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# **Herbivory and fire interact to affect forest understory habitat, but not its use by small vertebrates**

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*Short title:* Fire-herbivory interactions drive vegetation but not fauna

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## Abstract

Herbivory and fire are two disturbances which often co-occur, but studies of their interactive effects are rare outside of grassland ecosystems. We experimentally tested the interactive effects of prescribed fire and macropod herbivory on forest understory vegetation and its vertebrate fauna. Fire and herbivory interacted synergistically to affect forest understory vegetation, with palatable plants showing poor post-fire recovery in un-fenced sites compared with herbivore exclusion sites. Despite this strong interactive effect on vegetation, small vertebrates responded to the individual, and not the interactive effects of disturbance. The native insectivorous mammal *Antechinus stuartii* was more frequently encountered on large herbivore exclusion sites, as was the introduced European rabbit. In contrast, the small skink *Lampropholis delicata* was more common on sites with high densities of large herbivores. Skinks, snakes and European rabbits were also more active on burnt than unburnt sites. Our results suggest that it may be necessary to manage the macropod herbivore population after fire to prevent the decline of palatable plants, and maintain the dense habitat required by some small mammals. However, as the invasive rabbit was most active in macropod-free sites after fire, any management must include control of both types of herbivores. A mix of understory densities may also need to be maintained to ensure the persistence of species preferring more open habitats. Our study demonstrates that interactive effects of disturbance on vegetation communities may not lead to predictable effects on animals, and highlights the importance of considering both multiple stressors, and multiple species, in the management of disturbance regimes.

## Keywords

Disturbance interaction, browsing, grazing, indirect effects, kangaroo, synergistic effects

## Introduction

Disturbance regimes play a central role in ecosystem dynamics (Willig and Walker, 1999). However, in many parts of the world, natural disturbance regimes have been disrupted, with unwanted outcomes for biodiversity (Hobbs and Huenneke, 1992, Sinclair and Byrom, 2006). Thus, many biodiversity conservation programs aim to reinstate natural disturbance regimes (Fuhlendorf *et al.*, 2010, Noss *et al.*, 2006), but achieving this in systems where multiple disturbances co-occur may be difficult. Co-occurring disturbances can interact to produce distinctly different outcomes from what would be expected based on individual effects (Didham *et al.*, 2007, Tylianakis *et al.*, 2008) and a poor understanding of these interactions can lead to unexpected and undesirable management outcomes (Lindenmayer *et al.*, 2010, Tylianakis *et al.*, 2008).

The importance of disturbance interactions for structuring grasslands and heathlands has been widely recognised, and re-establishing fire-grazing interactions is identified as a priority for maintaining biodiversity in these habitats (Fuhlendorf *et al.*, 2010, Van Langevelde *et al.*, 2003). However, understanding of how fire and herbivory interact to affect species in forested habitats remains limited (Foster, Barton and Lindenmayer, 2014, Royo *et al.*, 2010, Wisdom *et al.*, 2006). As the interactive effects of fire and herbivory depend on the scale, intensity and timing of these disturbances, the outcome of interactions can be highly variable (Fuhlendorf *et al.*, 2010, Wisdom *et al.*, 2006). For example, at a local-scale, deer browsing after fire suppressed dominant shrub species, increasing herbaceous plant richness in a forest understory (Royo *et al.*, 2010). Conversely, heavy macropod herbivory following fire limited grass and forb recovery (Tuft, Crowther and McArthur, 2012). At a larger scale, Bailey and Whitham (2002) found that elk (*Cervus canadensis*) browsed more heavily in areas of aspen (*Populus tremuloides*) that burned at high intensity, compared with moderate intensity. This

heavy browsing reversed the positive effect of browsing on arthropod richness that occurred after moderate intensity fire. While such studies indicate that fire-herbivory interactions are likely to be prevalent in forested ecosystems (Royo and Carson, 2006), investigations of animal responses to the combined effects of these disturbances remain rare (Foster *et al.*, 2014, Wisdom *et al.*, 2006).

We combined prescribed fire and large herbivore exclusion treatments to test the interactive effects of fire and herbivory on understory vegetation and small vertebrates in a temperate forest ecosystem. As the management of disturbances is often targeted at plants, with the assumption that this will also cater for the needs of animals (Clarke, 2008), it is important to understand whether such assumptions are valid, and whether fauna respond in a predictable way to disturbances. Our study addressed the following questions: (1) How do fire, herbivory and their interaction affect understory habitat structure at the site level? (2) How do these disturbances affect site occupancy by small vertebrate fauna? We expected that vertebrate species would respond differently to the experimental treatments due to differences in their habitat and dietary preferences, and that these responses would be mediated by changes in vegetation structure. For example, we expected that both fire and herbivory would reduce understory cover, and lead to negative effects on site occupancy by vertebrates preferring dense understory habitats (Table 1). We provide recommendations for biodiversity conservation based on our findings.

## **Materials and methods**

### ***Study site***

We conducted our study in Booderee National Park (BNP); a ~6 500 ha peninsula in south-eastern Australia (35°10'S, 150°40'E). We established sites within *Eucalyptus pilularis* forest, which is the most widespread vegetation type in BNP (Taws, 1998). An intensive fox (*Vulpes*

*vulpes*) baiting program has been conducted in BNP since 1999 to protect native species from predation (Dexter *et al.*, 2012). Over the last decade, there has been a tenfold increase in native herbivores in BNP (predominantly swamp wallaby, *Wallabia bicolor*, and eastern grey kangaroo, *Macropus giganteus*), which is attributed to reduced predation by foxes (Lindenmayer *et al.*, 2014). Small-scale enclosure trials indicate that this high abundance of herbivores could be driving changes in vegetation composition (Dexter *et al.*, 2013), and there is concern about flow-on effects for smaller vertebrates, which include a number of threatened species (Dexter *et al.*, 2012). As fire is a naturally occurring disturbance within BNP, occurring both as wildfire and low-intensity prescribed burning (Lindenmayer *et al.*, 2008), it is important to understand how native herbivores interact with fire regimes.

### ***Study design***

We quantified the interactive effects of fire and herbivory on vegetation and small vertebrates using a randomised blocked experiment. We combined three levels of large herbivore enclosure and two levels of burning treatment in a factorial design (Appendix 1). We replicated each treatment combination across four blocks to give 24 sites. For the enclosure treatments, we excluded macropod herbivores from 25 × 25 m sites, using 1.1 m tall wire fencing, in June 2012. We created three levels of herbivore enclosure treatment: high activity (open treatment – no fence), intermediate activity (partial treatment – sites were fenced but gates opened and closed at two month intervals to simulate lower herbivore pressure), and no large herbivores (enclosure treatment). For the burnt treatments, we conducted 50 × 50 m burns in August 2012, with the 25 x 25 m site in the centre of the burnt area. Fire was low-intensity, removing approximately 95% of understory vegetation and did not reach the canopy (scorch height 1.5 - 4 m) or burn large logs.

## 99 **Data collection**

100 We surveyed understorey vegetation prior to treatment in April/May 2012 and repeated  
101 surveys biannually until May 2014. We sampled four  $3 \times 3$  m quadrats in each site, with each  
102 quadrat at least 1.5 m from the fence. We recorded four vegetation variables, representing  
103 important attributes of fauna habitat; total understorey projective cover (%), projective cover  
104 of bracken (*Pteridium escelentum*) (%), understorey height (averaged across 10 locations per  
105 quadrat using the stick-and-disc method of Smit *et al.* (2001); disc 100 mm diameter, 4.7 g  
106 weight) and litter depth (averaged across 10 locations per quadrat).

107

108 We surveyed macropod herbivore activity by counting scats along two  $25 \times 2$  m transects  
109 ( $100 \text{ m}^2$ ) per site, summing counts to give one count per site. As macropods defecate more  
110 while feeding than resting (Johnson, Jarman and Southwell, 1987), pellet counts can give a  
111 comparative measure of macropod feeding pressure between sites (Howland *et al.*, 2014). We  
112 surveyed transects every two months from August 2012 to May 2014, removing scats after  
113 each survey to avoid re-counting. We also monitored European rabbit (*Oryctolagus*  
114 *cuniculus*) activity using these transects, counting the number of rabbit diggings every two  
115 months from June 2013 to May 2014.

116

117 We surveyed site use by small mammals through live trapping in April/May 2012 and then  
118 every six months until May 2014. For each survey, we set eight Elliott traps per site for four  
119 consecutive nights. We ear marked animals with a permanent marker to identify recaptures  
120 within a survey.

121

122 We monitored reptiles using iron sheeting as artificial substrates. We set out four  $1 \times 1$  m  
123 sheets per site in July 2012, and checked them on two consecutive mornings approximately  
124 every two months from October 2012 to May 2014. To minimise biases due to time of day,

we rotated the order of site checking so that each site had one early morning and one late morning check per sampling period. To avoid non-independence of counts within a survey, we used the maximum value of the two consecutive counts for each species. Weather conditions meant that some surveys returned few individuals. Therefore, for data analysis, we excluded surveys with fewer than three detections for that species.

To measure arthropod prey availability, we sampled ground-dwelling beetles and spiders using pitfall traps, counting the total captures per trap. We deployed four 250ml (100 mm diameter) traps per site (2/3 filled with non-toxic polyethylene glycol solution) for two weeks in November 2012 and 2013.

### ***Data analysis***

To assess how fire-herbivory interactions affected habitat structure (question 1), and fauna occupancy (question 2) we tested treatment effects on dependent variables using linear mixed models (LMMs) for vegetation variables and generalised linear mixed models (GLMMs) with Poisson errors for animal counts. Vegetation variables were understory cover (%), understory cover excluding bracken (%; total understory cover minus cover of bracken), understory height (m), and leaf litter depth (mm). We analysed understory cover excluding bracken because bracken is a dominant, unpalatable species which could mask responses of other plants. Bracken also provides little of the ground-level structure important for small vertebrates (Bennett, 1993). Animal count variables were macropod scats, rabbit diggings, antechinus captures, delicate skink (*Lampropholis delicata*) and eastern small-eyed snake sightings (*Cryptophis nigrescens*), and spider and beetle captures.

We fitted each dependent variable with the full fixed effects model of herbivores\*burning\*time, and random effects of block/site/quadrat for vegetation and

block/site for animal variables to account for the repeated measures. A first-order autoregressive covariance structure on the random effects was trialled for the vegetation LMMs but was not used as it did not improve model fit ( $\Delta AIC < 2$ , Pinheiro and Bates, 2000). We did not define a covariance structure for animal responses as inspection of residuals indicated little evidence of temporal autocorrelation, and methods for fitting such structures with GLMMs are not well developed (Zuur *et al.*, 2009). We used Akaike information criterion, corrected for small sample size (AICc), to select the most parsimonious model from all possible subsets of the full model (19 models) (Burnham and Anderson, 2002). If models within two AICc of the top ranked model included predictors not included in the top model, we also discussed these alternate models. We excluded pre-treatment surveys from analyses to avoid spurious time  $\times$  treatment interactions.

The properties of some animal variables meant that adjustments to the full model were necessary. Specifically, to adjust for over-dispersion of macropod scat data ( $\phi = 6.9$ ), rabbit digging data ( $\phi = 2.7$ ) and arthropod data ( $\phi = 3.1$ ), we added an observation-level random effect to the models for these variables (Harrison, 2014). Further, for the macropod model, we divided the partial herbivore treatment into two categories: partial – open months, and partial – closed months, to better describe this treatment. As there were low numbers of macropod scats in exclosure and partial – closed month treatments, they were excluded from this analysis. For the GLMM of antechinus captures, we ran model selection on all subsets of the full model of herbivores\*burning\*time, plus an alternate model with ‘season’ substituted for ‘time’ (giving 33 different models for comparison). This accounted for the strong seasonal variation in antechinus abundance (Lazenby-Cohen and Cockburn, 1991). Finally, as low mean counts for the two reptile species meant some models including the burn.time fixed effect did not converge, we excluded five models for the delicate skink and three models for the small-eyed snake from model comparisons. LMMs were performed using the lme

function in the package MASS, GLMMs using the glmer function in the package lme4 and AICc model ranking using the package AICcmodavg, within R version 3.0.1 (R Core Team, 2013).

## Results

### *Vegetation structure*

Vegetation structure responded both to the burning and herbivore exclosure treatments, as well as their interaction (Table 2). Understory vegetation cover at unburnt sites declined in open and partial treatments over time, but remained stable in exclosure sites (Fig. 1a). After an initial reduction after fire, a similar decline was observed for burnt, open sites. However, burnt partial and exclosure sites remained stable. (Fig. 1a, Appendix 2). When bracken was excluded from understory cover, there was a strong exclosure  $\times$  time interaction, as cover on open and partial exclosure sites declined or remained low, while on full exclosure sites cover increased through time (Fig. 1b, Appendix 2). The burning  $\times$  time interaction was also important, as non-bracken vegetation increased over time on all burnt sites. Compared with other treatments, burnt, open sites had a high proportion of bracken, with very little non-bracken vegetation present across all time periods (Fig. 1b). Both understory height and leaf litter depth responded to the burning  $\times$  time interaction, but not to any other interaction terms (Table 2). Understory height was reduced by fire but had recovered after 21 months (Fig. 2a). Litter depth recovered more slowly, remaining lower in burnt than unburnt sites across all time periods (Fig. 2b). The second ranked model for understory height also included an exclosure main effect, where vegetation was slightly taller on exclosure than on open sites (Appendix 2).

## *Vertebrate responses*

Exclosure treatments successfully excluded macropod herbivores, with very low scat counts in exclosure treatments (**Error! Bookmark not defined.** $\bar{x} = 0.71 \pm 0.52$ ). When partial treatment gates were open, scat counts were 56% lower in partial than in open treatments (Fig. 3a). Macropods also responded to burning, showing higher activity in burnt than unburnt sites (Table 2, Fig 3). There were three competing models for rabbit diggings, with models including time, time plus exclosure and time plus burning all explaining similar levels of variation in the data (Table 2). Rabbit activity peaked in summer and tended to be higher in sites without macropods (partial and full exclosure treatments) and in burnt sites (Fig. 4, Appendix 2).

Brown antechinus captures were highest in herbivore exclusion sites, and in Autumn (May) surveys (Table 2, Fig. 5). The second ranked model also included burning as a fixed effect (Table 2), where antechinus captures were slightly lower in burnt than unburnt sites (Appendix 2). Both the delicate skink and the eastern small-eyed snake were encountered more frequently in burnt sites than unburnt sites (Table 2, Fig. 6, Appendix 2). Delicate skink numbers also tended to be higher in open and partial than in full exclosure sites and were higher in the first survey (three months post-fire), than at any other time (Table 3, Fig. 6). Beetles and spiders captures were 65% higher in the first year (2012, **Error! Bookmark not defined.** $\bar{x} = 31.3 \pm 3.1$ ) than the second (2013,  $\bar{x} = 18.9 \pm 1.96$ ), and the second ranked model indicated that captures were also slightly higher in burnt than in unburnt sites (Table 2, Appendix 2).

## **Discussion**

Fire and herbivory can interact strongly in space and time to shape the structure of vegetation communities (Koerner and Collins, 2014, Royo and Carson, 2006, Van Langevelde *et al.*,

2003). However, animal responses to the fire  $\times$  herbivory interaction are rarely studied (but see Fuhlendorf *et al.*, 2010, Kimuyu *et al.*, 2014, Kutt and Woinarski, 2007). In our experimental test of the interactive effects of fire and large herbivores, we found that forest understory structure responded to the fire  $\times$  herbivore exclosure interaction, but vertebrate site occupancy was affected only by the individual effects of disturbance. This suggests that local changes in vegetation structure may not be an adequate predictor of animal responses to disturbance and that animals warrant individual consideration for the management of ecosystems that are subject to both recurring fire and herbivory.

#### ***Question 1: Changes to habitat structure***

As expected, fire and herbivory both affected habitat structure, and effects differed with disturbance type. The limited recovery of non-bracken vegetation on burnt sites with high densities of large herbivores (Fig. 1), was consistent with previous studies (Meers and Adams, 2003, Tuft *et al.*, 2012). Both of these previous studies attributed the stronger effect of herbivory on burnt sites to greater herbivore pressure, driven by the attraction of herbivores to the fresh plant growth following fire. This is a commonly reported mechanism explaining fire  $\times$  herbivore interactions (Klop, van Goethem and de Jongh, 2007), for which we also found evidence, as indicated by macropod activity being greatest on recently burnt sites (Fig. 2b).

In contrast to the non-bracken vegetation, bracken recovered well in burnt, open sites, and made up a large proportion of the vegetation in these sites (Fig. 1). Bracken can regenerate rapidly following fire and suppress other plants. However, after an initial post-fire pulse, bracken cover usually declines over time, as other plants become dominant (Tolhurst and Turvey, 1992). Our results indicate that abundant macropod herbivores may be disrupting this successional process by selectively feeding on more palatable vegetation, maintaining the

bracken-dominated understory. As prescribed fire is commonly used in this system to reduce forest fuel loads and promote vegetation heterogeneity and floristic diversity (Morrison *et al.*, 1996), our results suggest that herbivore management following fire may be important to maintain a heterogeneous forest flora.

## ***Question 2: Habitat use by vertebrates***

Despite the strong effect of the fire  $\times$  herbivory interaction on vegetation, habitat use by vertebrates was affected only by the individual effects of disturbances and not their interaction. The increased rabbit activity we observed on herbivore exclusion and recently burnt sites was consistent with previous studies of small herbivore responses to large herbivore removal (Keesing, 1998) and fire (Leigh *et al.*, 1987, Moreno and Villafuerte, 1995). Competitive release of small herbivores following a reduction in large herbivore densities can result in increased herbivory by small herbivores, with subsequent impacts on vegetation communities (Legendijk, Page and Slotow, 2012). Our results suggest that control of native macropod herbivores may favour introduced rabbits, particularly after fire when fresh plant growth is abundant. Therefore, management of the native herbivore population should carefully consider the potential for competitive release of the European rabbit, which is a destructive pest species in Australia (Davey *et al.*, 2006).

*Antechinus* responded positively to large herbivore exclusion, with more individuals captured in sites without macropod herbivores, regardless of burning treatment. Despite the small size of our exclosures, this response likely indicates a preference for herbivore exclusion areas, as antechinus have small foraging ranges (approximately 0.4 ha for females and 0.9 ha for males, Lazenby-Cohen and Cockburn, 1991). Further, our result is consistent with Pedersen *et al.* (2014), who found that antechinus captures were negatively correlated with wallaby density. The preference of antechinus for sites without large herbivores may have been due

to the dense understory cover in enclosure sites (Bennett, 1993, Knight and Fox, 2000), providing increased foraging habitat (antechinus are scansorial) and/or greater protection from predators (e.g. Stokes *et al.*, 2004). Other studies have found that some small mammal species prefer habitats with lower densities of large herbivores (Bush *et al.*, 2012, Keesing, 1998, Kutt and Gordon, 2012), but our study is the first to experimentally demonstrate this response to macropod herbivores.

Contrary to other studies from south-eastern Australia (Fox, 1982, Lindenmayer *et al.*, 2008), we found only weak support for a negative response of antechinus to fire. This was likely due to the low intensity, small-scale fires used in our study. The availability of arthropod prey (Table 2, Appendix 2), combined with the persistence of logs and the proximity of unburnt vegetation to burnt areas in our study, may have sufficiently maintained habitat quality for antechinus. It is likely that antechinus may have responded more strongly to a larger-scale, or higher intensity burn (Lindenmayer *et al.*, 2008, Penn *et al.*, 2003).

Delicate skinks were more common in open than in herbivore exclusion sites, and both delicate skinks and small-eyed snakes were more common in burnt than unburnt sites. The negative response of delicate skins to herbivore exclusion was likely due to increased shading from recovering vegetation, which could have reduced the thermal suitability of the environment for this heliothermic species (Howard, Williamson and Mather, 2003). The positive response of the delicate skink to burning was contrary to our expectation for this species, which generally recovers slowly from fire, in response to the slow accumulation of leaf litter (Taylor and Fox, 2001). Our result may therefore reflect a change in micro-habitat use following burning, rather than a change in site occupancy. Burning reduced litter depth, and in the absence of suitable leaf-litter habitat, the delicate skink may have increased its use

of the artificial survey substrates for shelter, basking and foraging, as found by Croft, Reid and Hunter (2010).

A lack of alternative refuges also may explain the higher numbers of small-eyed snakes under the artificial substrates in burnt sites. However, there are two other possible explanations for this response: First is that the small-eyed snake was more common after burning as a result of reduced shading of substrates, which provided warmer, more desirable diurnal refuges (Webb *et al.*, 2004). Second, the density of skinks, a key prey item for small-eyed snakes (Shine, 1984), may have attracted snakes to the substrates in burnt sites. Previous studies of small-eyed snakes show that reduced shading after fire can improve the thermal properties of diurnal refuges (Webb *et al.*, 2005), but large wildfire can lead to population declines, possibly due to increased predation (Webb and Shine, 2008). While the possible biases in our reptile sampling technique mean results should be interpreted with caution, the greater numbers of reptiles in burnt sites and skinks in the open treatments, indicate that maintaining areas of open understory may be important for the persistence of reptiles in these forests (Webb *et al.*, 2005).

### ***Conservation implications***

Our results have four key implications relevant to the conservation of ecosystems subject to both recurrent fire and herbivory. First, the dominance of bracken and limited recovery of other vegetation in burnt, open sites indicates that short-term management of abundant macropod herbivores following prescribed fire may be useful for the conservation of structurally and floristically complex vegetation. Second, the preference of antechinus for herbivore exclusion sites suggests that management of native herbivores to promote dense understory habitat is also likely to benefit small mammals dependent on such habitats. Third, the increased rabbit activity we observed on recently burnt sites, and sites without

macropods, suggests that any plan to improve the post-fire recovery of vegetation by controlling native herbivores also should include management of rabbits. Fourth, the positive response of reptiles to the open understory of burnt sites and sites with more macropods differed from the antechinus response, and suggests that a mixed management scenario might be more appropriate.

While our experiments were small-scale, the contrasting responses of different species to herbivory and fire indicate that a mixed management strategy promoting a heterogeneous understory may be important for the persistence of all species in our study. Heterogeneous landscapes have commonly been suggested as a desired goal of land management, as such landscapes are more likely to allow the co-existence of species with different niches, as well as species that require a mix of habitats (Law and Dickman, 1998, Stein, Gerstner and Kreft, 2014). In Australian landscapes, fire patch-mosaics have been recommended to promote fauna diversity, although key questions around the appropriate spatial and temporal scales of such mosaics remain unanswered (Allouche *et al.*, 2012, Clarke, 2008, Driscoll *et al.*, 2010). While not designed to address questions of spatial scale, our study suggests that maintaining a mix of habitat types and conditions may be important for fauna in forested systems.

Although both fire and herbivory are often actively managed in forested systems (Gordon, Hester and Festa-Bianchet, 2004, Morrison *et al.*, 1996), these processes are usually considered independently (Royo and Carson, 2006, Wisdom *et al.*, 2006). However, the interactive effects of fire and herbivory observed in our study indicate that integrating large herbivore management with fire management practices is likely to be important for achieving vegetation heterogeneity in forests. This could be through the fire-dependent management of herbivores (e.g. controlling large herbivores across only part of a burn or after only some prescribed burns), or through planning fires to consider large herbivore behaviour (e.g.

354 reducing the edge-area ratio of prescribed burns, as macropods can be reluctant to enter open  
355 areas and so feed more heavily at the edge (While and McArthur, 2006)). Our study shows  
356 the value of experimental studies that quantify disturbance responses both individually and  
357 collectively, and highlights the importance of considering both multiple stressors, and  
358 multiple species, in the management of disturbance regimes.

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540

## Tables

Table 1. Predicted effects of fire and large herbivores on habitat and food resources for vertebrates and the corresponding predicted responses of two small mammal and two reptile species, based on their diet and habitat preferences. Habitat preferences are attributes which have been associated with higher abundance in forest habitat for that species.

Response group	Habitat preference	Diet	Predicted response	
			Fire	Herbivores
<i>Habitat and food resources</i>				
Understory cover			-	-
Understory height			-	-
Leaf litter depth			-	none
Fresh plant growth			+	-
Invertebrate prey			-	-
<i>Vertebrates</i>				
European rabbit ( <i>Oryctolagus cuniculus</i> )	Open understory <sup>a</sup>	Forbs and grasses <sup>b</sup>	+	-
Brown antechinus ( <i>Antechinus stuartii</i> )	Dense, complex understory <sup>a,c</sup>	Invertebrates <sup>c</sup>		
	Tall understory <sup>d</sup>		-	-
	Abundant logs <sup>d</sup>			
Delicate skink ( <i>Lampropholis delicata</i> )	High canopy cover <sup>e</sup>	Invertebrates <sup>e</sup>		
	Deep litter <sup>f,g</sup>		-	?
	Tall understory <sup>g</sup>			
Eastern small-eyed snake ( <i>Cryptophis nigrescens</i> )	Warm diurnal refuge <sup>h</sup>	Skinks <sup>h</sup>	+	?

<sup>a</sup>Catling and Burt (1995), <sup>b</sup> Davis, Coulson and Forsyth (2008), <sup>c</sup> Bennett (1993), <sup>d</sup> Knight and Fox (2000), <sup>e</sup> Bragg, Taylor and Fox (2005), <sup>f</sup> Taylor and Fox (2001), <sup>g</sup> Howard *et al.* (2003), <sup>h</sup> Webb *et al.* (2004),

Table 2. Model rankings for linear mixed models (LMMs, vegetation) and generalised linear mixed models (GLMMs, animals), testing the fixed effects of burning (B - burnt or unburnt), enclosure (E - open, partial or full enclosure), time (T - sampling event - categorical), and their interactions on vegetation structure and animal occurrence. For brown antechinus, we also ran model ranking on all subsets of a model with season (S - autumn or spring) substituted for time (i.e. B\*E\*S), to account for the strong seasonal variation in the abundance of this species. K is the number of parameters estimated in the model,  $\Delta$  AICc is the change in Aikake's Information Criterion (corrected for small sample size) from the best-ranked model. AICcWt is the Aikine Weight of the model, LL is the Log-likelihood.

Data	Model terms	K	$\Delta$ AICc	AICcWt	LL
<i>LMMs</i>					
Understory cover	B + E + T + B:T + E:T + B:E + B:E:T	28	0	0.97	-1454.7
Cover excluding bracken	B + E + T + B:T + E:T	20	0	0.74	-1389.6
Vegetation height	B + T + B:T	12	0	0.61	266.5
	B + E + T + B:T	14	1.59	0.28	267.8
Litter depth	B + T + B:T	12	0	0.82	-429.5
<i>GLMMs</i>					
Macropod scats	B + E <sup>a</sup> + T	15	0	0.6	-500.6
Rabbit diggings	T	9	0	0.37	-441.0
	E + T	11	1.09	0.21	-439.2
	B + T	10	1.64	0.16	-440.7
Brown antechinus	E + season	6	0	0.36	-172.0
	B + E + season	7	1.4	0.18	-171.5
Delicate skink	B + E + T	13	1.01	0.46	-162.8
	B + T	11	1.35	0.39	-165.3
Eastern small-eyed snake	B	4	0	0.67	-60.4
Beetles and spiders	T	5	0	0.61	-187.4
	B + T	6	1.85	0.24	-187.0

<sup>a</sup> Compares only partial-open months with open treatment (see methods)

# Figures

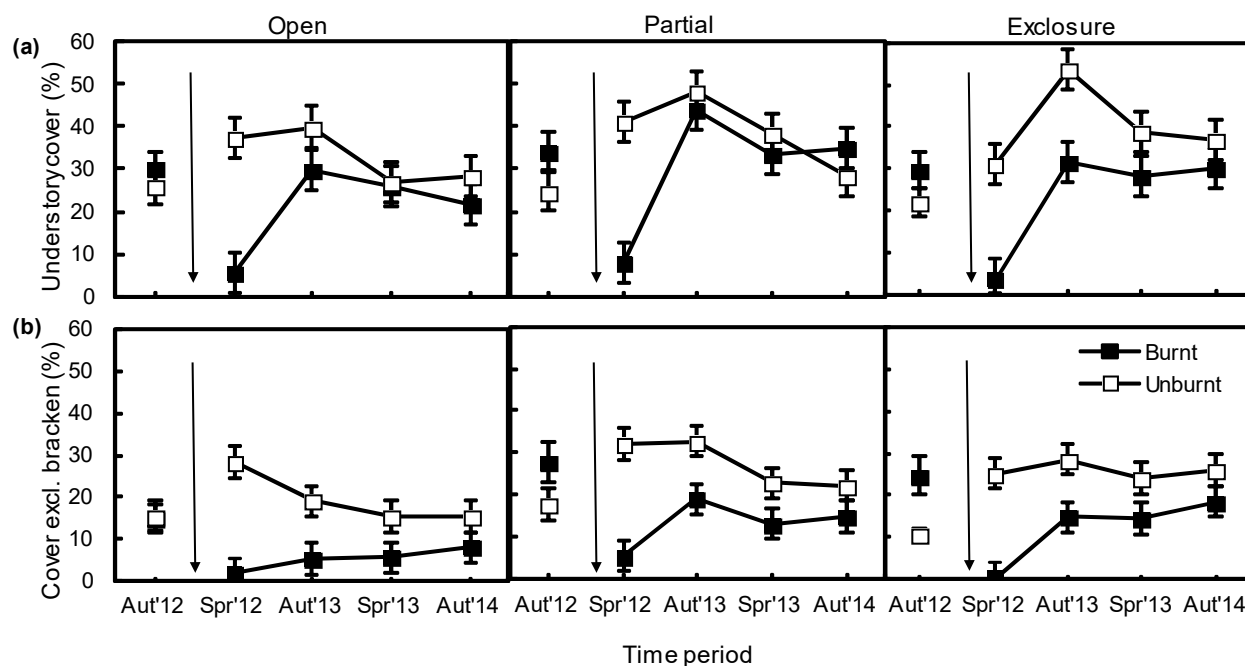


Figure 1. Vegetation structural responses to exclosure and burning treatments across sampling periods, (a) total understory percent cover, and (b) understory percent cover, excluding bracken (*Pteridium esculentum*). Values post-treatment are predicted means and estimated SE from the top-ranked models. Pre-treatment data (May 2012) were not included in the LMM, but are presented here (mean and SE) to allow comparison with post-treatment data. Arrows indicate timing of prescribed burning.

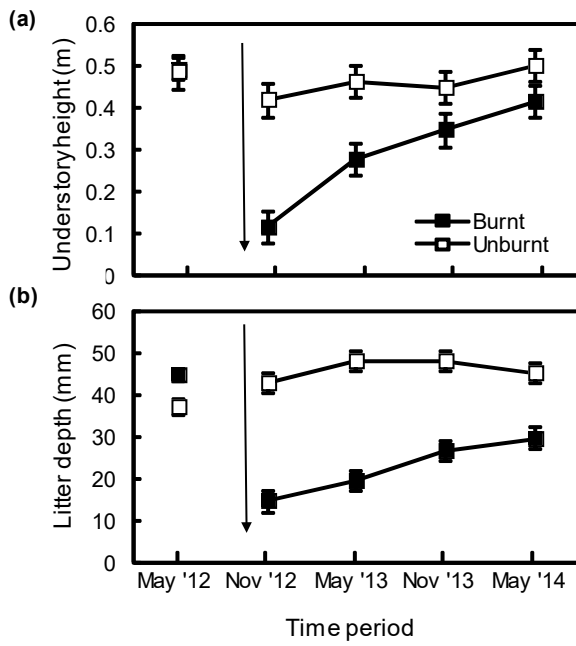


Figure 2. Response of understory height (a) and leaf litter depth (b) to burning treatment across time periods. Values post-treatment are predicted means and SE from the top-ranked models. Pre-treatment data (May 2012) were not included in the LMM, but are presented here (mean and SE) to allow comparison with post-treatment data. Arrows indicate timing of prescribed burning.

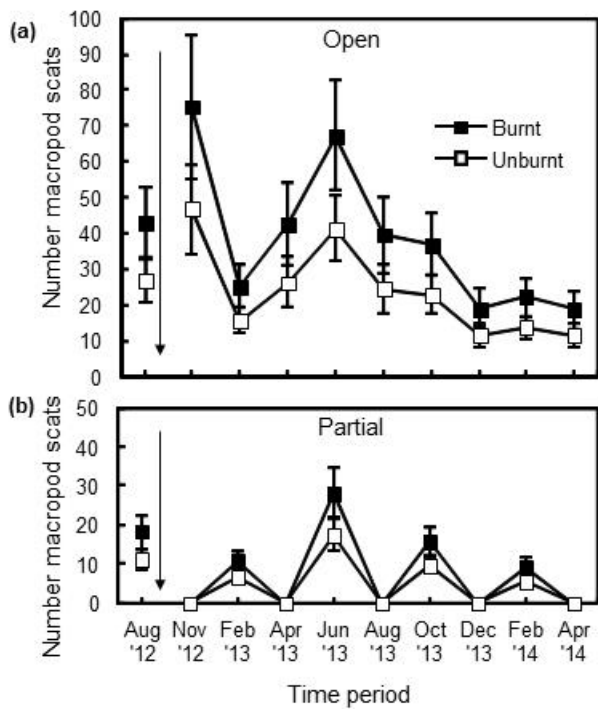


Figure 3. Number of macropod scats in burnt and unburnt sites through time in open (a) and partial exclusion sites (b). Note that closed months of the partial exclosures (Nov 2012, Apr 2013 etc.), and full exclosure sites were not included in the analysis as means for this group were too low to allow model fit. Values for open sites and partial-open months are predicted means and estimated SE from the top-ranked model. Arrows indicate timing of prescribed burning (note Aug '12 counts were after implementation of herbivory treatments but before burning treatment).

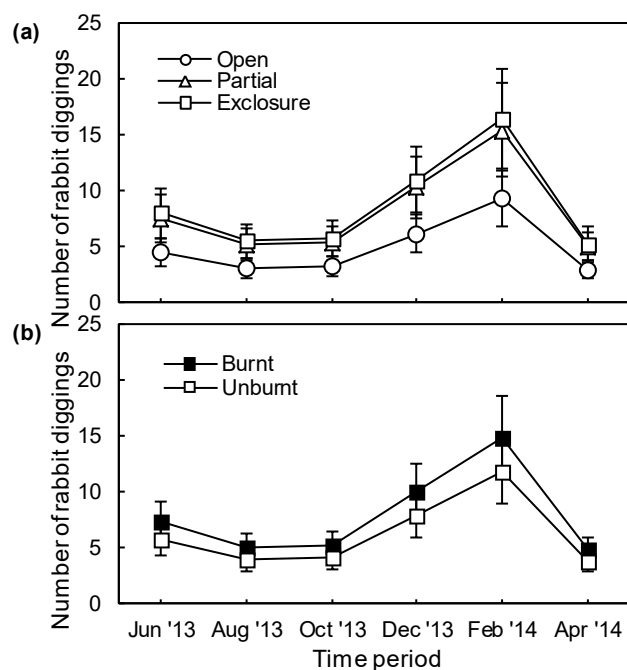


Figure 4. Number of rabbit (*Oryctolagus cuniculus*) diggings per site in the different enclosure treatments (a) and burning treatments (b) over time. Values are predicted means and estimated SE from the 2<sup>nd</sup> (a) and 3<sup>rd</sup> (b) ranked models respectively. The effect of time alone (first-ranked model) can be clearly seen in both plots.

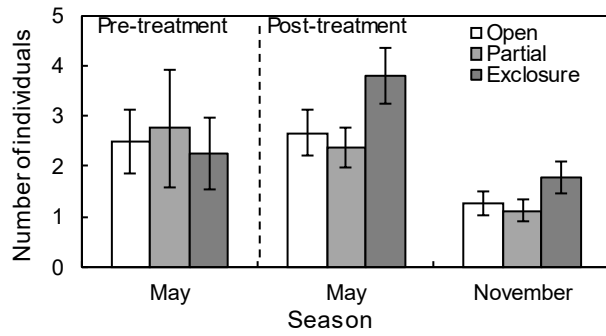
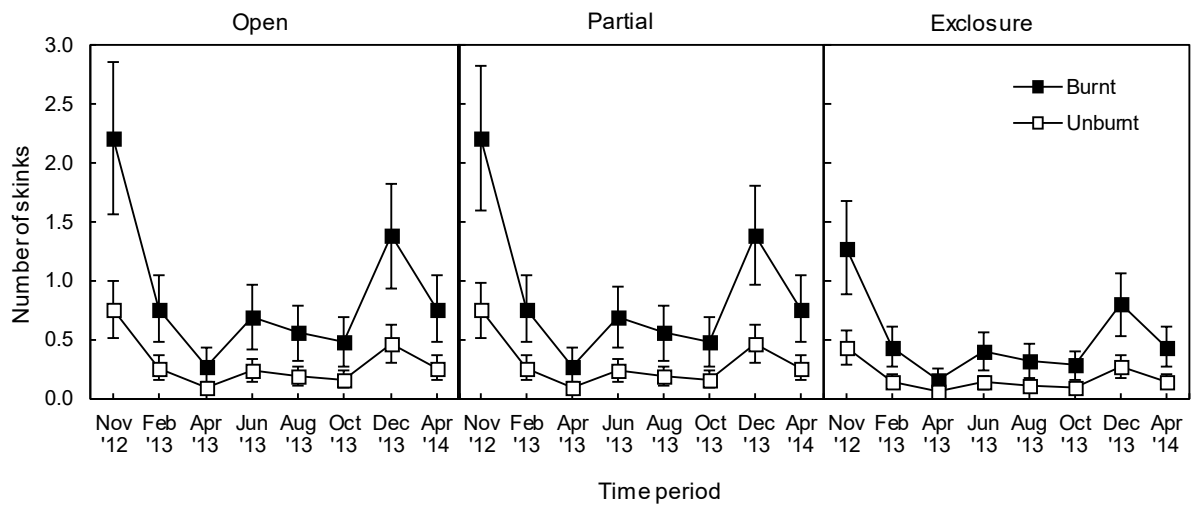


Figure 5. Number of individual brown antechinus (*Antechinus stuartii*) captured per site in different seasons and herbivory treatments. Values post-treatment are predicted means and SE from the top-ranked model based on two years of data (November 2012 to May 2014). Pre-treatment data (May 2012) were not included in the GLMM, but are presented here (mean and SE) to allow comparison with post-treatment data.



595

596 Figure 6. Number of delicate skinks (*Lampropholis delicata*) detected under artificial

597 substrates in the different burning and exclosure treatments across time. Values are predicted

598 means and SE from the top-ranked model.