding. Existing machinery for reseeding ripped warrens is currently available, but it may be more economically viable to combine seeding with warren ripping by attaching a seed box to the rippers. The planting of an intermediate perennial grass has been used successfully in the western United States for restoring degraded *Artemisia* shrub-steppe (Cox & Anderson 2004). Given the probable low success rate of restoring the prewarren vegetation in a single ripping and seeding operation, an alternative strategy might be to introduce an intermediate tussock grass such as Cereal rye (*Secale cereale*) which is used widely for reclaiming roadside batters. The addition of a perennial grass, albeit an exotic agricultural crop, will enhance landscape structure (sensu Ludwig & Tongway 1995) by increasing surface roughness, aid in the retention of soil and water (Hilty et al. 2003), and provide substantial litter to protect the soil against erosion and stimulate the growth of soil microbiota. Increased litter cover should also increase the C:N ratio of the surface soil, immobilizing any nitrogen in microbial biomass, and suppressing the growth of weedy annual species such as *S. barbatus* whose ability to respond earlier to small amounts of soil nitrogen gives them a competitive advantage over native perennial grasses (Paschke et al. 2000). An alternative technique in strategic situations where rabbits have exposed material of cultural or archeological significance may be to supply a supplementary carbon source such as starch or sucrose to the soil surface in order to manipulate the nitrogen levels, thus releasing native plants from competitive suppression (Blumenthal et al. 2003).

Rehabilitation of warren-affected soils by native plants may not occur in the short to medium term because of threshold changes in the morphology of the soil surface initiated by rabbit activity and perpetuated by domestic stock. We have shown that the quality of the soil surface in terms of microtopography, gravel, and cryptogamic cover is significantly lower on warren surfaces compared with nonwarren surfaces (Eldridge & Myers 1999; Eldridge & Simpson 2002). Cryptogams will not reestablish on active warrens but will reestablish gradually on abandoned intact warrens albeit slowly (D. J. Eldridge, personal observations). Ripping creates a range of microniches with differing levels of light, temperature, and evaporation, favoring some cryptogamic types such as mosses which recover quickly in woodland soils. In the semiarid woodlands a successional change in the vegetation is preceded by an increase in moss and cyanobacteria cover which is likely to stabilize surface soils, enhancing the development of a stable lichen crust (Eldridge & Greene 1994).

In summary, we argue that destruction of rabbit warrens is an essential precondition of any successful rabbit eradication program. Ripping will increase surface roughness and may stimulate natural succession of soil crust species necessary to restore a viable surface crust. Although we acknowledge that ripping will likely create some short-term increases in the dominance by annual weeds, we anticipate that under appropriate (low risk) grazing levels by domestic animals, that native grasses and forbs will eventually predominate, though we anticipate over long time periods. Given the paucity of desirable plant seeds in the active soil seed bank on the ripped warrens, augmentation of seeds in selected areas might be a viable management option. Nonetheless, the restoration of rabbit-impacted soils is likely to be a slow process.

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