



Vegetation changes associated with cattle (*Bos taurus*) and wombat (*Vombatus ursinus*) activity in a riparian forest

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Burrows; Grazing; Mounds; Plant composition; Riparian; Soil disturbance; Wombat

Nomenclature

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Abstract

Question: Is the composition of groundstorey vegetation influenced by wombat burrowing and mound construction as well as streambank tracks by domestic cattle at high and low levels of usage?

Location: Sixteen streambank study sites in an agricultural area in Kangaroo Valley, southeastern New South Wales, Australia.

Methods: We examined the effects of cattle and wombats on vegetation by measuring plant and litter cover on three markedly different microsites; wombat mounds, the network of tracks used by both cattle and wombats to access pastures away from the riparian area, and control sites that were neither tracks nor mounds, and which were located 1–2 m away from mounds or tracks.

Results: We recorded significantly fewer vascular plant species on the mounds and tracks than on the control microsites, but there were significantly more species at sites of high cattle usage than low cattle usage. Plant cover on the control microsites was more than twice that on the mounds and tracks. The exotic plants, panic veldt grass (*Ehrharta erecta*) and kikuyu (*Pennisetum clandestinum*) were typical indicators of high cattle use sites, while wandering jew (*Tradescantia fluminensis*) and to a lesser extent the unpalatable, low-sprawling shrub mist-flower (*Ageratina riparia*) were indicators of low cattle use sites.

Conclusions: Our study demonstrates that there are few differences in plant community composition between microsites constructed by cattle and those of wombats. Both microsites supported a community that was a subset of the species pool in the surrounding vegetation. Cattle grazing since 1851 in Kangaroo Valley has probably reduced disturbance-sensitive plant species, resulting in an effect that is more apparent at the landscape scale. Further study should focus on the landscape-scale effects of cattle grazing to determine whether cattle or wombats are the major causes of ecosystem degradation in Australian riparian environments.

Introduction

The encroachment of agriculture onto land used by wildlife is a major cause of decline in many animal populations (Ottichilo et al. 2000). Agriculture typically reduces the extent of existing vegetation, rendering the local environment unsuitable for many species originally present (Dickman 2008). In Australia, some species such as the greater bilby (*Macrotis lagotis*) and burrowing bettong (*Bettongia lesueur*) have suffered substantial range extinctions and are now restricted to offshore islands (Southgate 1990). Other

species such as Bennett's wallaby (*Macropus rufogriseus*) and Tasmanian pademelon (*Thylogale billardierii*) thrive on the elevated productivity of the new monocultures and become pests (Statham & Statham 2009). In western USA, black-tailed prairie dogs (*Cynomys ludovicianus*) have largely retained their ranges, but have suffered widespread fragmentation of habitat and extinctions at the local population level (Sidle et al. 1991). One of the most adverse examples of agriculture, particularly grazing by domestic animals, has been the destruction of habitat when native animals and domestic cattle come into direct conflict

(Green et al. 2005). Increasing demand for agricultural products will likely exacerbate negative interactions between native and agricultural species and precipitate an increased demise of native species by landholders. One group of native species that have suffered from the encroachment of agriculture are those that modify the landscape by creating structures such as burrows or mounds. These disturbances are highly visible and often thought to damage pasture or reduce the grazing value for exotic animals. Conflict between cattle and plateau pika (*Ochotona curzoniae*) on the Tibetan Plateau, for example, has led to extensive poisoning programmes (Arthur et al. 2008).

A well-known but little-studied example of conflict between native animals and livestock occurs in southeastern Australia where the bare-nosed wombat (*Vombatus ursinus* Shaw) is thought to reduce the quality of agricultural pastures by grazing and burrowing (Marks et al. 1989; Temby 1998). Wombats occur in moderate densities (0.3 individuals per hectare) in temperate sclerophyll forests of southeastern Australia (McIlroy 1973). However, populations can occur in high densities (1.9 individuals per hectare) in riparian forests adjoining agricultural areas (Skerratt et al. 2004). In non-agricultural environments wombats forage on a range of fibrous, nutrient-poor native grasses (Evans et al. 2006). Close to agricultural areas, however, they tend to feed in areas of improved pasture dominated by introduced grasses with a high tissue nitrogen content (Triggs 2009). Over much of their range, wombats are regarded by farmers as pests because of their habit of damaging fences, which are often rabbit-proof and therefore costly to erect and maintain (Marks et al. 1989; Marks 1998). Wombats also construct large burrows that are usually excavated into the sides of streambanks, but occasionally are dug in adjoining agricultural land.

Little is known about the extent to which cattle and wombats interact, or the extent to which wombats may be responsible for altering the quality of riparian habitats. Landholder surveys undertaken within the distributional range of wombats in eastern Australia have consistently highlighted a range of grievances towards wombats while the potential impacts of domestic cattle are not acknowledged (Marks et al. 1989; Borchard & Collins 2001). These concerns range from wombats spreading parasites and diseases to livestock, to scratching and fouling pasture with faecal matter, to eroding streambanks by their burrowing activities.

Studies of the impact of cattle have generally shown substantial reductions in riparian zone complexity wherever they are introduced (Belsky et al. 1999). Cattle grazing and trampling can change the quantity and composition of plant species, alter surface litter cover

(Schulz & Leininger 1990; Kramer et al. 2007) and reduce soil quality (Tollner et al. 1990). Cattle grazing in riparian zones can also reduce the richness and abundance of terrestrial invertebrate communities by reducing habitat structure and complexity (Kramer et al. 2007). Cattle also create a network of well-worn tracks within their grazing areas that are also used by wombats, complicating the issue of the interactive effects of wombats and cattle on riparian systems. Domestic cattle range in adult body weight from about 350 kg to 580 kg. The average weight of bare-nosed wombats is about 26 kg, but weights of up to 35 kg are not uncommon (Triggs 2009).

Our study aimed to determine whether there is an association between the use of streambanks by wombats and cattle and the composition of groundstorey plants at the level of wombat- and cattle-created microsites (wombat mounds, wombat/cattle tracks). To explore the possible direct effects of wombat and cattle activity in riparian environments we examined differences in plant assemblages and structure at sites subjected to two levels of use by cattle (low and high). We predicted that the composition of plant species associated with high cattle use sites would differ from that at low-use sites. We also measured leaf litter cover to explain potential mechanisms for any observed differences in plant species.

Studies worldwide suggest that animal-created structures often support unique assemblages of plants (Rogers et al. 2001). We expected, therefore, that both mounds and tracks would support unique assemblages of groundstorey plants species, compared with those in the surrounding landscape, because of the combined effects of soil mixing (bioturbation), trampling and soil compaction on soil processes such as infiltration. We examined these predictions at 16 sites in Kangaroo Valley of southeastern Australia, an area that supports a large population of wombats and has a long history of grazing by cattle.

Methods

Study sites

Sixteen sites were chosen, each comprising a 100-m section of streambank, extending up the bank to the point where the slope was level. The streams ranged from deeply-incised and relatively straight with steep streambanks up to 31°, to meandering and sinuous, with more gently sloping banks slopes of 12°. The distance from the water's edge to the edge of the bank ranged from 7 m for the steeper banks to 17 m for the gently sloping banks. Sites were separated by distances ranging from 320 m to 1000 m. The minimum distance between sites was based on the maximum distance travelled by radio-collared wombats (300 m) in an earlier study undertaken in Kangaroo Valley (Giles & Lonnon 1999). The 16 sites were separated by

standard agricultural fencing that provided boundaries for cattle.

The study sites were classified as 'low' ($n = 8$) or 'high' ($n = 8$) cattle use, defined in an earlier study (Borchard et al. 2008). Low cattle usage sites supported an average of 5.4 ± 4.1 (mean \pm SE) head \cdot d $^{-1}$ over the past 15 yr compared with 79.3 ± 4.1 head \cdot d $^{-1}$ from the high cattle use sites based on independent data from landholders. The low-use cattle sites were characterized by intermittently-used cattle tracks, with impacts restricted to the tracks and relatively undisturbed inter-track soil surfaces. Tracks in the high-use sites showed obvious signs of cattle use, and the intervening soils and vegetation were heavily modified by cattle, ranging from faecal spoilage to trampling and overgrazing.

Plant, soil and litter cover

In 2009, over a 2-wk period in the growing season we measured plant and litter cover at each site on three markedly different microsites: (1) wombat mounds (Fig. 1a); (2) the network of cattle tracks that provide access to pasture away from the riparian area and are also used by wombats to link their burrows (Fig. 1b); and (3) control sites that were neither tracks nor mounds, and which were located 1–2 m away from mounds or tracks. These microsites were located either near the streambank ('near'), defined as within 5 m of the water's edge, or 'far', located 15 m or more from the stream edge and generally very close to the upper bank. At each of the 16 sites there were three groups of the three microsites close to and far from water. The cover of all vascular plants, by species, and the cover of litter and bare ground were measured at all microsites with a 1 m \times 0.25 m quadrat. The quadrat was placed at a defined location within each microsite and only plants that were rooted within the quadrat were measured.

Classification of the vegetation assemblages

To test whether vegetation assemblages differed among microsites, each plant recorded on a mound, track and non-mound non-track microsite was assigned a value that related to its morphological, reproductive or dispersal attributes. Twenty-six ecological and morphological attributes (Table 1) were scored for the 67 species identified across the 16 sites. The attributes that were selected were based on functional traits regarded as important in terms of their response to disturbance and as predictors of invading plant species in other ecological studies (McIntyre et al. 1999, 2005; Eldridge & Simpson 2002). Assessments of field specimens were complemented by information obtained from the literature (Harden 1990–1995).



Fig. 1. Photographs of (a) a wombat mound at a low cattle site, showing encroachment of *Ehrharta erecta* and (b) a worn track at a high cattle site, showing *Pennisetum clandestinum* growing across the streambank as well as in the track microsite. Bars, 0.5 m.

Statistical analyses

We used a mixed-models ANOVA approach (Minitab Inc., State College, PA, US) to test for differences in the cover of litter, plants, bare ground and the number of species, species richness (Margalef's index) and species evenness (Pielou's index) in relation to cattle use (high, low), distance to water (near, far), and microsite (track, mound,

Table 1. Total cover (%) of plants by traits in relation to microsite (control, mound, track), stream location (stream, top) and cattle usage (high, low).

Attribute	Microsite					Stream location		Cattle usage			
	Control	Mound	Track	$F_{2,56}$	P	Stream	Top	High	Low	$F_{2,56}$	P
Annual	0.4	1.3	0.3	–	n.s.	0.2	1.0	0.9	0.4	–	n.s.
Perennial	77.4 ^a	33.2 ^b	28.3 ^b	26.85	< 0.001	46.7	45.9	50.3	42.3	–	n.s.
Native	13.7 ^a	5.0 ^b	3.4 ^b	3.95	0.002	8.0	6.8	5.9	8.8	–	n.s.
Exotic	64.1 ^a	29.4 ^b	25.2 ^b	15.56	0.001	39.0	40.2	45.3 ^a	33.9 ^b	3.37	0.059
Monocotyledon	66.9 ^a	28.0 ^b	23.9 ^b	20.46	0.001	39.7	39.5	43.6	35.5	–	n.s.
Dicotyledon	10.4	6.2	4.7	–	n.s.	7.0	7.2	7.2	7.0	–	n.s.
Ascending	47.8 ^a	16.5 ^b	11.7 ^b	6.61	0.001	18.6	20.8	22.9	16.5	–	n.s.
Prostrate	30.0 ^a	17.9 ^b	16.9 ^b	13.6	0.001	28.4	26.2	28.3	26.3	–	n.s.
Animal assisted	31.4 ^a	14.8 ^b	12.6 ^b	4.36	0.001	16.7	22.5	30.1	9.1	–	n.s.
Unassisted	43.8 ^a	19.1 ^b	15.1 ^b	11.25	0.001	28.9	23.1	20.2	31.8	–	n.s.
Wind assisted	2.6	0.6	0.9	–	n.s.	1.4	1.3	0.9	1.8	–	n.s.
Awn	3.5	2.2	1.3	–	n.s.	0.7	3.9	3.4	1.2	–	n.s.
Burr	1.1	0.2	0.03	–	n.s.	0.7	0.2	0.8	0.1	–	n.s.
Hairy pappus	6.1	1.9	3	–	n.s.	3.6	3.7	3.7	3.6	–	n.s.
No ornament	67.2 ^a	30.2 ^b	24.3 ^b	20.45	0.001	42.0	39.2	43.3	37.9	–	n.s.
Wing	0.02	0	0.03	–	n.s.	0.0	0.0	0.0	0.0	–	n.s.
Dry dehiscent	8.9	1.5	4	–	n.s.	3.3	6.4	5.8	3.8	–	n.s.
Dry indehiscent	65.3 ^a	29.8 ^b	23.8 ^b	17.72	0.001	40.1	39.1	43.7	35.5	–	n.s.
Succulent indehiscent	3.7	3.2	0.8	–	n.s.	3.6	1.5	1.8	3.4	–	n.s.
Fibrous root	69.3 ^a	28.2 ^b	23.7 ^b	18.84	0.001	40.0	40.8	43.9	36.9	–	n.s.
Tap root	8.5	6.3	4.9	–	n.s.	7.0	6.2	7.4	5.8	–	ns
0–10 cm	6	2.2	1.8	–	n.s.	2.6	4.0	2.4	4.2	–	n.s.
10–20 cm	0.7	0.2	0.4	–	n.s.	0.2	0.7	0.5	0.4	–	n.s.
20–30 cm	3.7	1.1	1.4	–	n.s.	1.8	2.4	2.0	2.2	–	n.s.
30–50 cm	46.7 ^a	20.2 ^b	17.6 ^b	11.29	0.001	30.9	25.4	25.3	31.0	–	n.s.
>50 cm	20.7 ^a	10.8 ^b	7.5 ^b	2.55	0.03	11.5	14.5	21.0	5.0	21.7	0.001

Different superscripts within an attribute indicate a significant difference in that attribute for a given factor at $P = 0.05$; n.s. = not significant.

non-track/non-mound control) and their two-way and three-way interactions. The first stratum considered differences between high and low cattle usage, and a second stratum was an error term only, which accounted for the variance among the three replicate groups of microsites at each of the 16 sites ($df = 32$). The third stratum considered distance from the stream edge and its interaction with cattle usage. The fourth stratum considered microsite effects (mound, track, control) and its two-way and three-way interactions with cattle usage and distance to stream edge. All data were tested for homogeneity of variance using Levene's test (Minitab 1997). Litter cover was \log_{10} transformed before ANOVA.

We used permutational multivariate analysis of variance (PERMANOVA, Anderson 2005) with the Bray–Curtis similarity coefficients, to test whether the composition of plants of different attributes or traits (based on their cover) varied in relation to cattle usage, distance to stream edge and microsite (and their interactions). The PERMANOVA model had a similar multistratum structure as that described above for the univariate analyses, except that we averaged over the three replicate groups of microsites at each of the 16 sites in order to simplify the analyses.

The degree of association of plant species with respect to cattle usage, distance from stream edge and microsite (and their interactions) was measured using Indicator-Species Analysis (Dufrene & Legendre 1997). Indicator values (IV) combine information on relative abundance and frequency of species, and the indicator value is maximal ($IV = 100\%$) when all individuals of a given species are restricted to a particular treatment (e.g. high cow usage), and all samples from the particular treatment contain an occurrence of that species. Species data were randomized among the treatments and a Monte Carlo randomization procedure performed with 1000 iterations in order to determine the statistical significance of the indicator values. Indicator value analysis was performed using PC-ORD (McCune & Mefford 1999) with a data matrix consisting of the average abundance of each species.

Results

Effect of microsite, cattle usage and streambank position

We recorded significantly fewer vascular plant species on the mounds (2.7 ± 1.7 ; mean \pm SE) and tracks (2.7 ± 1.6)

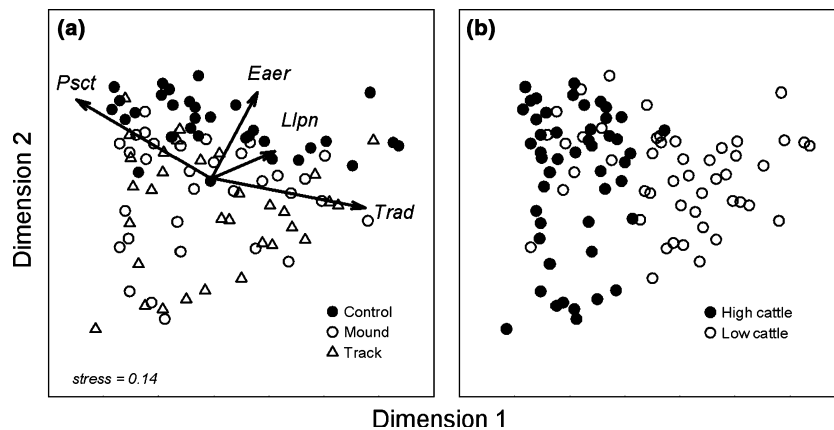


Fig. 2. The first two dimensions of the MDS biplot of species cover showing differences between (a) mound, track and control microsites and (b) high and low cattle usage. Vectors for those species with correlation coefficients > 0.40 with the main axes are shown. Trad = *Tradescantia fluminensis*, Eaer = *Ehrharta erecta*, Lpn = *Lolium perenne*, Psct = *Pennisetum clandestinum*.

than on the control microsites (3.3 ± 1.8 ; $F_{2,184} = 7.50$, $P = 0.001$; Fig. 2). There were significantly more species at high cattle usage (3.3 ± 0.16) than the low cattle usage (2.5 ± 0.11) sites ($F_{1,14} = 4.35$, $P = 0.056$, Fig. 2) but no effect in relation to streambank position ($P = 0.43$). There were no significant differences in richness (Margalef's index) or evenness in relation to cattle usage, microsites or distance from stream edge ($P > 0.05$).

In general, there were substantial differences in plant cover between microsites, with the major differences being between the off-mound, off-track controls and the mounds and tracks. Plant cover on the control microsites (79.4 ± 2.1) was more than twice that on the mounds (34.3 ± 2.7) and tracks (29.5 ± 2.5 ; $F_{2,184} = 188.65$, $P < 0.001$). There was no effect of cattle usage ($P = 0.14$) or streambank location ($P = 0.41$) on plant cover. Consequently, there was more bare soil on the mounds (40.9 ± 2.9) and tracks (31.8 ± 3.2) than the control microsites (2.47 ± 0.43 ; $F_{2,184} = 71.4$, $P < 0.001$), but again no cattle usage or streambank effects ($P > 0.51$). Litter cover increased from control (17.9 ± 1.9) through mound (24.8 ± 2.7) to track (37.8 ± 3.0) microsites ($F_{2,184} = 22.3$, $P < 0.001$) and was substantially greater at the low cattle sites than at high cattle sites (33.7% vs 20.1% respectively; $F_{1,14} = 4.70$, $P = 0.048$).

The PERMANOVA analyses of plant cover indicated a significant effect of microsite on plant community structure [pseudo $F_{2,56} = 4.81$, $P(\text{perm}) < 0.001$], with similar plant composition between track and mound microsites [$t = 1.08$, $P(\text{perm}) = 0.39$], which both differed from the control microsites ($P = 0.001$; Fig. 2). The main difference resulted from a dominance by *Tradescantia fluminensis* (IV = 45.6, $P = 0.004$) on control microsites, but no species was strongly indicative of tracks or mounds. We also

detected significant differences in plant community composition in relation to cattle usage [pseudo $F_{1,14} = 7.35$, $P(\text{perm}) = 0.001$; Fig. 2]. Indicator species analysis showed that *Pennisetum clandestinum* (IV = 74.9, $P < 0.001$) and *Ehrharta erecta* (IV = 48.0, $P = 0.039$) were significant and indicators of high cattle sites, with large indicator values. Although other species were significant indicators (Table 1), the indicator values were relatively small. *Tradescantia fluminensis* was a significant indicator of low cattle usage sites (IV = 70.6, $P < 0.001$) and a significant indicator of non-track/non-mound (control) microsites (IV = 63.6, $P = 0.001$; Table 1).

Plant traits in relation to mound position, cattle usage and microsite

For any plant traits (Table 1), there were no differences in cover between sites close to, and those far from, the stream edge ($P > 0.05$, Table 2). The cover of exotic plants was significantly greater at the high cattle sites (45.3%) than the low cattle (33.9%) sites [pseudo $F_{1,4} = 3.29$, $P(\text{perm}) = 0.048$] and there was four times greater cover of large (> 50 cm tall) plants at the high cattle sites than at the low cattle sites [pseudo $F_{1,4} = 13.57$, $P(\text{perm}) < 0.001$]. The cover of plants with animal-assisted dispersal mechanisms was greater at the high cattle usage sites than the low cattle usage sites on tracks and control sites, but there were no differences on the mounds [cattle usage by microsite interaction: pseudo $F_{2,56} = 3.89$, $P(\text{perm}) = 0.004$]. Overall, therefore, control sites were not characterized by a plant community with a unique suite of plant attributes. Rather, they tended to be higher in cover of relatively tall, ascending or prostrate, fibrous, monocotyledonous, perennial plants (Table 2).

Table 2. Species that were significant indicators of different cattle usage, streambank location and microsite.

Species	Cattle usage	Indicator value (%)	P
Cattle usage			
<i>Pennisetum clandestinum</i>	High	74.9	< 0.001
<i>Bromus cartharticus</i>	High	27.1	< 0.001
<i>Rumex brownii</i>	High	18.9	0.006
<i>Prunella vulgaris</i>	High	18.7	< 0.001
<i>Cynodon dactylon</i>	High	18.7	0.004
<i>Modiola caroliniana</i>	High	17.2	0.015
<i>Paspalum dilatatum</i>	High	12.5	0.024
<i>Hypochaeris radicata</i>	High	12.5	0.028
<i>Tradescantia fluminensis</i>	Low	70.6	< 0.001
<i>Ageratina riparia</i>	Low	20.0	0.027
<i>Pseudoanthemum variabile</i>	Low	15.1	0.030
Stream location			
<i>Lomandra longifolia</i>	Stream	18.6	0.006
<i>Entolasia marginata</i>	Stream	15.9	0.023
<i>Persicaria prostrata</i>	Stream	14.6	0.014
<i>Geranium solanderi</i>	Top	29.2	0.010
<i>Modiola caroliniana</i>	Top	16.4	0.010
Microsite			
<i>Tradescantia fluminensis</i>	Control	48.4	0.003
<i>Commelina cyanea</i>	Control	34.9	0.018

Discussion

There were three main results of our study. First, both high cattle use sites and low cattle use sites had similar plant cover, although high cattle use sites supported more species that tended to differ in their composition. Second, tracks and mounds had similar plant composition, but had substantially less cover, and supported a subset of those in the surrounding vegetation. Third, plant cover and composition did not change with increasing distance from the stream edge. Overall, contrary to our predictions, mounds and tracks did not support a unique spectrum of plant species compared with the surrounding vegetation. However, they did support substantially reduced plant cover, which likely resulted from continual disturbance, particularly by cattle.

Effects of cattle usage on plant cover and composition

Overgrazing by cattle has long been implicated in habitat degradation and substantial reductions in plant and animal diversity and abundance (FAO 2007), processes known to favour the spread of invasive exotic plants. Our observation of greater cover of exotic plants is therefore not surprising. We detected no significant effects of cattle on plant cover when averaged across all microsites. However, we detected more species and 33% greater cover of

exotic plants at the high cattle sites, a typical consequence of high cattle usage (Noy-Meir et al. 1989). Our results are consistent with those from a range of riparian agricultural environments where grazing has been shown to reduce plant vigour and biomass, and alter species composition (Kauffman & Krueger 1984; Young-Mathews et al. 2010).

High cattle usage sites had a different composition of plant species, mainly grasses. The erect *Ehrharta erecta* and the prostrate grass *Pennisetum clandestinum* were typical indicators of high cattle use sites, while *Tradescantia fluminensis* and to a lesser extent the unpalatable, low sprawling shrub *Ageratina riparia* were indicators of low cattle use sites. *Ehrharta erecta* is a highly invasive exotic grass that spreads through grassy woodlands, forests and heathlands. Although a strong competitor in shaded areas (McIntyre & Ladiges 1985), it is replaced by *P. clandestinum* in more open sites. *Pennisetum clandestinum*, a vigorous nitrophilous grass of improved pastures, is extremely grazing-tolerant (McIntyre et al. 2005) and has likely spread to disturbed streambanks through stoloniferous growth (Jackson & Jacobs 1985). The fleshy nature of *T. fluminensis* makes it vulnerable to cattle trampling so it is not surprising that it is an indicator of low cattle usage sites. Anecdotal evidence however, suggests that high stocking rates can destroy large infestations of *Tradescantia*. Disturbances created by wombats and cattle therefore may create the only gaps for other plants to establish. *Ageratina riparia* is an indicator of moist conditions and disturbed stream margins (Robinson 1991) and would be expected to be removed by high cattle usage.

Not unexpectedly, plants at high cattle use sites had some attributes suggestive of animal-assisted dispersal (Table 1) such as adhesive seeds (McIntyre et al. 1995). We did not detect any differences in the cover of species with awned seeds, which would be expected given that animals are their principal vectors of dispersal (McIntyre et al. 2005). In contrast with low cattle use sites, high use sites had a greater cover of taller (>50 cm) plants, consistent with studies of cattle grazing in riparian areas (Paine & Ribic 2002). Although tall plants may have a competitive advantage under moderate levels of grazing (Weiher et al. 1999), they are generally selected against by heavy grazing because of the high cost of investing in support structures (Lehsten & Kleyer 2007). This suggests to us that either the relatively high levels of grazing were too low to induce lodging in taller riparian plants or that more than a century of grazing has selected for grazing-resistant taller plants, which is a more likely scenario. Finally, we cannot account for the lack of a significant difference in relation to streambank position, but it may be an artefact of the particular sites we studied. There were few differences in topography among the sites, and high water flows were probably too

intermittent to influence the vegetation (Nilsson et al. 1996).

Differences in plant communities among microsites

Animals can have substantial and enduring effects on riparian ecosystems, ranging from the creation of a complex networks of tracks at landscape scales to specific patch-level effects on vegetation and ecosystem processes (Naiman & Rodgers 1997). Despite the marked differences in microsite morphology, we found very few differences in plant community structure, apart from less cover and fewer species on mounds and tracks. Cattle grazing has been a substantial land use in Kangaroo Valley since 1821 (Griffith 1986). Anecdotal evidence suggests that wombat populations may have benefited from the conversion of forested land to managed pasture, but the suite of plants on streambanks has remained relatively stable since the first half century of agricultural expansion. It is likely, therefore, that disturbance-sensitive species were filtered out by grazing and trampling many years ago.

We could attribute reduced richness on tracks and mounds to the more extreme disturbances experienced by plants growing in these microsites. Species growing on the mounds and tracks need to tolerate not only continual herbivory, but must also tolerate inundation of soil caused by frequent burrowing by wombats. Regular soil movement on the mounds of the American badger (*Taxidea taxus*), for example, has been shown to induce marked shifts in the composition of mound-resident plants (Platt 1975). We expected reduced cover and richness on the mounds, given that digging and mound construction by animals are known to influence a range of soil properties such as porosity, bulk density and infiltration (Laundre 1993; Eldridge 2004; Eldridge 2009). Unexpectedly, however, wombat mounds did not support a unique species assemblage. Part of the reason for this may be that wombats forage relatively long distances from their mounds and, unlike other mound-producing semi-fossorial vertebrates such as the European rabbit (*Oryctolagus cuniculus*) (Eldridge & Simpson 2002), Plains vizcacha (*Lagostomus maximus*) (Arias et al. 2005), Prairie dog (*Cynomys* spp.) (Ceballos et al. 1999) and Banner-tailed kangaroo rat (*Dipodomys spectabilis*) (Guo 1996) do not graze on their own mounds.

At landscape scales, wombat mounds contribute in excess of 260 t·ha⁻¹ of loose soil (Borchard & Eldridge 2011) to the riparian system, and re-excavation and reworking of burrows result in an ever-changing mound surface. Soil ejected from the burrows acts as an environmental filter (*sensu* Keddy 1992) by reducing the photosynthetic capacity of plants, particularly short plants with prostrate growth forms. Regular inundation with soil may

advantage plants that are taller, given that reduced soil moisture and carbon starvation resulting from inundation with soil would occur later in larger plants (Lambers et al. 2008). Potentially, therefore, mounds could be selecting for taller plants while the surrounding plant community could be selecting for shorter, grazing-tolerant species. This is consistent with our trait results where we found a lower cover of prostrate plants on the mounds and tracks, though we are unable to interpret the observation of a lower cover of tall plants on the mounds and tracks. Mounds would also be expected to support a greater number of species that are poorly adapted to low light levels (Seifan et al. 2010). Unpublished data from mounds at our sites reveals that two exotic plants, the shrub *Ligustrum sinense* and the sub-shrub *Sida rhombifolia*, the native tussock grass *Lomandra longifolia* and native shrub *Hymanthera dentata* were able to tolerate limited burial by mound soil. Burial alters a range of soil properties, increasing soil temperature, reducing oxygenation and changing soil moisture levels (Maun 1998). These woody plants may be able to tolerate burial by shifting the allocation of below-ground resources to above-ground tissues (Maun 1998).

We found no difference between mounds and tracks in relation to vascular plants at the microsite scale. Consequently, it is difficult to separate out the relative effects of wombats from those of cattle. Certainly the soil-disturbing effects of wombats are marked (Borchard & Eldridge 2011), but only at the scale of the mounds. When one takes into account the extent of track formation by cattle (119 t soil·ha⁻¹; Borchard & Eldridge 2011), it is clear that they have a markedly greater effect on ecosystem processes at landscape scales than is apparent from the study of vascular plants alone. The network of tracks at the study sites was used by both wombats and cattle. We suspect, however, that cattle are responsible for most of the track formation, although the extent to which wombats contribute to their formation is uncertain. We are unaware of any studies of track formation by native vertebrates, including wombats. Observations at cattle-free sites containing wombats indicate that wombat tracks consist of a slight flattening of the vegetation but are not concave like those of cattle. We believe therefore that the effect of wombats on existing cattle tracks is minimal, particularly given the low foot pressure of wombats (16–96 kPa) compared with cattle (132–250 kPa; Scholefield & Hall 1986). Similarly, effects at larger scales, which we can only speculate upon, suggest a more pronounced effect of cattle grazing. Prolonged cattle grazing increases the spread of *P. clandestinum*, producing a highly productive sward that outcompetes other species, probably by reducing light levels. This is combined with increases in the cover of *Tradescantia* in shaded areas as a result of its unpalatability to wombats

and cattle, which allows it to outcompete native species (Standish et al. 2001).

In summary, our study has demonstrated that there are few differences in plant community composition between structures constructed by cattle and those of wombats. Both were similar in that they supported a community that was a subset of the species pool in the surrounding vegetation (*sensu* Seifan et al. 2010). Further study should focus on the landscape-scale effects of cattle grazing to determine whether cattle or wombats are the major causes of ecosystem degradation in Australian riparian environments.

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