Synergistic interactions between fire and browsing drive plant diversity in a forest understory

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Abstract

Questions: Does browsing by large herbivores affect forest understory diversity by modifying assemblage dominance? Does fire interact with browsing to affect forest understory diversity? Does this interaction occur via a numerically-mediated or functionally-moderated pathway?

Location: Booderee National Park, Jervis Bay Territory, south-eastern Australia

Methods: We tested the interactive effects of fire and browsing by native herbivores on understory plant diversity using a randomised blocked experiment in an open eucalypt forest. We monitored the percentage cover of every vascular plant species in 24 sites over four experimental blocks. We applied a different treatment to each of the six sites in the four blocks. Treatments were a factorial combination of three levels of herbivory treatment (open, partial exclosure, full exclosure) and two levels of prescribed fire treatment (burnt, unburnt).

Results: Browsing increased plant community dominance and reduced evenness and diversity, but only in burnt sites. Heavy browsing following fire created an understory dominated by an unpalatable, fire resistant fern species (bracken, *Pteridium esculentum*). This fire-browsing interaction was driven by both numerically-mediated and functionally-moderated pathways: Fire both increased local browsing intensity, and amplified the per-unit effect of herbivores on the plant community.

Conclusions: The altered competitive environment after fire, combined with heavy post-fire browsing created a depauperate understory, dominated by bracken fern. The ability of bracken to supress the establishment of other plants means that, once established, this fern-dominated understory may be difficult to reverse. Our results demonstrate the key role of fire-browsing interactions in forest vegetation dynamics and highlight the importance of integrating large herbivore management with fire planning in forest ecosystems.

Key words

Alternate stable states; Browsing; Community structure; Dominance; Disturbance interaction; *Eucalyptus* forest; Herbivory; Macropod; Plant diversity; *Pteridium esculentum*; Understory

Nomenclature

Robinson (1991)

Running Head

Fire-browsing interactions

Introduction

Herbivory is a core process driving the structure and diversity of plant communities in many ecosystems worldwide (Milchunas et al. 1988; Hester et al. 2006; Borer et al. 2014). In forested systems, selective browsing by large herbivores can have transformative effects, altering canopy tree species dominance and driving cascading effects through the rest of the ecosystem (Royo & Carson 2006; Holm et al. 2013; Côté et al. 2014). Browsing has also been shown to exert strong effects on forest understory vegetation. However, there is little agreement among studies about whether browsing enhances or reduces the diversity of forest understory plants. Positive effects (Royo et al. 2010a), negative effects (Rooney & Waller 2003; Jenkins et al. 2014), and no effect (Kerns et al. 2011) of browsing on understory plant diversity have all been reported, with discrepancies between studies attributed to differences in herbivore densities, ecosystem productivity, disturbance history and other site-dependent variables (Hester et al. 2006; Royo et al. 2010a).

While the net effects of herbivory on plant diversity are variable, it has been suggested that most responses can be explained by effects on plant species dominance

(Hester et al. 2006). In systems where herbivores selectively feed on dominant plant species, they will reduce assemblage dominance, and increase resource availability for competitively inferior plants, thereby increasing diversity (Côté et al. 2004; Hester et al. 2006). However, when the dominant species are unpalatable, herbivores will have the opposite effect. A number of recent studies from grassland systems have supported this hypothesis, finding that the effects of herbivory on ground-level light availability (which is driven by the abundance of dominant species), consistently explained herbivory effects on plant diversity, despite the sites having a wide range of abiotic conditions and disturbance histories (Borer et al. 2014; Eby et al. 2014; Koerner et al. 2014).

Understanding the effects of grazing and browsing can be useful for predicting the outcomes of management interventions (Hester et al. 2000). Such predictions, however, are complicated by the fact that herbivory can interact strongly with other episodic disturbance events (e.g. fire, timber harvest, drought; Royo & Carson 2006; Wisdom et al. 2006). These interactions can produce vastly different outcomes than would be predicted from studies of individual effects, and can lead to unintended management outcomes (Tylianakis et al. 2008). Ecological disturbances can interact via two main pathways: an interaction chain (a numerically-meditated process), and an interaction modification (a functionally-moderated process) (Didham et al. 2007). In the context of disturbance-grazing interactions, a numerically-mediated interaction could occur through disturbance changing the local abundance of herbivores, in turn affecting vegetation. A functionally-moderated interaction would occur if disturbance modified the per unit effect of herbivores on vegetation.

Both these interaction pathways are commonly described in studies of fire-grazing interactions, although they are not often explicitly identified as such. For example, patch burning of grasslands can initiate a numerically-mediated fire-grazing interaction; fire stimulates fresh growth which attracts large herbivores (Allred et al. 2011). The resulting concentration of herbivores increases local grazing intensity, while reducing it elsewhere, which increases vegetation heterogeneity (Fuhlendorf et al. 2006). By modifying the competitive interactions among plant species, or selectively acting on some plant traits, fire can also have a functionally-moderated effect on plant responses to herbivory. For example, in a North American mesic grassland, annual burning amplified the negative effect of grazing exclusion on plant diversity (Eby et al. 2014). This was due to the dominant grass species in the system being both a post-fire increaser and highly palatable. These two functional traits gave this grass species a competitive advantage following fire and allowed it to dominate the plant community in the absence of herbivores (Eby et al. 2014).

As disturbances can interact with the life history traits of organisms, as well as with each other, predicting the outcomes of disturbance interactions is problematic, even if plant traits are well understood (Royo & Carson 2006). Therefore, understanding such interactions requires manipulative experiments that are able to test the non-additive effects of these processes (Didham et al. 2007; Tylianakis et al. 2008). Manipulative tests of the interactive effects of herbivory and disturbance have become reasonably common in grassland systems (e.g. Fuhlendorf et al. 2006; Collins & Calabrese 2012; Koerner & Collins 2014), but remain rare in forested systems (Wisdom et al. 2006; Royo et al. 2010a). The high densities of large herbivores in many forests worldwide (Côté et al. 2004), and the prevalence of active fire management in forest ecosystems (Stephens & Ruth 2005; Boer et al. 2009), mean that improving our understanding of the effects of fire-browsing interactions on vegetation dynamics is of high importance for the management of forest ecosystems (Wisdom et al. 2006).

We studied the effects of fire × browsing interactions on plant diversity in a temperate forest understory, testing the hypothesis that effects on plant diversity would be similar to those described for grassland ecosystems. Our study had three main predictions: (1) That browsing by large herbivores would affect plant diversity by modifying assemblage dominance. Specifically, as the dominant understory species in our study system was of low palatability (*Pteridium esculentum,* Di Stefano & Newell 2008; Fletcher et al. 2011), we predicted that browsing would increase assemblage dominance and reduce diversity. We also predicted that: (2) fire would amplify the effects of browsing on plant diversity, and that (3) this interaction would occur via both numerically-mediated and functionally-moderated pathways. The numerically-mediated effect would be driven by more herbivores browsing in burnt sites, while the functionally-moderated effect would be driven by fire amplifying the effects of herbivory on *P. esculentum* dominance.

Methods

Study site

We conducted this study in Booderee National Park (BNP); a ~6 500 ha peninsula in south-eastern Australia (35°10′S, 150°40′E, Fig. 1). The most widespread vegetation type in the park is open eucalypt forest (Taws 1998). This forest type is dominated by *Eucalyptus pilularis, Corymbia gummifera and E. botryoides* in the overstory (> 10 m), *Banksia serrata, Acacia longifolia* and *Monotoca elliptica* in the midstory (2 – 10 m) and *Lomandra longifolia* and *P. esculentum* in the understory (< 2 m) (Taws 1998; Lindenmayer et al. 2008).

An intensive baiting program targeting the introduced red fox (*Vulpes vulpes*) has been in place within the park since 1999 to protect native small mammal species from predation (Dexter et al. 2012). As hunting has been long discontinued and dingoes (*Canis lupus dingo)* now occur only rarely in the park, the removal of foxes means that predation pressure on herbivores is low (Lindenmayer et al. 2014). Since the removal of foxes, there has been a tenfold increase in the numbers of native macropod herbivores within the park (Dexter et al. 2012; Lindenmayer et al. 2014). The most common of these macropods are the swamp wallaby, *Wallabia bicolor*, a generalist browser, and the eastern grey kangaroo, *Macropus giganteus*, a grazer (Davis et al. 2008; Dexter et al. 2013). Small-scale exclosure trials have indicated that the current high abundance of these herbivores could be driving a decline in some plant species (Dexter et al. 2013).

Study design

We quantified the interactive effects of fire and large herbivores on understory plant diversity using a randomised, blocked experiment. We examined three levels of herbivory treatment and two levels of burning treatment in a factorial design (Fig. 1). We replicated each of these six treatment combinations across four experimental blocks to give a total of 24 sites. For the herbivory treatments, we manipulated the density of macropods within 25 × 25 m plots using exclosure fences to produce three levels of herbivory: full herbivory (open treatment), intermediate herbivory (partial treatment – plots were fenced but gates opened and closed at two month intervals to simulate lower browsing pressure), and no herbivory (exclosure treatment). We constructed exclosure fences in June 2012 using 1.1 m tall feral-proof stock fencing, which we found to be effective at excluding macropods (see results). For the burning treatments, we conducted 50 × 50 m, low severity burns across half of the herbivore treatment sites in August 2012. Burns removed approximately 95% of understory vegetation from the site and did not reach canopy foliage (tree scorch height 1.5 - 4 m).

Data collection

We surveyed understorey vegetation prior to treatment implementation in April/May 2012 (austral autumn) and repeated surveys three months after burning, and then every six months until May 2014. To capture variation within each site, we sampled vegetation using four small quadrats, rather than one large quadrat in each site. We placed four 3 x 3 m quadrats at fixed locations in each site, with one quadrat in each of the four quarters of the site, ensuring each was at least 1.5 m from the fence. For each quadrat, we visually estimated the projective cover of each vascular plant species, using the same observer for all estimates. Prior to any data processing, we averaged the cover values of each plant species across the four quadrats to give one value for the 36 m^2 area sampled in each site. We used these site-level data to calculate four standard metrics of community diversity: species richness (species/ 36 m^2), species diversity (Simpson's reciprocal index - *1/D*), evenness (Simpson's evenness – $E_{1/D}$), and assemblage dominance (Berger-Parker index – d) (Magurran 2004).

We surveyed site use by macropod herbivores by counting their scats along two 25 × 2 m transects (100 m^2) in each site, summing counts to give one overall count per site. We surveyed transects every two months from August 2012 to May 2014. We removed scats from transects after each survey to avoid double counting. For analysis, we summed the two scat counts preceding each vegetation survey to give an estimate of the average level of herbivore activity in a site leading up to each sampling event.

Data analysis

We tested the effects of herbivory, fire and their interaction on plant species richness, diversity, evenness and dominance using linear mixed-models (LMMs) in R (R Core Team 2013). The full model for these analyses included the fixed effects of herbivory × fire × time, plus the pre-treatment value (to account for any pre-existing differences between sites), and random effects of block/site. Instead of the categorical herbivory treatments, we used the scat counts at each site as our measure of herbivory. This allowed us to account for variation in herbivore pressure both between and within levels of the herbivore exclosure treatments, and also to test whether the relationship between herbivore pressure and plant diversity metrics differed between burnt and unburnt sites (i.e. whether there was a functionally moderated interaction). Prior to inclusion in the model as a fixed effect, scat count data were natural log (ln) transformed to reduce skew, and standardised by centring, and dividing by two standard deviations to allow comparison of the main effects of fire and herbivory and aid in interpretation of interaction terms (Gelman & Hill 2007). After checking the fit of the full models by inspecting residual plots (Zuur et al. 2009), we used the "dredge" function in the package "MuMIn" (Barton 2014) to rank all possible subsets of the full model, based on minimising Akaike's Information Criterion, corrected for small sample sized (AICc) (Burnham & Anderson 2002).

As our study included repeated measures at sites, we tested for temporal autocorrelation between repeated measures at sites using the "acf" function in R (R Core Team 2013). Autocorrelation for all variables was low, and including a first-order autoregressive correlation structure on the random effects did not improve the fit of the LMMs. Therefore, we did not include correlation structures in our final models (Pinheiro & Bates 2000). We also considered fitting the species richness data with a generalised linear mixed-model (GLMM), with Poisson errors, which is often used for count data. However, this was not used in the final analysis as the characteristics of a Poisson distribution (skewed distribution and heteroscedasticity) were not evident in our data (Zuur et al. 2009), and a trial GLMM showed poor fit at the extremities when compared with the LMM.

To assess whether fire also interacted with herbivory via a numerically-mediated pathway, we tested whether fire increased herbivore activity (as measured from scat counts) within the different exclosure treatments. We used GLMM with a Poisson error distribution and a log-link function for this analysis, with exclosure treatment × fire × time as fixed effects and block/site as random effects. As very low scat counts in exclosure treatments ($\bar{x}$ = 1.78 ± 0.53, 59% of counts = 0) led to complete separation of factor combinations (Gelman & Hill 2007), the exclosure treatment was excluded from this analysis. Scat count data were found to be over-dispersed, which we accounted for by including an observation-level random effect in our model (Harrison 2014).

We tested for differences in community composition among the six treatment combinations both pre- (May 2012) and post-treatment (May 2014), using nonparametric blocked multi-response permutation procedures (MRBP, McCune & Grace 2002) in PC-ORD (McCune & Mefford 2006). We excluded rare species (those occurring at 2 or fewer sites) from the site × species matrix and relativized abundances within sites, prior to analysis (McCune & Grace 2002). If MRBP indicated significant differences in species composition among treatments, we then used indicator species analysis (Dufrene & Legendre 1997) to identify individual species associated with the different treatments. We used the function "multipatt" in the R package "indicspecies" (De Cáceres & Legendre 2009), which allows the identification of species associations with combinations of groups (treatments) rather than just a single group (De Cáceres et al. 2010). We set the maximum number of groups (treatment combinations) to be combined to three as this allowed us to identify associations with both individual treatment combinations, as well as with complete factors in the factorial design. We accounted for the blocked structure of sites by constraining permutations within, rather than among blocks. Significance was determined from 9999 permutations of the data.

Results

Effect of browsing and fire on plant diversity metrics

We detected 111 understory plant species over five surveys in the two-year study period (Appendix S1). In the top-ranked LMMs, fire modified the effect of herbivory on plant community diversity, evenness, and dominance and this interaction was consistent across time (Table 1, Fig. 2, Appendix S2). Plant species diversity, evenness and dominance were not related to herbivore activity on unburnt sites, but burnt sites had lower community diversity and evenness and higher assemblage dominance as herbivore activity increased (Table 1, Fig. 2). This indicates a functionally moderated interaction. The difference in community diversity and evenness between burnt and unburnt sites varied through time and was highest 15 months post-fire. In contrast, the highest-ranked model for assemblage dominance indicated that the effect of fire was consistent across time; at high levels of herbivory, the relative abundance of the dominant species was 30 % higher in burnt than unburnt sites (Fig. 2). This increase in assemblage dominance was driven by *P. esculentum,* which comprised approximately 70 % of the vegetation cover in burnt-open sites, but less than 40 % in burnt and unburnt exclosure sites (Fig. 3). In contrast to the other diversity metrics, none of the models for species richness with ΔAICc < 2 included the herbivory × fire interaction (Appendix S2), and the effects of fire were short-term, with species richness of burnt sites returning to the level of unburnt sites within 15 months (Table 1).

Effect of fire on herbivore activity

Fire affected herbivore activity levels, with both the first and second ranked models showing that scat counts were higher on burnt than unburnt sites (Table 2), indicating a numerically-mediated interaction between fire and herbivory. In the first-ranked model, this effect was consistent across time, but in the second-ranked model, this difference was significant only in the period from three to nine months post-fire, where counts in burnt sites were more than double those in unburnt sites (Table 2, Fig. 4).

Effect of browsing and fire on plant species composition

Species composition did not differ among experimental treatments prior to treatment implementation in May 2012 (MRBP, $P = 0.15$). However, by May 2014, species composition differed significantly among treatments (MRBP, $P = 0.004$). Pairwise comparisons revealed that burnt-open sites had significantly different species composition to all other treatment combinations (all $P < 0.05$). Burnt partial and burnt exclosure sites also differed significantly in composition ($P = 0.03$).

Indicator species analysis identified six individual species that were associated with the experimental treatments, each of which was positively associated with three of the treatment combinations (all $P < 0.05$, Appendix S1). The fern *P. esculentum* was positively associated with both burnt and unburnt open sites, as well as burnt partial sites. Conversely, the grass *Themeda australis* and the herb *Galium propinquum* were associated with both burnt and unburnt exclosure treatments, as well as unburnt partial treatments. A further three species were associated with burnt exclosure treatments but differed in their other associations; the small tree *Synoum glandulosum* was also associated with burnt partial and unburnt exclosure sites, the sub-shrub *Marsdenia suavolens* was also associated with unburnt exclosure sites and burnt open sites, and another small tree *Persoonia linearis* was associated with all burnt treatments.

Discussion

We tested plant diversity responses to browsing and the fire-browsing interaction using a manipulative experiment in a temperate forest understory. As predicted, where browsing increased plant community dominance, it reduced plant diversity and evenness. Prescribed fire interacted strongly with browsing, with herbivore activity affecting these measures of plant diversity only in burnt sites. This fire-browsing interaction was generated through a combination of numerically-mediated and functionally-moderated pathways; fire both increased herbivore activity levels, and increased the per-unit effect of herbivores on the plant community.

Effect of browsing and fire

Browsing had little effect on the plant community in the absence of fire, but browsing in burnt environments increased community dominance, reduced plant community evenness and diversity, and altered species composition. Specifically, browsing in burnt environments increased the dominance of the fern *P. esculentum* and reduced the abundance of a number of palatable grasses and herbs. This pattern was consistent with previous studies where plant diversity responses to grazing depended on the effect of grazing on the dominant plant species (Mathisen et al. 2010; Royo et al. 2010a; Borer et al. 2014). As suggested by Royo et al. (2010a), the variable effect of browsing on the dominant plant species can potentially explain the wide range of reported effects of large herbivores on forest plant diversity. In systems where large herbivores have been at high abundances for extended periods, understories are largely dominated by a few unpalatable species; this is the case in many forested systems of North-America (Tremblay et al. 2006; Rooney 2009) and Europe (Kirby 2001) where deer are highly abundant. In such systems, continued browsing maintains the dominance of unpalatable species, while herbivore exclusion can allow palatable species to recover, thereby increasing plant species richness and evenness. In systems where large herbivores are not highly abundant, browsing may help to maintain understory diversity by reducing the dominance of fast-growing palatable species, particularly following disturbance (Royo et al. 2010a).

Despite having strong effects on plant community diversity and evenness after fire, we found that browsing did not affect plant species richness, either with or without burning. Mathisen et al. (2010) reported a similar result for moose browsing in Swedish pine forest. This may be because much of the vegetation in both the study by Mathisen et al. (2010) and in our study was comprised of shrubs (Appendix S1). Browsing is often not lethal for established individuals of woody plant species (Hester et al. 2006). Thus, in forest systems with woody understories, browsing will affect the relative cover of different species more strongly than the relative number of individuals. In addition, as shrubs are slow-growing and long-lived compared with many herbs and grasses (McFarland 1998), the two-year time frame of our study may have been insufficient for differences in colonisation and extinction rates to become apparent.

Interaction pathways

The stronger effect of herbivory on vegetation after burning occurred both via numerically-mediated and functionally-moderated pathways. Burning both increased the herbivore activity at a site (Fig. 4), and increased the per unit effect of herbivore activity on the vegetation (Fig. 2). The attraction of large herbivores to recently burnt patches has been well documented in grassland ecosystems (Allred et al. 2011), and has also been shown for some forest-dwelling ungulates (Fisher & Wilkinson 2005). However, previous studies of macropod herbivores following fire have found little effect of large wildfires on macropod densities (Garvey et al. 2010; Arthur et al. 2012). These contrasting results indicate that fire-browsing interactions driven by the attraction of herbivores to burnt areas may be more likely to occur following small, patchy fires (as occurs with prescribed burns), than following large-scale wildfires. The effects of prescribed fire on browsing intensity should therefore be considered in fire planning in these systems, especially where herbivores are particularly abundant.

The greater per-unit effect of herbivores on vegetation in burnt than in unburnt sites was likely due to the competitive release of *P. esculentum* following fire. After fire (and other disturbances), *Pteridium* species can rapidly regenerate from below-ground rhizomes and dominate recently disturbed environments (Skre et al. 1998; Spencer & Baxter 2006). However, in the absence of further disturbance, the dominance of *P. esculentum* usually declines with time since fire, as other plants become more established (Spencer & Baxter 2006). In our study, browsing maintained assemblage dominance two years after fire, with *P. esculentum* comprising almost 70 % of understory vegetation cover in burnt, browsed (open) sites, compared with less than 40 % in burnt, un-browsed sites (Fig. 3). The dominance of *P.*

esculentum could have important consequences for the ability of the vegetation to recover to its pre-fire state, as *P. esculentum* can form a shade canopy which supresses the establishment of other plants (Tolhurst & Turvey 1992). Therefore, our results suggest that heavy browsing after prescribed fire may lead to an understory dominated by a few fire- and browsing-resistant species, which could be difficult to reverse.

An understory dominated by browse- and fire-resistant plants was suggested by Wisdom et al. (2006) as a likely outcome of low serverity forest fires under moderate or high herbivory. Previous studies of the individual effects of chronic herbivory (Rooney 2001) and reoccurring fire (Spencer & Baxter 2006) have documented transitions towards depauperate understories dominated by ferns (*Dennestaedtia* and *Pteridium* respectively). Our study, and an earlier pilot study (Dexter et al. 2013), show that, in concert, fire and herbivory can have synergistic effects, creating a depauperate, fern-dominated understory over a relatively short time period. Our results also show that at low levels of herbivory, differences in vegetation diversity between burnt and unburnt sites are small. Therefore, in forests where predation by foxes and dingoes keeps macropod herbivores at low densities, fire-browsing interactions may have limited effects on vegetation diversity.

Although the timeframe of our study means we cannot predict whether the effects of these fire-browsing interactions will persist in the long-term, alternate stable states driven by chronic herbivory have been documented from a range of forest ecosystems worldwide (Royo & Carson 2006; Raffaele et al. 2011; Tanentzap et al. 2011; Hidding et al. 2013). These systems are characterised by understories with low floristic diversity which are dominated by a few, unpalatable species (de la Cretaz & Kelty 1999; Horsley et al. 2003). Once such states have developed, legacy effects can prevent the recovery of plant diversity, even if herbivore densities are reduced (Royo et al. 2010b). Preventing the development of such states through the integrated management of disturbances such as herbivory and fire is therefore of key importance for the conservation of diverse forest understory flora (Royo & Carson 2006; Wisdom et al. 2006).

Can effects on dominance always be used to predict the outcome of fire-browsing interactions?

We were able to predict the outcome of the fire-browsing interaction in our study. However, this was most likely due to the particularities of our study system rather than a predictability of fire-browsing interactions in general. In our study system, the most dominant and widespread understory species is *P. esculentum*, which is of low palatability (Di Stefano & Newell 2008) and responds positively to fire (Spencer & Baxter 2006). Therefore, both fire and browsing acted to increase the dominance of *P. esculentum*, and their functionally-moderated effects were synergistic. In addition, fire increased browsing activity, meaning that the numerically-mediated interaction between fire and browsing also had positive synergistic effects.

By contrast, in many other systems, the outcomes of fire-browsing interactions will be far less predictable. For example, in a system where fire and browsing act antagonistically (e.g. fire increases dominance, but browsing has the opposite effect, as in Eby et al. 2014), where more than one species is dominant (and fire or browsing responses differ between these species) and/or where functionally-moderated effects are in opposition to numerically-mediated effects, the outcome will depend on the balance of these opposing effects. Further, fire and browsing may interact in more subtle ways, such as modifying the strength of each other's effects on dominant species. For example, the tissues of plants regenerating after fire often lack the physical and chemical defences of mature plants, meaning generally unpalatable plants can be highly palatable after burning (Augustine & McNaughton 1998). If differences in palatability between species are reduced, herbivores feed less selectively, so the strength of browsing effects on assemblage dominance can be reduced or even eliminated

(Augustine & McNaughton 1998). In addition, low severity fires, such as prescribed burns can have different effects on the plant community than high severity fires that often occur as wildfire (Morrison 2002). Different fire severities may therefore have differing effects on dominant species, and so the outcomes of fire-browsing interactions are likely to vary with fire severity. Therefore, predicting the outcome of fire-browsing interactions will only be possible in some ecosystems, and where there is detailed knowledge of the palatability and functional traits of plant species. Outside of these systems, manipulative experiments will continue to be critical to improving understanding of the dynamics of fire-browsing interactions.

Conclusion

In forested systems that are dominated by unpalatable, fire-resistant plant species, prescribed fire and browsing are likely to interact synergistically to increase assemblage dominance and reduce plant community diversity. In such systems, integrated management of fire and large herbivores will be necessary to prevent the development of an understory dominated by a narrow set of fire tolerant, unpalatable species. In forested ecosystems where unpalatable, fire resistant species are not dominant, the outcome of fire-browsing interactions will not be so easy to predict. Therefore manipulative studies which can examine both the individual and interactive effects of these disturbances, and their interaction pathways, will continue to play a central role in developing our understanding of fire-browsing interactions in forest ecosystems.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Plant species list

Appendix S2. Tables of model rankings

Tables

Table 1. Estimates of coefficients (Est.), their standard errors (SE) and probabilities for the top-ranked linear mixed model testing the effects of fire (burnt or unburnt), large herbivore activity (scats per 100m^2, ln transformed), time since fire (3, 9, 15 or 21 months) on plant species richness (species / 36 m^2), diversity (Simpson's reciprocal index, *1/D*), evenness (Simpson's evenness, $E_{1/D}$) and dominance (Berger-Parker, *d*). Pre-treatment values were included as a fixed effect to account for pre-existing differences between sites. Reference states for comparisons were unburnt sites three months post-fire. Random terms for each model were block/site.

		Species richness				Diversity (1/*D*)				Evenness ($E_{1/D}$)				Dominance (*d*)			
Fixed effects		Est.	SE	df	*P*	Est.	SE	df	*P*	Est.	SE	df	*P*	Est.	SE	df	*P*
Intercept		6.15	5.33	66	0.253	2.25	0.72	64	0.003	0.075	0.024	64	0.002	0.266	0.078	67	0.001
Pre-treatment value		0.85	0.19	18	<0.001	0.39	0.20	18	0.060	0.373	0.168	18	0.040	0.296	0.126	18	0.030
Fire		-9.40	1.45	18	<0.001	1.04	0.53	18	0.066	0.095	0.020	18	<0.001	0.107	0.031	18	0.003
Herbivores (ln transformed)						0.28	0.48	64	0.558	0.012	0.016	64	0.455	-0.022	0.046	67	0.636
Time since fire	9 months	0.50	0.78	66	0.523	-0.43	0.48	64	0.378	-0.016	0.020	64	0.410	0.115	0.038	67	0.003
	15 months	-0.25	0.78	66	0.749	-0.02	0.48	64	0.973	0.001	0.020	64	0.975	0.063	0.038	67	0.100
	21 months	1.17	0.78	66	0.139	0.13	0.49	64	0.785	0.001	0.020	64	0.973	0.053	0.039	67	0.177
Fire:Herbivores(ln)						-1.68	0.64	64	0.011	-0.059	0.021	64	0.006	0.209	0.061	67	0.001
Fire:Time	B:9m	6.67	1.10	66	<0.001	-1.69	0.67	64	0.014	-0.110	0.028	64	<0.001				
	B:15m	10.33	1.10	66	<0.001	-1.88	0.67	64	0.007	-0.126	0.028	64	<0.001				
	B:21m	10.92	1.10	66	<0.001	-1.67	0.69	64	0.018	-0.122	0.028	64	<0.001				

Table 2. Results of generalised linear mixed models testing whether fire affected the level of herbivore activity (scats per 100m^2) in the different exclosure treatments (open or partial exclosure) through time (3, 9, 15 or 21 months post-fire). Full exclosure treatments were not included in this analysis due to very low values ($\bar{x}$ = 1.78 ± 0.53). Reference states for comparisons were unburnt, open sites three months post-fire.

		Top ranked model				Second ranked model			
Fixed effects		Est.	SE	Z	*P*	Est.	SE	Z	*P*
Intercept		4.26	0.23	18.8	<0.001	4.36	0.25	17.2	<0.001
Fire		0.46	0.20	2.2	0.025	0.27	0.33	0.8	0.408
Exclosure (partial)		-1.63	0.20	-8.0	<0.001	-1.63	0.20	-8.1	<0.001
Time since fire	9 months	-0.51	0.24	-2.1	0.038	-1.04	0.32	-3.2	0.001
	15 months	-0.25	0.24	-1.0	0.306	-0.20	0.31	-0.7	0.515
	21 months	-0.89	0.24	-3.6	<0.001	-0.81	0.31	-2.6	0.010
Fire:Time	B:9m					1.01	0.44	2.3	0.022
	B:15m					-0.09	0.43	-0.2	0.831
	B:21m					-0.18	0.44	-0.4	0.690

Figures

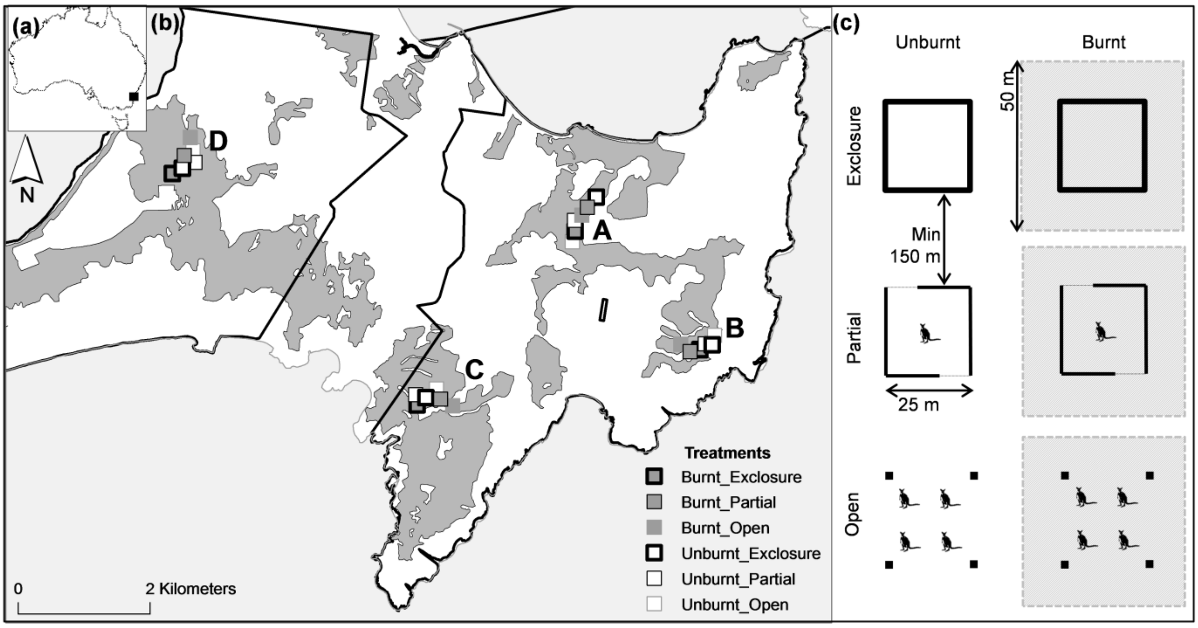


Figure 1. Study location and design showing (a) location of Booderee National Park in south-eastern Australia, (b) location of the four experimental blocks (A-D) within Booderee National Park, and (c) a schematic diagram of the factorial design showing the experimental treatments and their arrangement within the four experimental blocks (not to scale, exact spatial arrangement of sites varies between blocks). Dark grey shaded area in (b) shows the extent of the *Eucalyptus pilularis* forest type within BNP, black outline indicates park boundary, light grey shading depicts ocean.

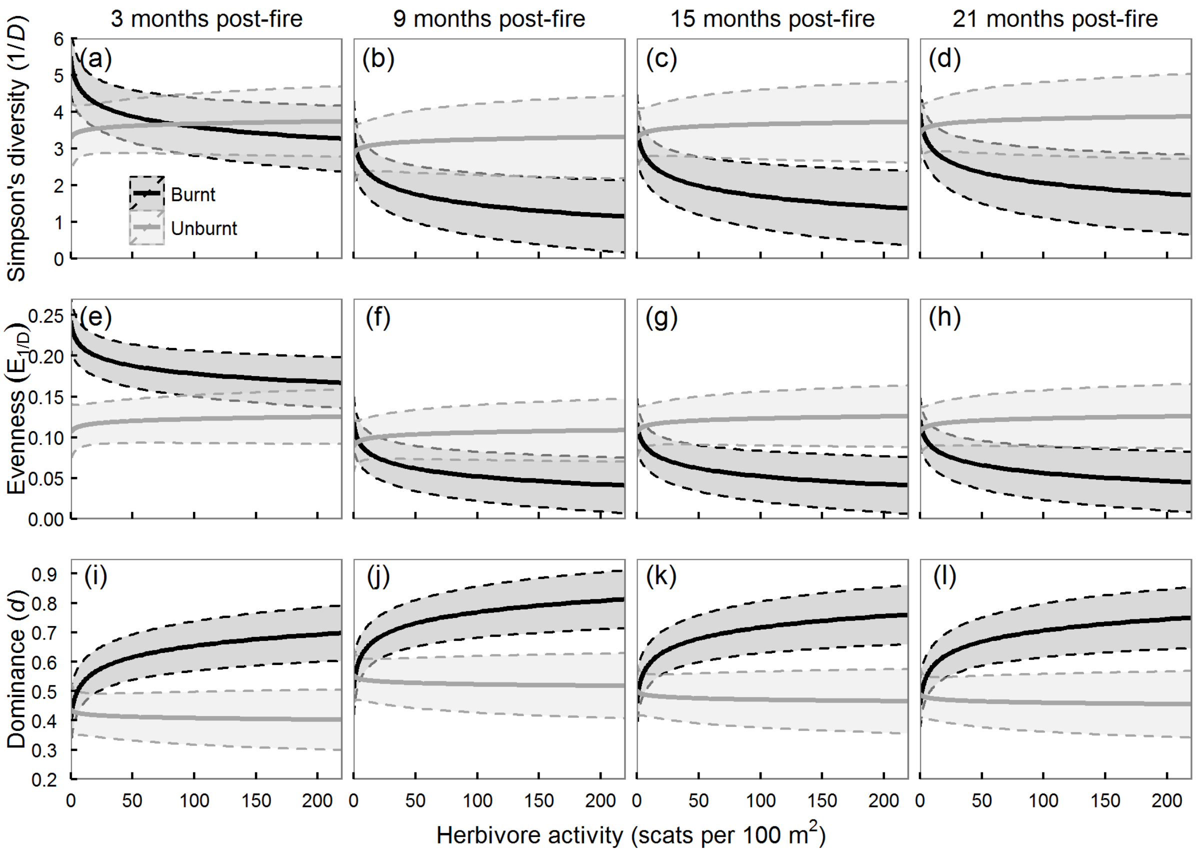
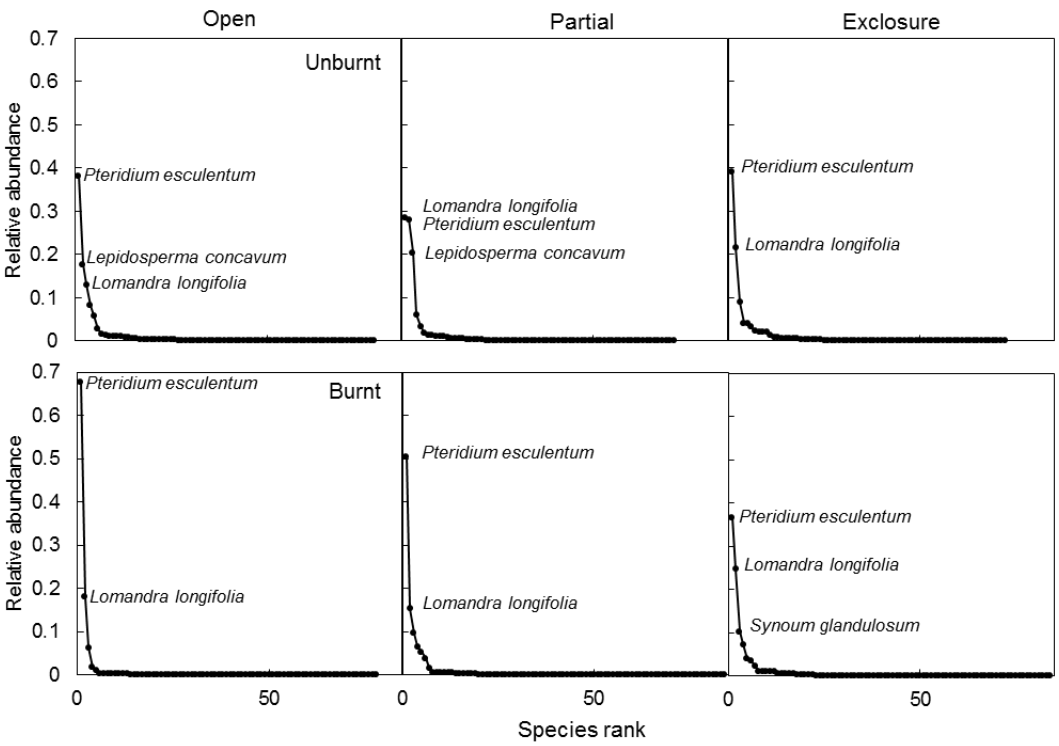


Figure 2. Response of plant community diversity (Simpson's reciprocal index, *1/D*, a-d), evenness (Simpson's evenness, $E_{1/D}$, e-h) and dominance (Berger-Parker, *d*, i-l) to fire (burnt or unburnt) and herbivore activity through time. Values are predicted means and 95 % confidence intervals from the top-ranked model for each metric. Pre-treatment values were fixed at the mean for all predictions (3.15 for diversity, 0.106 for evenness and 0.53 for dominance).



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609 Figure 3. Species rank-abundance curves for burnt and unburnt sites under each of the

610 herbivory treatments in the final survey period (May 2014). Species with relative abundances

611 > 0.1 are identified on each plot.

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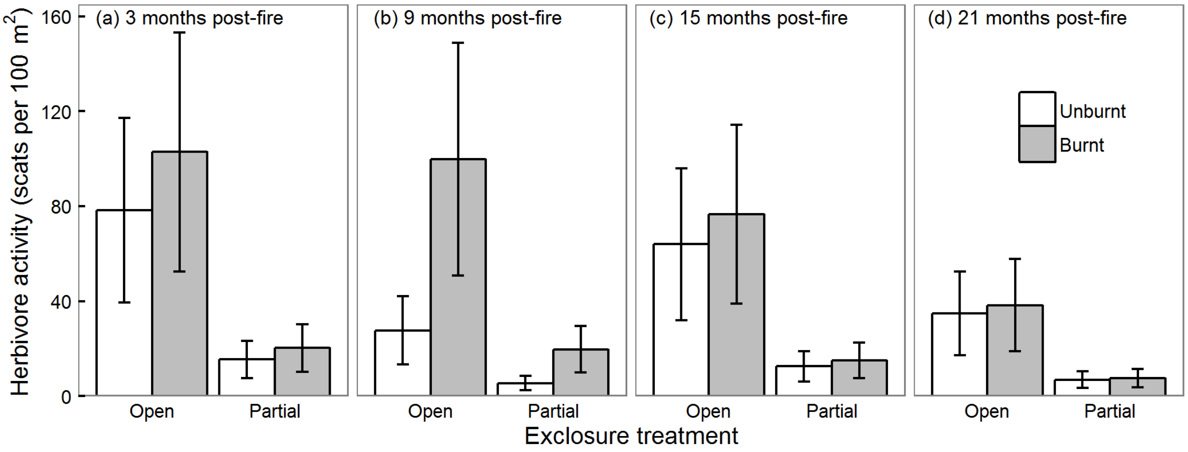

Figure 4. Herbivore activity in each of the experimental treatment combinations over time. Values are the predicted mean scat count and 95 % confidence intervals based on the second-ranked generalised linear model. Full exclosure treatments were not included in this analysis due to very low values ($\bar{x}$ = 1.78 ± 0.53).