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ORIGINAL PAPER

Density-dependent grazing impacts of introduced European rabbits and sympatric kangaroos on Australian native pastures

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Abstract Little information is available on relationships between pest animal density and damage in natural ecosystems. Introduced European rabbits, *Oryctolagus cuniculus*, cause severe damage to Australian native vegetation but density–damage relationships are largely unexplored. There are no recognized simple methods to estimate their impacts on native pastures, due in part to confusion with grazing impact of other herbivores. We tested simple quantitative sampling methods using multiple small quadrats to detect site differences in pasture cover, pasture species richness and dung pellet density of herbivores, from which rabbit density and relative abundance of larger herbivores were estimated. Native pasture cover and species richness declined exponentially with increasing rabbit density, within the range of 0–5 rabbits ha^{-1}, while cover of unpalatable exotic pasture species increased. By contrast, kangaroo abundance was positively related to palatable native pasture cover and negatively related to cover of unpalatable weeds, and had no negative effect on native pasture cover or species richness that was discernable against a background of low to moderate rabbit densities. Perennial native forbs and perennial grasses replaced invasive Wards weed as the dominant ground cover at low rabbit densities. We conclude that, regardless of previous grazing history, contemporary kangaroo grazing pressure and weed invasion, the severely degraded state of native pastures was perpetuated by rabbits. The effect of rabbits on native pasture can be recorded in a simple manner that is suitable for identifying density–damage relationships in the presence of other herbivores and changes over time. This method is seen as particularly useful in setting target densities below which rabbits must be managed to maintain native plant communities and ecosystem function in southern Australia. It may also be useful to demonstrate rabbits' impacts in other regions, including optimum densities for plant biodiversity benefits in their native European range.

Keywords Biodiversity · Exotic species · Herbivory · Pasture damage · Plant cover · Species richness

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Introduction

Exotic herbivores, unrestrained by natural ecological processes and plant defences, frequently damage native plant communities to a greater extent than native herbivores (Parker et al. 2006; Oduor et al. 2010). Their preferential grazing can reduce abundance and species richness of native pasture species and promote less-palatable exotic competitors, with compounding effects on other ecosystem processes (Balvanera et al. 2006; Isbell et al. 2011). Although this is a well-recognised global problem, there is little information on the relationship between exotic herbivore density and damage (Nunez et al. 2010). Consequently, managers have difficulty determining what level of control is necessary to protect native species or promote their recovery, and funding agencies are unable to make well-informed decisions about resource allocation for competing programs. Herbivores may be managed on the basis that partial control provides incremental recovery but plant functional responses can vary greatly (Hone 2007; Norbury et al. 2015). Threshold densities for preventing damage to palatable species may be very low (e.g. Lange and Graham 1983; Alverson et al. 1988; Denham and Auld 2004; Bird et al. 2012; Mutze et al. 2016) and partial herbivore control may indirectly advantage moderately palatable exotic plants (Norbury et al. 2015) and release them to outcompete native species (Nunez et al. 2008).

Introduced European rabbits, *Oryctolagus cuniculus*, cause severe damage to Australian native vegetation (Leigh et al. 1987; Williams et al. 1995; Cooke 1998; Denham and Auld 2004; Cooke et al. 2010; Bird et al. 2012). Their impact on trees and large shrubs is often readily apparent from rabbit bite-marks on basal stems, lower branches and seedlings, and the absence of juvenile cohorts where long-lived seed-bearing adult plants are common (Cooke et al. 2010; Mutze et al. 2016), thereby suppressing recruitment of a wide range of perennial species (reviewed in Cooke et al. 2012; also Bird et al. 2012; Forsyth et al. 2015; Mutze et al. 2016). The impact on pastures and small shrubs is more obscure, because a significant component of damage may simply be removal of flowers and seed heads (Leigh et al. 1987), and favored species such as terrestrial orchids may be completely eliminated or suppressed below detectable levels despite high remaining pasture biomass (Mutze et al. 2008; Bird et al. 2012). Nevertheless, rabbit impacts on native pasture communities have been recorded in a wide variety of Australian habitats including arid shrublands (Foran et al. 1985), sandy mallee woodland (Cochrane and McDonald 1966), semi-arid grassland (Leigh et al. 1989) and sub-alpine heath (Leigh et al. 1987). Rabbit grazing and digging activity around warrens also alters soil characteristics and soil seed banks to favour germination and growth of exotic weeds over native species (Eldridge et al. 2006), slowing recovery after native plant communities have been degraded by rabbit grazing. Of the 121 threatened or endangered Australian native plant species for which rabbits are a recognized threat (DEWHA 2008), more than 50 % are grasses, forbs or low-growing shrubs that remain vulnerable to rabbits at all growth stages. These threats are likely to be grossly under-reported because it is difficult to quantify rabbit density in native vegetation, and there are no simple repeatable methods to estimate rabbit impact on native pasture.

In the arid rangelands of southern Australia, most habitats occupied by rabbits also support domestic livestock and sympatric populations of one or more large macropod species: red kangaroos, *Macropus rufus*, euros, *Macropus robustus,* western grey kangaroos, *Macropus fuliginosus*, or eastern grey kangaroos, *Macropus giganteus* (Van Dyck and Strahan 2008). There is a high degree of dietary overlap between rabbits, livestock and these macropods (Short 1985; Dawson and Ellis 1994, 1996; Van Dyck and Strahan 2008). In conservation reserves established on former livestock grazing lands, over-abundant large macropods have been shown to impede recovery of degraded native pastures (e.g. Norbury et al. 1993; de Preu 2006), while other studies have found sympatric rabbit populations to be the main influence on native species recovery (Leigh et al. 1989; Mutze 2006). Kangaroos may be maintained at elevated numbers by permanent water supplies developed to support earlier use for livestock production, and feral livestock, particularly goats, *Capra hircus*, may remain common. Therefore, it is often unclear which herbivores must be managed to promote vegetation recovery, and to what levels (de Preu 2006; Hone 2007).

The critical characteristic of any method for measuring herbivore impact on pasture composition is that it can be used to quantify differences that are related to herbivore density and, in particular, to demonstrate quantifiable changes in pasture composition following changes in herbivore density. We aimed to develop a simple method that could be adapted for routine vegetation surveys or detailed research projects to distinguish rabbit impacts from those of other herbivores. From the range of possible approaches we chose to measure pasture cover and species richness using small quadrats. This approach has greater sensitivity than point-quadrats or biomass estimates for recording uncommon species and those with small leaf area (Godinez-Alvarez et al. 2009). While the method is not new, its use to simultaneously estimate plant cover and species richness, rabbit density (Mutze et al. 2014a) and relative abundance of other herbivores (Johnson and Jarman 1987; Landsberg and Stol 1996) in the same small quadrats offered a novel approach for estimating density-dependent impacts of multiple herbivores. Having arrived at a method that seemed practical, we tested it in vegetation associations where differences in shrub recruitment had been observed between rabbit-control and no-control treatments (Mutze et al. 2008) to ask whether it was sensitive enough to measure density-dependent herbivore impacts on native pasture.

Methods

Study sites

Responses of native vegetation communities to effective rabbit control may take many years to become evident because of slow plant succession. Therefore, comparison of sites in close proximity which have similar vegetation communities, soil and climate, but different history of rabbit control and levels of rabbit abundance, offered the most practical means of assessing whether there were measurable relationships between rabbit density and native pasture species richness and cover. If effective and practical assessment methods were developed they could then be used, before and at suitable times after specific projects to control rabbits, to see whether or not pasture species richness and cover had improved.

This study was undertaken in conjunction with work conducted to quantify the effects of rabbits on perennial trees and shrubs (Mutze et al. 2016). That is, study sites were chosen based on tree and shrub communities without reference to pasture communities. In all, we established 12 sites to quantify herbivore effects on pastures in semi-arid rangeland plant communities on Ikara Flinders Ranges National Park in South Australia (31°25′S 138°42′E, mean annual rainfall approximately 250 mm). Field-work was undertaken in autumn and spring of 2012.

The native vegetation of Ikara Flinders Ranges National Park was heavily degraded by sheep and cattle grazing during early pastoral expansion into inland South Australia in the mid 1800s and those effects were compounded by the subsequent arrival of rabbits. Livestock were removed after the Park was established in 1970. Feral goats were abundant during the 1980s but were reduced to low numbers in the 1990s by intensive control programs, and remained uncommon in the study area (de Preu 2006). The dramatic impact of rabbit haemorrhagic disease (RHD) on rabbit numbers in the Park in late 1995 (Mutze et al. 2014b) and widespread rabbit control between 1994 and 2001 across 200 km^2 of the Park (de Preu 2006), followed by partial recovery of some of those rabbit populations (Mutze et al. 2014b), produced a large number of comparable sites in close proximity with substantial differences in rabbit density. The sites chosen were in open shrubland consisting primarily of *Eremophila alternifolia*, *Acacia ligulata*, *Callitris glaucophylla*, *Senna artemisioides artemisioides* or *Dodonaea lobulata*. The understory on each of these sites included open tussock grasses and forbs with a highly variable proportion of exotic and native species.

Pasture cover and species richness

Pasture composition was recorded during spring when pastures would usually have been at their peak. Rainfall during the 6 months before the study began was above average but rainfall from July to October was only 13 % of the long term average (BOM 2016) and, as a result, pastures had been grazed down and annual species had begun to dry off.

Pasture cover was recorded in 0.1 m^2-quadrats dropped from chest-height at intervals of either 5 or 10 paces, depending on the size of the survey area (1–2 ha), along a series of linear transects walked back and forth across each site to give an approximately even distribution throughout the survey area. To avoid bias, we navigated to a local feature and stayed close to the chosen line of walk, taking care not to favour more open areas nor to look down and select the position relative to pasture species observed. Once dropped, the quadrat was adjusted to free it from vegetation that held it above the soil surface, taking care not to move it laterally. The percentage cover within the quadrat was estimated visually, by species, including grasses, forbs, low-growing shrubs, cryptogam, organic litter and bare ground. All standing vegetation of up to 0.4 m height within the quadrat was recorded, including overhanging plants rooted outside of the quadrat. For each component within the quadrat we estimated the percentage area of the quadrat it covered. When looking down at the quadrat, only the top layer was scored so that the total value for the quadrat was 100 %. If any species was estimated at less than 1 % of the quadrat area it was recorded as a 'trace'. Unrecognized species were recorded by number and voucher specimens were taken for subsequent identification. Herbivore dung pellets present within the quadrat were counted but not scored as part of percentage cover. When two observers were involved, the first few quadrats at each site were assessed by both observers to ensure that estimates were consistent. One hundred pasture quadrats were scored at each site.

Herbivore abundance

Herbivore abundance was estimated from dung pellet density, counted in autumn to estimate mean density in summer/autumn and counted again in spring to estimate density in winter/spring. In both seasons, dung was counted on at least 100 × 0.1-m^2 quadrats in each site or combination of subsites. In spring, quadrats used for pasture assessment were included as part of the total sample. Rabbit density was estimated from dung pellet density (Mutze et al. 2014a). Rabbit dung is quite persistent and estimates using this method are influenced by population density during the previous 2 years (Mutze et al. 2014a), so considerable overlap is expected in estimates taken 6 months apart from the same areas. Dung counts can also be used to census populations of most larger Australian herbivores (Johnson and Jarman 1987; Landsberg and Stol 1996) so macropod, goat and sheep dung pellets were also counted. Observations made during previous long-term studies at Ikara Flinders Ranges National Park (Mutze et al. 2014b) indicated kangaroo dung may be less persistent than rabbit dung due to more rapid consumption by termites, but the effect had not been quantified so dung counts for species other than rabbits were not converted to animal densities. The common large macropods in the tussock grassland sections of the Park used for this survey, euros and red kangaroos, occur in approximately equal densities (de Preu 2006). Their dung was not differentiated by species and combined dung pellet counts were used as an index of kangaroo abundance. However, kangaroo dung counts were, mistakenly, not recorded at three sites during spring surveys, so those sites were excluded from analyses involving spring kangaroo dung counts.

Data analysis

Variation in the relationships between kangaroo dung counts and rabbit density within sites during autumn and spring were examined by simple linear regression to determine whether mean values for these parameters could be used in vegetation analyses.

We then used statistical models comparing variation in plant cover and species richness to rabbit density and/or kangaroo dung counts. We used models with both rabbit and kangaroo terms, and first order interactions with plant species or species groups where appropriate, to determine which aspect of herbivore abundance, if any, could best explain plant species richness and cover. We also considered each herbivore term in separate models, to see how individual herbivore abundance was related to species richness and cover, even if not the best explanatory variable. Relationships between herbivore abundance and species richness, taken as the number of pasture species recorded per site, were considered in generalized linear mixed models (GLMMs) with Poisson error structure and log-links (Crawley 1993). Pasture cover was examined using GLMMs with normal errors and log-links which provided a better fit to the data, across all analyses, than alternative logistic and linear models tested. Separate models were considered for cover of exotic weeds, native grasses, and a third category of native forbs and low-growing shrubs. Within each of the three groups, for species found at four or more sites, variation in slope and mean cover between species was tested.

Results

Herbivore abundance

Rabbit dung counts in spring were highly correlated with rabbit dung counts at the same sites in autumn (Spring counts = 1.21 × Autumn counts + 0.14, R = 0.96, $P < 0.001$). The data indicated that there were no major site-specific seasonal changes in rabbit density, so mean rabbit density estimates were calculated from the combined data and used as a variable to explain pasture species richness and cover.

At those sites where kangaroo dung was counted in both spring and autumn, dung counts in spring were poorly correlated with kangaroo dung counts in autumn ($R = 0.58$, $F_{1,7} = 3.58$, $P = 0.10$). Kangaroo dung counts during spring were also independent of rabbit dung counts ($R = -0.18$, $F_{1,7} = 0.2$, $P > 0.6$) but during autumn, kangaroo dung counts were negatively related to rabbit dung counts ($R = -0.63$, $F_{1,10} = 18.8$, $P < 0.02$) (Fig. 1). Since rabbit grazing primarily occurs within 150–200 m of permanent burrow systems (Leigh et al. 1989; Williams et al. 1995) and there were no major site-specific seasonal changes in rabbit density, this suggests that there were seasonal changes in the areas where kangaroos foraged, with kangaroos grazing less in areas with higher rabbit density during summer/autumn. Consequently, the autumn and spring kangaroo dung counts were considered separately in analyses of kangaroo effects on vegetation.

Only trace amounts of goat dung were found at one site. No dung of other vertebrate herbivores was recorded.

Plant species richness

Species richness of native grasses ($\chi^2 = 5.1$, $P < 0.03$) and native forbs ($\chi^2 = 6.4$, $P < 0.02$) was lower at sites with higher rabbit density, but the number of weed species was independent of rabbit density ($\chi^2 = 0.41$, $P > 0.5$) (Fig. 2a). There was some evidence of more native grass species at sites with high kangaroo dung counts in autumn ($\chi^2 = 4.2$, $P < 0.05$) (Fig. 2b) but autumn kangaroo dung counts and rabbit densities were correlated and rabbit densities were the better explanatory variable. Species richness was not related to spring kangaroo dung counts in any of the three pasture categories (all $\chi^2 < 1.6$, $P > 0.2$) (Fig. 2c).

Amongst native pasture species found at fewer than four sites, 10 forbs and two grasses were recorded only at rabbit densities below 1 rabbit ha^{-1}. Three forbs were found only at 1–2 rabbits ha^{-1}, and one forb at one site below 2 rabbits ha^{-1} and one site above 2 rabbits ha^{-1}, but no native species were recorded exclusively at sites exceeding 2 rabbits ha^{-1}. The only exotic weed recorded at fewer than four sites, *Echium plantagineum*, was recorded at two sites, both having >3 rabbits ha^{-1} (Table 1).

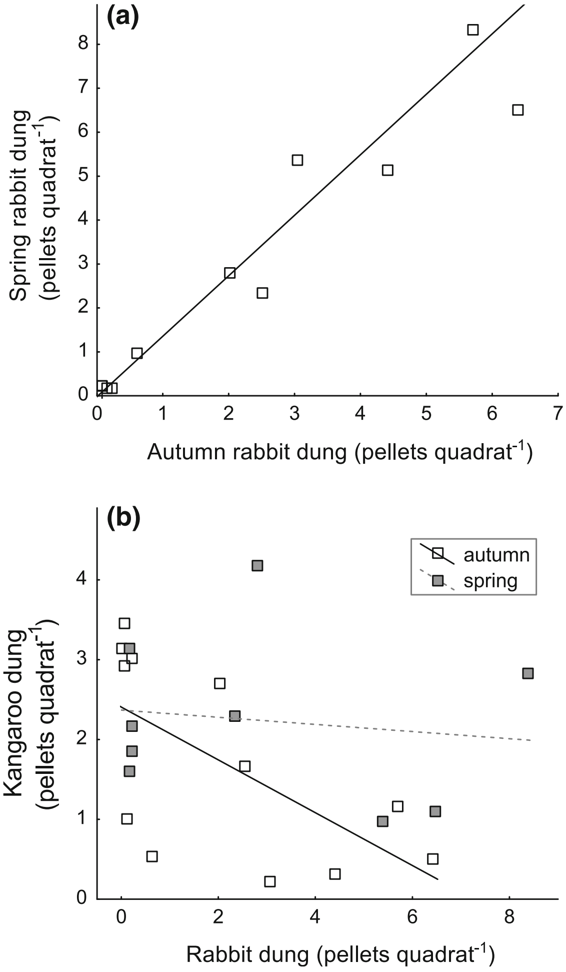

Fig. 1 Between season and between species relationships in herbivore dung counts at Ikara Flinders Ranges National Park; **a** between autumn and spring rabbit dung counts and **b** between mean rabbit dung counts and kangaroo dung counts in autumn and spring

Perennial native grass cover

The palatable perennial grasses belonging to the genera *Rytidosperma* (syn. *Danthonia*), *Austrostipa* and *Enneapogon* were heavily grazed in some areas and difficult to identify to species level at times, so native grass cover analyses were conducted at genus level (Table 1). Mean grass cover varied between genera ($F_{1,21} = 116$, $P < 0.001$), with the highly palatable *Rytidosperma* and *Austrostipa* (Cunningham

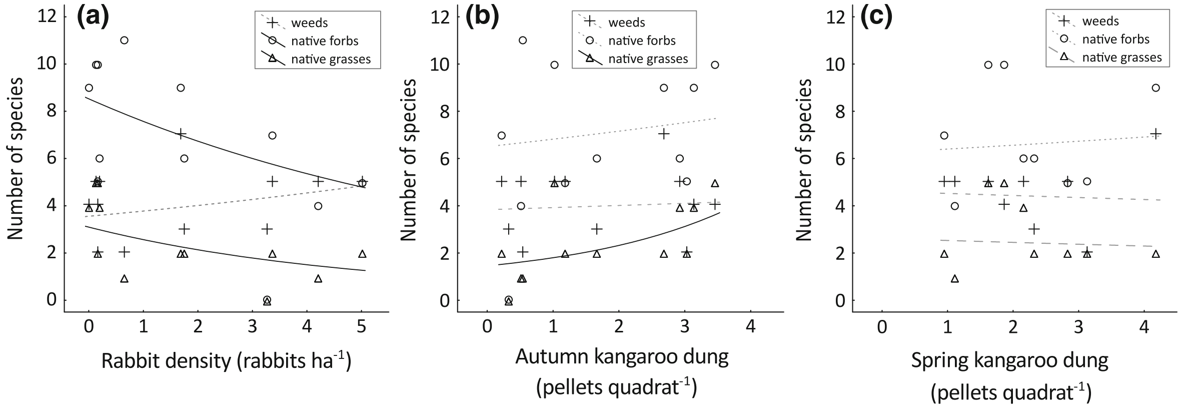

Fig. 2 Relationships between pasture species richness and herbivore abundance at Ikara Flinders Ranges National Park for **a** rabbits, **b** kangaroos in autumn, and **c** kangaroos in spring. *Regression lines* shown for significant ($P < 0.05$, *solid lines*) and non-significant ($P > 0.05$, *grey dashed lines*) exponential relationships

et al. 2011) being the least prevalent, and declined exponentially with increasing rabbit density ($F_{1,21} = 63, P < 0.001$) (model $R^2 = 0.87$) (Fig. 3a). Grass cover was positively related to autumn kangaroo dung counts in models without a rabbit term ($F_{1,21} = 5.6$, $P < 0.03$, model $R^2 = 0.66$) (Fig. 3b) but there was no effect of kangaroo dung counts on grass cover in any of the models that included a rabbit term (all $P > 0.6$). Grass cover was not related to spring kangaroo dung counts in any model tested (all $P > 0.12$) (Fig. 3c).

We found marginal evidence that the effect of rabbits varied between native grasses; *Cymbopogon ambiguous*, an unpalatable colonising species (Cunningham et al. 2011), increased with rabbit density while the three more-platable genera declined. Given the limited data, a common slope was fitted for the three palatable genera and a different slope for *Cymbopogon* (Fig. 3a), explaining an additional 2.3 % of model deviance ($F_{1,20} = 4.27$, $P = 0.05$). Nevertheless, *Cymbopogon* was only found at sites with 0.0–1.7 rabbits ha^{-1}. We found no evidence that the relationship between kangaroo dung counts and grass cover varied among grass species (all $P > 0.35$).

Native forb cover

Two palatable copperburrs, *Sclerolaena patenticuspis* and *S. obliquicuspis,* were common at the sites and, being very similar in appearance and difficult to distinguish where they had been heavily grazed, they were included in cover analyses at genus level. Other genera were separated by species (Table 1).

Mean native forb cover varied among species ($F_{8,47} = 3.51$, $P < 0.01$) and declined exponentially with increasing rabbit density ($F_{1,47} = 8.0, P < 0.001$, model $R^2 = 0.39$) (Fig. 3d) or, in separate models, increased exponentially with increasing autumn kangaroo dung counts ($F_{1,47} = 10.5$, $P < 0.001$, model $R^2 = 0.41$) (Fig. 3e) but neither term reduced model deviance significantly when added to a model that included a parameter for abundance of the other herbivore, and the species + autumn kangaroo dung count model provided a marginally better fit. Interaction terms between individual plant species and herbivore measures were not significant in any models tested (all $P > 0.5$), indicating that the herbivore effects were fairly consistent across the common native forbs. Forb cover was not related to spring kangaroo dung counts in any model tested (all $P > 0.5$) (Fig. 3f).

Exotic weed cover

The exotic weeds in the study area included the palatable annual grasses *Bromus* and *Avena* and legumes belonging to the genus *Medicago* that are common agricultural pasture species. All had begun to die back due to dry early spring weather, were heavily grazed and difficult to identify, so were entered in analyses as 'exotic annual grasses' and 'medics', respectively.

Table 1 Pasture species recorded in Ikara Flinders Ranges National Park

Pasture group	Species
Species recorded at 4 or more sites	
Native grass	*Rytidosperma caespitosum*
	Austrostipa spp.
	Cymbopogon ambiguus
	Enneapogon avenaceus
Native forb	*Abutilon halophilum*
	Hyalosperma demissum
	Pimelia simplex
	Ptilotus obovatus
	Sclerolaena obliquicuspis
	Sclerolaena patenticuspis
	Sida petrophila
	Sida spodochroma
	Solanum ellipticum
	Vittadinia cuneata
Exotic weed	*Bromus spp.*
	Asphodelus fistulosus
	Carrichtera annua
	Centaurea melitensis
	Herniaria hirsuta
	Medicago spp.
	Marrubium vulgare
Species recorded at fewer than 4 sites	
Native grass	*Aristida nitidula*
	Enneapogon polyphyllus
Native forb	*Atriplex stipitata*
	Cheilanthes austrotenuifolia
	Enchylaena tomentosa
	Eriochiton sclerolaenoides
	Euphorbia drummondii
	Euphorbia tannensis
	Lotus cruentus
	Rhagodia spinescens
	Sida fibulifera
	Sida intricata
	Solanum sturtianum
	Solanum quadriloculatum
Exotic weed	*Echium plantagineum*

Many of the exotic plants were not palatable. In particular, Wards weed, *Carrichtera annua*, is the locally dominant annual forb, with highly aromatic unpalatable foliage that dies off in late spring, leaving dense, dry, standing stems with persistent seed pods (Cunningham et al. 2011). *Carrichtera* is grazed very little by rabbits or kangaroos (Cooke et al. 2012). At the time of survey, it had matured and begun to drop its leaves but still contributed more to total pasture cover than any other species or species group (Fig. 3). Preliminary analyses indicated marginally different herbivore effects between all weed species (species × slope $P = 0.05$) but only the regression slope for *Carrichtera* differed significantly from zero. The between-species models were simplified to fit one slope for *Carrichtera* and a different, common slope for other weed species, without significantly increasing error deviance.

Carrichtera cover was substantially lower at sites where autumn kangaroo dung counts were high, but cover of other weeds was slightly higher at those sites (Fig. 3h), with a highly significant difference between slopes ($F_{1,39} = 10.9$, $P < 0.002$, model $R^2 = 0.63$). The relationships were reversed but less pronounced for rabbit densities (Fig. 3g); mean weed cover varied between species ($F_{6,40} = 47.1$, $P < 0.001$) and was higher at high rabbit densities ($F_{1,40} = 4.1$, $P < 0.05$, model $R^2 = 0.33$) but the difference in slopes between *Carrichtera* and other weeds was not significant ($F_{1,39} = 2.8$, $P = 0.1$). There was no effect of rabbit density on weed cover in models that included autumn kangaroo dung counts (all $P > 0.38$).

In models which included spring kangaroo dung counts as the only explanatory variable, differences in slopes between weed species were highly significant ($F_{6,21} = 10.8$, $P < 0.001$). Given the restricted sample size, some of these differences may be artefacts of over-parameterization but the model could not be simplified to compare the slope for *Carrichtera* to a common slope for other weeds without significantly increasing error deviance ($F_{5,21} = 5.5$, $P < 0.003$). Weed cover was not related to spring kangaroo dung counts in any model that included rabbit density or autumn kangaroo counts (all $P > 0.09$).

Discussion

This study demonstrated that the effect of rabbits on native pasture cover and species richness can be quantified in the presence of substantial populations of large native herbivores, using simple techniques suitable for identifying density–damage relationships and changes in pasture composition over time. This

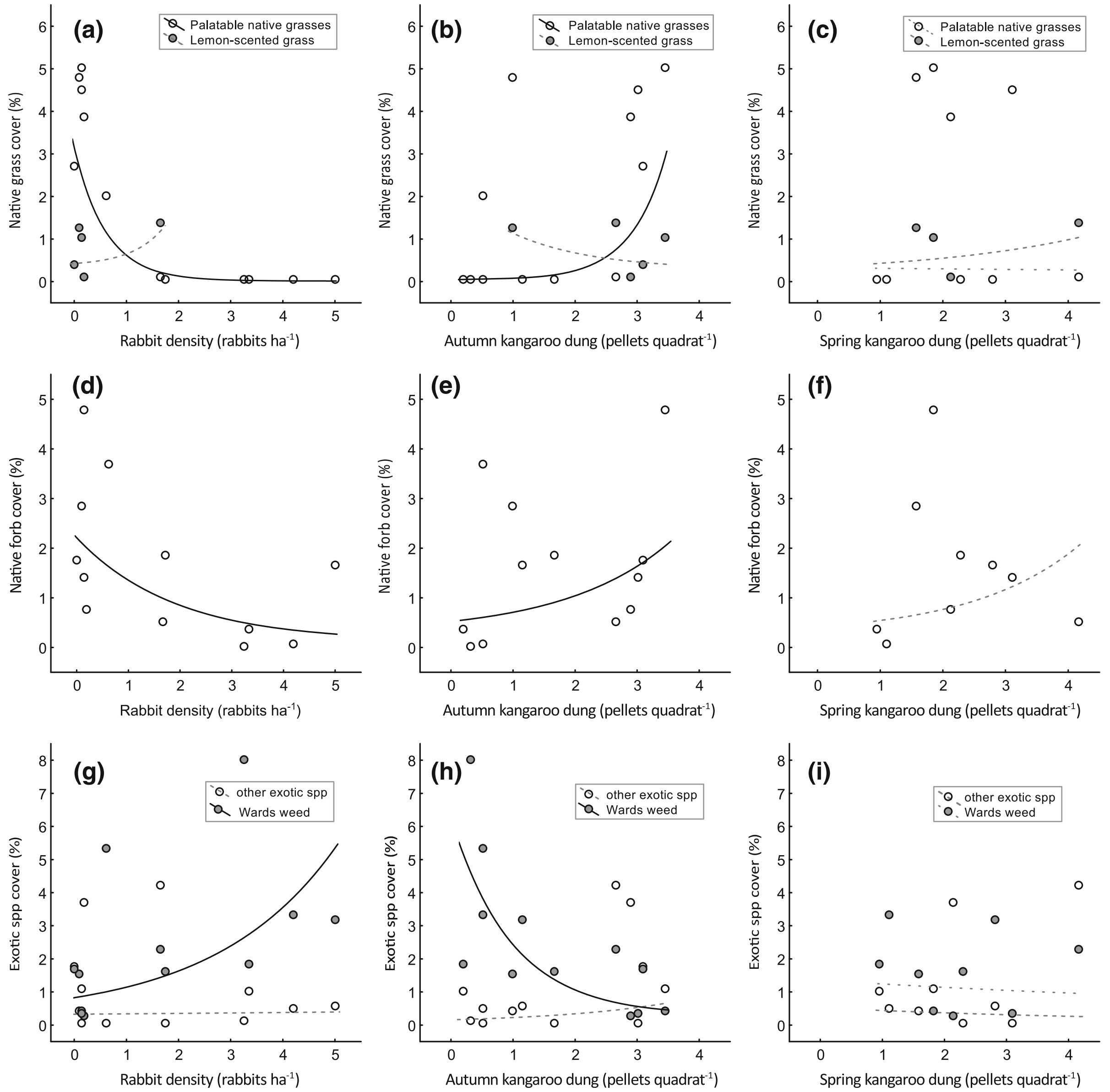

Fig. 3 Relationships between total pasture cover and herbivore abundance at Ikara Flinders Ranges National Park for perennial native grasses, native forbs and exotic plants, respectively, with (**a**, **d**, **g**) rabbits, (**b**, **e**, **h**) kangaroos in autumn and (**c**, **f**, **i**) kangaroos in spring. Relationships for lemon-scented grass, *Cymbopogon ambiguous,* and Wards weed, *Carrichtera annua,* are shown separately because their relationships with at least one index of herbivore abundance were significantly different from other species in their groups. *Regression lines* shown for significant ($P < 0.05$, *solid lines*) and non-significant ($P > 0.05$, *grey dashed lines*) exponential relationships

method is seen as particularly useful in setting estimates of maximum densities below which rabbits must be managed to maintain native plant communities, and hence ecosystem function (Friedel and James 1995; Balvanera et al. 2006; Isbell et al. 2011), in southern Australia.

The method may also be applicable to demonstrate the positive and negative impacts of low-density rabbit populations in other regions. For example, rabbits play a critical role in maintaining plant biodiversity in parts of their European range (review in Delibes-Mateos et al. 2008), maintaining spatial heterogeneity in plant height and nutrient availability (Olofsson et al. 2008). The benefits may be maximized under moderate rabbit grazing (Zeevalking and Fresco 1997) but relationships between plant biodiversity and rabbit density remain largely undefined.

Herbivore impacts on pasture composition in Ikara Flinders Ranges National Park

From our analyses, rabbit grazing reduced native plant species cover by approximately 50 % at 1 rabbit ha^{-1}, and by almost 90 % at 5 rabbits ha^{-1}. Native pasture cover declined due to both declining cover of widespread species and reduced occurrence of less-common species, and native species richness was almost halved at 5 rabbits ha^{-1}. Conversely, exotic weed species richness increased at higher rabbit density. The suppressive effect of rabbit density was most pronounced on perennial native grasses, *Rytidosperma*, *Austrostipa* and *Enneapogon*, but we did not find a significant effect of rabbit density on the less palatable grass *Cymbopogon* (Fig. 3a). *Cymbopogon* is often restricted to creeklines and rocky terraces (Cunningham et al. 2011) so it is unclear from these data whether it is suppressed at the higher rabbit densities we recorded, or whether our sites with higher rabbit density were in areas that did not suit its slightly restrictive habitat preferences. Perennial grasses are critical components of semi-arid woodlands and shrublands, as the basis of sustainable grazing, and influence water infiltration, soil stability and nutrient distribution, and hence recruitment of woody perennials and the scale and functioning of habitat patches (Friedel and James 1995) so their re-establishment is an important step in ecosystem recovery.

During summer/autumn, kangaroos exhibited inverse relationships to those of rabbits with native pastures and weeds. In particular, high kangaroo dung counts were associated with high cover of native grasses and forbs, and low *Carrichtera* cover. By contrast, no relationships were apparent between kangaroo abundance during winter/spring and pasture composition. We take this as evidence that rabbits damaged native pastures, that rabbit density largely determined the cover and richness of native species, and that kangaroos foraged in the areas where native pasture remained least damaged by rabbits, avoiding heavily rabbit-grazed areas during the usual period of pasture shortage in summer/autumn, but foraging more broadly when annual pastures grew in winter/spring. Our data indicate that native forbs and perennial grasses replace *Carrichtera* as the dominant ground cover at low rabbit densities (Figs. 3a, d, g); that is, regardless of previous grazing history, contemporary kangaroo grazing pressure and weed invasion, the severely degraded state of these native pastures is perpetuated by rabbits. Alternative explanations for these statistical relationships, for example, that kangaroo grazing favours native grass growth and suppresses Wards weed, that kangaroos out-compete rabbits in grassy areas and force them to occupy the poorer pastures dominated by Wards weed, or that rabbits prefer Wards weed pastures and competitively exclude kangaroos from those areas in summer, are improbable and largely disproved by the increase in kangaroo numbers, increase in native grasses and forbs, and reduction in weeds (de Preu 2006; Mutze 2006; Mutze et al. 2008) that has occurred in the Park where rabbits have been controlled or fenced out.

Mean macropod densities in the tussock grasslands of Ikara Flinders Ranges National Park used for the vegetation survey are approximately 11 euros km^{-2} and 14 red kangaroos km^{-2} (de Preu 2006), both of which are extremely high compared to most areas within the arid pastoral zone of southern Australia (DENR 2012). Nevertheless, on the basis of relative food intake, their combined density equates to approximately 9 sheep-equivalents km^{-2} (Munn et al. 2013), which is only slightly more than half of the maximum sheep stocking rate permitted by government leasehold agreements on adjoining properties. Rabbit densities of 1–5 rabbits ha^{-1} equate to 9–45 sheep-equivalents km^{-2} (Cooke 2014). So even without taking into account the highly selective grazing behaviour of rabbits, given that they consumed up to five times as much as kangaroos where they were at the highest densities, their powerful influence on vegetation might be expected based on food intake alone.

Not all exotic species were suppressed by rabbits; cover estimates for species other than Wards weed were independent of rabbit density and the highest individual weed cover estimate occurred at moderate rabbit density (Fig. 3g). Declining weed cover at very high rabbit density might be expected, as rabbits at first favor weed invasion by selectively grazing the more palatable native pasture species, but at high rabbit densities remove all but the least palatable weeds. Due to that same effect, weed biomass may increase initially in response to a reduction in rabbit grazing intensity (Cooke 1998), but over time it is likely that unpalatable weeds will be replaced, at least in part, by the more palatable native forbs, shrubs and grasses (Cochrane and McDonald 1966; Cooke 1998; de Preu 2006). In less degraded Australian native pastures, reduction in rabbit density leads to increases in cover, biomass, flowering and species diversity of native forbs, and changes in the proportions of more-palatable and less-palatable native species, rather than changes in weed prevalence (Leigh et al. 1987).

It remains likely that some pasture species are severely suppressed by both rabbits and kangaroos at the densities recorded, to the extent that they were not detected at any site. Darling pea, *Swainsona sp*, for example, formed dense 300-mm-tall mats inside ungrazed exclosures on the Park following good rains in 2010, but outside of exclosures was only observed during the previous 20 years as occasional heavily-grazed plants in rabbit-controlled areas (G. Mutze, unpublished data). Kangaroos clearly compete for pasture biomass with other large herbivores (e.g. Edwards et al. 1996), and must add considerably to pasture off-take in areas occupied by rabbits. Nevertheless, Leigh et al. (1989) found that the effects of kangaroos on species composition and biomass in semi-arid grasslands was generally much less than rabbits, and in this study kangaroo grazing had no negative effect on native pasture cover or species richness that was measurable against a background of low to moderate rabbit grazing.

In the absence of livestock, rabbit impact on pastures was easy to discern with moderate sample sizes. For each sample point, it took approximately 2 h for two observers to measure pasture cover in 100 quadrats. The time invested also provided an estimate of herbivore abundance. On pastoral properties where livestock also graze native pastures, larger sample sizes may be necessary to disentangle the effects of rabbit and kangaroo density from complex interacting influences of stocking rates, large feral herbivores, distance from permanent water and irregular rainfall (e.g. Friedel 1997). In this regard, it is worth noting that repeated highly-detailed attempts to demonstrate gradients in Australian arid-zone pasture composition due to grazing by larger herbivores around permanent water points, at sites within the geographic range of rabbits but without accounting for rabbits' impact, have been largely unsuccessful (reviewed by Fensham and Fairfax 2008).

Wider implications for biodiversity in Australian landscapes

The rabbit-density-dependent rate of decline in native pasture found in this study is of particular interest because it matches, almost identically, the rabbit-density-dependent decline in recruitment of perennial shrubs and trees previously recorded at this site and in higher rainfall sites in coastal South Australia, central Victoria (Mutze et al. 2016), and southern Victoria (Forsyth et al. 2015), and at 200 other sites in temperate eastern Australia (Cooke et al. 2010). Collectively, the available data indicate that in a wide variety of temperate and arid zone Australian vegetation communities, rabbits severely reduce vegetation condition at densities of <1 rabbit ha^{-1}, taking out the most palatable native species and often reducing biodiversity long before they affect plant biomass (Lange and Graham 1983; Leigh et al. 1989; Denham and Auld 2004; Bird et al. 2012). To put this in context, an average density of 1 rabbit ha^{-1} could be maintained by only one small warren every 300 m across a landscape, if each warren supported two breeding pairs, each producing two short-lived litters per year. Population densities ≥ 1 rabbit ha^{-1} are widespread in Australian pastoral rangelands (e.g. Leigh et al. 1989; Williams et al. 1995; Mutze et al. 2014a) and in native vegetation remnants in agricultural areas (Williams et al. 1995; Cooke et al. 2010; Bird et al. 2012). Rabbits therefore pose a severe biodiversity threat in areas where they might easily be thought not to be a problem, or might even remain unnoticed.

Based on our data, it seems likely that rabbits must be managed to densities of <0.5 rabbits ha^{-1} in order to maintain plant biodiversity in Australian native pastures. Nevertheless it remains possible that some species will be suppressed at 0.1 rabbits ha^{-1} and some may be able to tolerate densities of 1 rabbit ha^{-1}, and we recommend that future investigations should concentrate on that density range.

Finally, the strong negative relationship between rabbit and kangaroo abundance estimates during the usual period of summer/autumn food shortage, despite above-average summer rainfall, indicates significant competition for pasture between rabbits and large macropods in natural systems, as previously suggested by Mutze et al. (2008). This, in turn, suggests that rabbits' impacts on pasture may have played, and may continue to play, a greater role than is commonly recognized in range contractions and extinctions of smaller Australia native herbivores (Cooke 1998, 2015). The dramatic expansion in range of four species of threatened desert mammals in the 20 years since RHDV drastically reduced rabbit abundance in inland Australia (Pedler et al. 2016) is consistent with these views.

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