Foster, C. N., Barton, P. S., Robinson, N. M., MacGregor, C. I., & Lindenmayer, D. B. (2017) Effects of a large wildfire on vegetation structure in a variable fire mosaic. *Ecological Applications*, 27(8): 2369-2381.

DOI **https://doi.org/10.1002/eap.1614**

Article type : Articles

Running Head: Fire mosaics and vegetation structure

Monday, 28 August 2017

Effects of a large wildfire on vegetation structure in a variable fire mosaic

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Abstract

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Management guidelines for many fire-prone ecosystems highlight the importance of maintaining a variable mosaic of fire histories for biodiversity conservation. Managers are encouraged to aim for fire mosaics that are temporally and spatially dynamic, include all successional states of vegetation, and also include variation in the underlying "invisible mosaic" of past fire frequencies, severities and fire return intervals. However, establishing and maintaining variable mosaics in contemporary landscapes is subject to many challenges, one of which is deciding how the fire mosaic should be managed following the occurrence of large, unplanned wildfires. A key consideration for this decision is the extent to which the effects of previous fire history on vegetation and habitats persist after major wildfires, but this topic has rarely been investigated empirically.

In this study we tested to what extent a large wildfire interacted with previous fire history to affect the structure of forest, woodland and heath vegetation in Booderee National Park in south-eastern Australia. In 2003, a summer wildfire burnt 49.5% of the park, increasing the extent of recently burnt vegetation (< 10 years post-fire) to more than 72% of the park area. We tracked the recovery of vegetation structure for nine years following the wildfire and found that the strength and persistence of fire effects differed substantially between vegetation types. Vegetation structure was modified by wildfire in forest, woodland and heath vegetation, but among-site variability in vegetation structure was reduced only by severe fire in woodland vegetation. There also were persistent legacy effects of the previous fire regime on some attributes of vegetation structure including forest ground and understorey cover, and woodland midstorey and overstorey cover. For example, woodland midstorey cover was greater on sites with higher fire frequency, irrespective of the severity of the 2003 wildfire. Our results show that even after a large, severe wildfire, underlying fire histories can contribute substantially to variation in vegetation structure. This highlights the importance of ensuring that efforts to reinstate variation in vegetation fire age after large wildfires do not inadvertently reduce variation in vegetation structure generated by the underlying invisible mosaic.

Keywords:

Biodiversity, fire mosaic, invisible mosaic, prescribed burning, pyrodiversity, vegetation structure.

Introduction

A dominant premise in fire ecology is that managing ecosystems for pyrodiversity (variability in the spatiotemporal distribution of fires) will promote and maintain biodiversity (Martin and Sapsis 1992, Bradstock et al. 2005, Parr and Andersen 2006). This concept has led to the "variable mosaic" approach to fire management, where maintaining variability in both the visible fire mosaic (i.e. time-since fire, and fire size, severity, season and patchiness), and the underlying invisible mosaic (i.e. lengths of past inter-fire intervals, fire frequencies) across a landscape is promoted (Bradstock et al. 2005, Ponisio et al. 2016, Tingley et al. 2016). Yet, translating the variable mosaic concept into management prescriptions is challenging, as for most ecosystems, critical questions remain unanswered, including what temporal and spatial scale of variability will promote biodiversity, which elements of the fire mosaic will benefit which species, and how to manage tradeoffs between different components of the fire mosaic (e.g. time since fire, fire intervals and fire frequency)(Parr and Andersen 2006, Driscoll et al. 2010, Kelly et al. 2017). For example, management guidelines focused on fire intervals have often been derived from the fire responses of a few, well-studied plant species (Menges and Hawkes 1998, Bradstock and Kenny 2003, Duff et al. 2013), and recent studies have found that such guidelines may poorly represent the ecological requirements of other taxa, particularly those which rely on long-unburnt habitats (Berry et al. 2014, Robinson et al. 2014, Croft et al. 2016).

A further challenge to maintaining variable fire mosaics is the occurrence of large, unplanned wildfires (Kelly et al. 2017). Large wildfires create extensive areas of vegetation with uniform fire age and, in landscapes previously managed with a variable mosaic approach, can greatly reduce variability in the distribution of fire ages (the visible mosaic) available in a landscape. However, even very severe wildfires are usually heterogeneous, with different areas burning at different severities (Turner and Romme 1994, Perry et al. 2011, Leonard et al. 2014, Berry et al. 2015, Tingley et al. 2016), meaning that while large wildfires can homogenize fire age, there may not be a coincident reduction in the variability of vegetation structures within a landscape. Moreover, even in areas that are severely burnt by wildfires, legacy effects of previous vegetation on post-fire vegetation structure can be substantial (Franklin et al. 2000, Fontaine et al. 2009, Johnstone et al. 2016, Romme et al. 2016, Ton and Krawchuk 2016). Many legacy effects are likely to be related to previous fire history (the invisible mosaic), meaning that wildfires do not necessarily erase the effects of a previously established fire mosaic on vegetation structure. For example, both Pereoglou et al. (2011, coastal heathland), and Lindenmayer et al. (2012, fire-killed eucalypt forest) describe strong effects of pre-fire vegetation age on the availability of habitat structures for fauna after large wildfires. Similarly, Fontaine et al. (2009) found that after a large wildfire, mixed evergreen forests that had also burnt 15 years prior contained different habitat structures, and associated bird communities, than forest that had not burnt for decades prior to the wildfire. In contrast, Haslem et al. (2016, mixed eucalypt forest) found that properties of a recent severe wildfire overrode most effects of previous fire history on vegetation structure. There is therefore a need to better understand the extent to which wildfire modifies the effects of the previous fire history on habitat structure, and hence, whether it is important for post-wildfire management, and attempts to re-instate variability in time-since fire, to account for the established invisible mosaic.

We use a nine year study of vegetation recovery following a large, severe wildfire to test the effects of wildfire on vegetation structural attributes that are important for fauna. Our study addressed two key questions: (1) Do large, severe wildfires lead to reduced variability in vegetation structure, compared with unburnt sites? (2) Are the effects of pre-wildfire fire history on attributes of vegetation structure erased, modified or unaffected by the occurrence of a severe wildfire? We discuss our results in the context of post-wildfire management decisions, and particularly to what extent fire management following large wildfire events needs to account for the pre-fire mosaic to meet the needs of both fauna and flora.

Materials and Methods

Study site

We conducted this study in Booderee National Park, a ~ 6300 ha reserve located on a coastal peninsula approximately 200 km south of Sydney south-eastern Australia (35°40` S, 150°40` E, Fig. 1a). The area has a temperate maritime climate and an average rainfall of 1240 mm spread evenly throughout the year (Australian Bureau of Meteorology 2016). Booderee National Park is dominated by dry sclerophyll vegetation, including forest (36.2 % of the park area), woodland (12.9 %), heath (15.3 %) and shrublands (9.5%) (Fig. 1a, Taws 1997). Other, less-widespread vegetation formations include wet forest, rainforest and sedgeland. The distribution of vegetation types in the study region is determined predominantly by edaphic factors, with fire driving differences in vegetation within, rather than transitions among, these broad vegetation types (Beadle 1954, Keith 2004).

In this study, we focused on the three most widespread vegetation formations in Booderee National Park: forest (trees have touching crowns), woodland (trees have separated crowns and low stature) and heath (treeless, shrubs usually < 2m tall) (Taws 1997). The forest overstorey is dominated by *Eucalyptus pilularis*, *Corymbia gummifera*, and *E. botryoides*, the midstorey by *Banksia serrata*, *Acacia longifolia*, and *Monotoca eliptica* and the understory is dominated by *Pteridium esculentum* and *Lomandra longifolia.* The woodland overstorey is typically comprised of *Eucalyptus sclerophylla*, *Corymbia gummifera*, and *Banksia serrata*, the midstorey is dominated by *B. serrata* and *C. gummifera* and the understory is comprised of *P. esculentum, B. serrata*, *Lambertia formosa*, *Acacia longifolia*, *A. suaveolens*, and *Lomandra longifolia.* Heath comprises both wet and dry heath and is dominated by shrubs that are usually less than two meters tall, including *Banksia ericifolia*, *Allocasuarina distyla*, *Isopogon anemonifolius*, *Hakea teretifolia* and other *Leptospermum or Melaleuca* species. Overstorey species in the forest and woodland vegetation types (*Eucalyptus sp.*, *Corymbia sp*. and *B. serrata*) are able to re-sprout from above-ground epicormic buds after fire (meaning even severe fires are rarely stand-replacing), while the dominant species in heath vegetation regenerate from seed (*B. ericifolia, A. distyla*, *H. teretifolia*), or from underground lignotubers (*I. anemonifolius, Leptospermum* and *Melaleuca* species) (Kattge et al. 2011). For more detailed descriptions of the vegetation types see Taws (1997) and Lindenmayer et al. (2008b).

Fire in Booderee National Park

Booderee National Park has a well-documented fire history and records of fire perimeters and cause (wildfire or prescribed fire) have been maintained since 1957. A total of 230 fires was recorded between 1957 and 2012 (average of 4.18 per year), with a median fire size of 7.02 ha.

Most areas of the park have experienced between one and four fires in 55 years (equating to one fire every 13-55 years, Fig 1b), which is low-moderate compared with many studies of fire frequency in this region, where high fire frequency sites often have fire frequencies equating to more than one fire every five years (e.g. Morrison et al. 1995, Bradstock et al. 1997, Watson and Wardell-Johnson 2004, Penman et al. 2008). There have been only five large (> 500 ha) wildfires recorded since 1957, and these occurred in 1962, 1972 (two fires), 2002 and 2003. Since 1980, there have been more prescribed fires than wildfires within the park, and if the two large fires of 2002 and 2003 are excluded, more area has burnt under prescribed fire than wildfires in this time (Appendix S1: Fig. S1).

The 2003 wildfire occurred in early summer (mid-December), and burnt 49.5% of the park area (total fire extent was more than 2600 ha, Fig. 1b). Area calculations based on mapped fire perimeters (using ArcMap version 10.4.1) revealed that the 2003 wildfire reduced the area of vegetation with long (> 30 years since fire) and moderate time since fire (10-30 years post-fire) within the park by 49% and 69% respectively, and increased the extent of recently burnt vegetation (< 10 years post-fire) to more than 72% of the vegetated area (Fig. 2). The 2003 wildfire particularly impacted areas of heath vegetation, with the extent of moderate and long time since fire heath reduced by 92% and 61% respectively (Fig. 1, 2).

Data collection

We measured changes in vegetation structure at 67 sites which were established in 2003 (prior to the wildfire) to monitor biodiversity responses to fire (Lindenmayer et al. 2008a, Lindenmayer et al. 2008b, Lindenmayer et al. 2016). These sites were selected using a stratified, randomized approach, with the goal of distributing sites widely throughout the park, while ensuring representation of all major vegetation types. The park area was divided into polygons that were homogenous in broad vegetation type (Taws 1997), and time-since fire (four classes of time-since fire, as of early 2003), and a stratified-random sample of polygons was selected (forest = 20, woodland = 22 and heath = 25). Each site comprised a 100 m transect which was placed so that the full transect was situated within the selected polygon (Lindenmayer et al. 2008a). We surveyed vegetation in two 20 x 20 m quadrats which were located one on each side of the transect 20 m apart (i.e. between 20 - 40 m and 60 - 80 m).

For each of the 67 sites, we calculated the time-since fire (pre-wildfire fire interval) and fire frequency based on the mapped fires since 1957. These calculations were made as of the 21st December 2003 (the eve of the 2003 wildfire), so that interactions between the pre-wildfire fire history, and the 2003 wildfire could be tested. Sites that had not burnt in the record period were assigned the maximum interval of 46 years. Following the 2003 wildfire (2-6 weeks following fire), we visited each of the 67 sites to assess fire severity. Each site was assigned to one of three categories based on the post-fire vegetation state: unburnt, moderate (understorey burnt, midstorey may be scorched but some green material remaining), or severe (midstorey leaves totally consumed and/or overstorey burnt). None of the forest sites were recorded as burning at high severity in the 2003 wildfire. For heath sites, overstorey and midstorey are usually absent, and so the 2003 wildfire severity was assessed based on the patchiness of the burn (moderate = patchy burn, severe = whole site burnt). None of the 67 sites used in this study have been burnt since the 2003 wildfire.

One limitation with using long-term fire history data to investigate effects of fire regime on vegetation, is that the occurrence of fire (and hence fire regime variables) can be correlated with underlying environmental factors such as topography and soil type. Therefore, there is potential for fire effects to be confounded with these underlying factors. However, in our study, such confounding is unlikely as the fire history variables used in this study (fire frequency and time since fire) are not strongly correlated with underlying environmental variables (Appendix S1), likely due to the consistent prescribed burning and active wildfire control program within our study area.

We measured vegetation structural attributes at each site five times between June 2004 and May 2013. Surveys were repeated at one to four year intervals (median = 1.6 years) and all were led by the same field ecologist (CM). Due to the large number of sites surveyed, not all sites could be surveyed within the same season. However, survey timings were balanced across vegetation types and fire histories to ensure no annual or seasonal bias among treatments. We selected structural variables for measurement based on their established importance as habitat for fauna, and the ability to measure these variables consistently over time. For each survey, we visually estimated the projective foliage cover of the understorey (0 - 2 m), midstorey (2 - 10 m) and overstorey (> 10 m) strata in each 20 x 20 m quadrat. Using four 1 x 1 m plots in each quadrat (one in each corner of the 20 x 20 m quadrat), we also estimated the percentage cover of bare earth in the ground layer. Bare earth cover was chosen as it is an inverse measure of ground-layer habitat structure, and because leaf litter cover can be highly variable at small scales due to the presence of other (important) habitat features such as logs, rocks and grasses. In the first survey (2004-2005) and last survey (2012 - 2013) at each site we also recorded the number of logs (diameter > 10 cm, length > 1 m), and the number of live woody stems (in the classes < 15 cm, 15 – 30 cm and > 30 cm diameter at 1.3 m above ground level), in each quadrat. Logs and stems that were crossing the quadrat boundary were included in the counts if the mid-point was located within the quadrat. We averaged all cover estimates at the site level, and converted stem and log counts to densities (number m^{-2} and number ha^{-1} respectively) prior to analysis.

Data analysis

Question 1: Does severe wildfire reduce variation in vegetation structure among sites?

We tested the effect of 2003 wildfire on among-site variation in vegetation structure, using a multivariate approach, and analyzing each of the three vegetation types separately. We performed two multivariate tests for each vegetation type; a PERMANOVA (Permutational Analysis of Variance) to test for differences in multivariate centroids among groups, and a PERMDISP analysis (test of homogeneity of multivariate dispersions) to test for differences in within-group variability among groups. All multivariate analyses were based on site-site distance matrices (one for each vegetation type), using data from the first (2004-2005) and last (2012-2013) surveys at each site. Analyses were performed using the Vegan package (Oksanen et al. 2015) in R version 3.2.3 (R Development Core Team 2015). We calculated three separate distance matrices (one for each vegetation type), using Euclidean distance, and including the following variables: overstorey cover, midstorey cover, understorey cover, bare earth cover, log density, and the density of small (0 -15 cm), medium (15 - 30 cm) and large (> 30 cm), live woody stems. In heath sites, the variables overstorey cover, medium stem density and large stem density contained mostly zero values. Therefore we excluded overstorey cover, and combined all stem counts into a single stem density variable prior to calculating the distance matrix for heath sites. We standardized each variable prior to calculating the distance matrices to ensure equal weighting of each variable.

We used a PERMANOVA (Permutational Analysis of Variance, function - vegan::adonis) with 999 permutations to test for differences in the centroids of groups of sites, according to 2003 burn severity, the survey year, and their interaction. A significant difference among groups in this analysis would indicate that fire altered the relative availability of different components of vegetation structure.

We performed a PERMDISP analysis (test of homogeneity of multivariate dispersions, function - vegan::betadisper) (Anderson et al. 2006, Anderson and Walsh 2013) to test for differences in multivariate dispersion among groups of sites that were: unburnt, moderately burnt, or severely burnt in the 2003 wildfire, for both 2004 and 2012 surveys (6 groups total). Differences in dispersion among groups in this analysis would indicate that burnt sites were either more or less variable in vegetation structure than unburnt sites. Where differences in dispersion were detected, we then performed a permutation test (999 permutations) of pairwise comparisons among the six groups (function - vegan::permutest). We used principal components analysis (function - vegan::rda) to visualize multivariate results (Oksanen et al. 2015).

Question 2: Are effects of previous fire history on vegetation structure modified by severe wildfire?

We used linear mixed models to test whether the long-term fire history affected vegetation structural attributes, and whether these effects persisted after, or were modified by, the 2003 wildfire. Our analysis compared a candidate set of nine models for each vegetation type, which were based on three competing hypotheses:

1. No effect of previous fire history: once accounting for the severity of the 2003 wildfire (FS03), and temporal change (time), previous fire frequency or fire interval was not related to vegetation structural attributes.

   Base model (one model): FS03*time
2. Persistent effects: the previous fire history was associated with differences in vegetation structural attributes, and this effect was not modified by 2003 fire severity.

Additive models (three models): FS03*time + fire frequency (and/or) + fire interval

3. Interactive effects: pre-wildfire fire history variables affected vegetation structural attributes, and at least one of these effects was modified (erased, reduced or amplified) by 2003 fire severity.

   Interactive models (five models): FS03*time + fire frequency*FS03 (and/or) + fire interval*FS03

We performed this analysis for each of the vegetation types separately, for the response variables overstorey cover (forest and woodland only), midstorey cover, understorey cover, bare earth, log density (forest and woodland only), and total stem density (counts summed across the three size categories). We transformed variables (where required) to meet model assumptions (logit transformation for cover variables, log or square root transformation for density variables). We standardized both predictor and response variables, then fit linear mixed models using the function “lmer” (“lme4” package), with site as a random effect to account for temporal dependency due to repeated measures at each site. For variables measured in all five surveys, time (years since 2003) was fitted as a continuous variable and both linear and quadratic effects were included (i.e. time + time^2). For variables measured only in the first and last surveys (log and stem density), time was fitted as a categorical variable. We compared the three additive and five interactive models to the base model using the Akaike Information Criterion corrected for small sample sizes (AICc, using “dredge” in the package “MuMIn”) (Burnham and Anderson 2002). We discuss additive or interactive models only when they had an AICc value at least two points lower than the base model (Arnold 2010). We made predictions (with 95% confidence intervals) from the top-ranked model for each variable using the “predictInterval” function in the package “merTools”.

Results

Wildfire effects on variation in vegetation structure

The 2003 wildfire altered vegetation structure across all three vegetation types (PERMANOVA: all $P < 0.05$, Fig. 3). Differences between sites that did and did not burn in the 2003 fire tended to be larger in 2004 than 2012 (Fig. 3), although this was significant only for heath sites (P =

0.019). Bare earth characterized recently burnt sites in all vegetation types (2004 surveys of moderate or severe sites). However associations between fire severity and other vegetation structural variables differed among vegetation types (Fig. 3).

While wildfire altered multivariate vegetation structure in all three vegetation types, fire significantly affected among-site variability in vegetation structure only in woodland vegetation (test for homogeneity of multivariate dispersion: $P_{woodland} = 0.006$, $P_{heath} = 0.105$, $P_{forest} = 0.222$). In 2004, one year post-fire, there was no significant difference in multivariate dispersion between unburnt and moderately burnt (P = 0.16) or severely burnt (P = 0.18) woodland sites. Between 2004 and 2012, variation among severely burnt sites declined slightly (multivariate dispersion changed from 1.5 to 1.3), while the structure of unburnt woodland sites became more variable (multivariate dispersion of unburnt sites in 2012 was 3.2 - more than double that for severely burnt sites in 2012, P = 0.01, Fig. 3b).

Interactions between wildfire and previous fire history

The effect of the pre-wildfire fire history on vegetation structure, and the extent to which wildfire modified these effects, differed between structural elements and vegetation types. In forest vegetation, previous fire history influenced understorey and ground layer structures, but not midstorey or canopy cover (Table 1). Frequently burnt forest sites supported greater understorey cover and lower woody stem density than rarely burnt sites, but this effect was erased by the 2003 wildfire (Fig. 4a, d). By contrast, forest sites that were long-unburnt and rarely burnt prior to the 2003 wildfire had higher understorey cover and more bare ground respectively, regardless of whether a site burnt in the 2003 wildfire (Fig. 4b,c).

Previous fire history affected both the overstorey and midstorey cover of woodland vegetation, and these effects persisted in sites that were burnt in the 2003 wildfire (Table 1). Sites with a long pre-wildfire fire interval had greater overstorey and midstorey cover than sites with a short pre-wildfire interval, irrespective of whether a site burnt in the wildfire (Fig. 5a, c). Woodland midstorey cover also was greater in high fire frequency sites, again regardless of the 2003 fire severity (Fig. 5b). By contrast, the density of logs in woodland sites was higher on low fire frequency sites, and this effect was only evident on sites that did not burn in the 2003 wildfire (Fig. 5d).

In heath vegetation, the severity of the 2003 wildfire had a dominant effect on vegetation structure, and there were no persistent effects of previous fire history (Table 1, Appendix S2). The only strong association between heath vegetation structure and previous fire history was a greater density of woody stems in long-unburnt sites, and this effect was evident only in sites that did not burn in the 2003 fire (Fig. 6), indicating a time-since fire effect, rather than a fire interval effect.

Discussion

Wildfires can create large areas of vegetation of uniform fire age. However, whether or not such fires reduce variation in vegetation structure (and hence the diversity of habitat structures available to fauna) will vary depending on ecosystems, fire behavior, and previous fire history (Russell-Smith et al. 2003, Turner et al. 2003, Loepfe et al. 2010, López-Poma et al. 2014). We studied the effects of a large wildfire on vegetation structure within dry sclerophyll forest, woodland and heath vegetation types, where a variable mosaic of fire histories had previously been established. We found that while wildfire modified vegetation structure in all vegetation types, among-site variability in vegetation structure was reduced only in severely burnt woodland vegetation. In addition, analysis of individual vegetation structural attributes revealed associations between vegetation structure and long-term fire history that persisted even in severely burnt sites. Our results demonstrate that both variation in wildfire severity (including vegetation that escapes wildfire), and variation in the invisible mosaic of vegetation that does burn, can contribute substantially to among-site variability in vegetation structures following large wildfires. Identifying actions that can be implemented between large wildfires to both allow areas of vegetation to escape wildfires, and to maintain spatial variability in long-term fire history, will help to maintain variability in vegetation structures in landscapes facing large, unplanned wildfire events.

We found that while wildfire modified vegetation structure in all vegetation types, among-site variability in vegetation structure was reduced only in severely burnt woodland vegetation. Our finding that unburnt woodland vegetation had greater among-site variability in vegetation structure than severely burnt woodlands supports the idea that the capacity for long-unburnt vegetation to escape large wildfire may be an important determinant of the diversity of habitat structures available to fauna (Croft et al. 2016). The effects of fire on variability in forest vegetation structure were likely limited because no high severity (crowning) fire was recorded for forest vegetation in the 2003 wildfire, and also because the canopy tree species of forests in our study area (predominantly *E. pilularis* and *C. gummifera*) are rarely killed by fire (Benson and McDougall 1998). The result that the 2003 wildfire had strong effects on heath vegetation structure, but did not affect among-site variability that structure, may be due to the strong influence that pre-fire vegetation condition can have on the post-fire structure and composition of heath vegetation (Keith and Tozer 2012), and well as the simpler structure of heath vegetation in general, where most vegetation is in a single, dense strata (Barton et al. 2014). Overall, a large, severe wildfire had only limited effects on among-site variability in vegetation structure. Further, as there were differences in vegetation structures associated with wildfire severity, is it possible that the heterogeneous severity of the wildfire may have actually increased vegetation heterogeneity at the landscape scale.

We found there were many effects of the pre-wildfire fire history (the invisible mosaic) on structural attributes of forest and woodland vegetation that were unaffected by the severity of a major wildfire. For example, high fire frequency was associated with low bare earth cover in forest vegetation, irrespective of the 2003 wildfire severity. While it is possible that this association was due to high ground cover (caused by environmental factors such as moisture availability) driving higher fire frequency, we believe this is unlikely due to the low correlations between fire frequency and environmental variables in our study (Appendix S1). Rather, this association is likely to be driven by long-term effects of fire on litter dynamics. Although fire increases bare ground in the short-term by consuming leaf litter and grass cover, this effect lasts only a few years in dry-sclerophyll vegetation (Fig4c, Appendix S2), (Price and Bradstock 2010). In the longer-term, high fire frequency can reduce litter decomposition rates by altering the soil microclimate, reducing the nitrogen content of litter, and/or by reducing the abundance of litter-dwelling and litter-foraging fauna (York 1999, Brennan et al. 2009, Penman and York

2010, Nugent et al. 2014), all of which could increase litter accumulation, and could explain the reduced bare earth cover we found on frequently burnt sites.

Pre-wildfire fire history also had effects on vegetation cover that were not modified by the 2003 wildfire. Increasing length of the pre-wildfire fire interval was associated with increasing understorey cover in forests, and increasing overstorey and midstorey cover in woodlands. Fire frequency also was positively associated with midstorey cover in woodlands. Both the associations between vegetation cover and fire history, and the differences in these associations between vegetation types are likely to be underpinned by differences in vegetation composition, and associated differences in the fire response traits of species (Bradstock and Kenny 2003, Clarke et al. 2015). For example, a long inter-fire interval in woodlands likely allows a greater proportion of plants (and particularly obligate seeding species) to reach heights where they enter the midstorey, while high fire frequency may favor particular midstorey species that survive fire, such as *Banksia serrata* (Bradstock and Myerscough 1988). Persistent effects of long-term fire history on vegetation structure, despite the occurrence of a large, severe wildfire, indicate that variability in the invisible fire mosaic may be an important factor in maintaining vegetation heterogeneity in our study system.

We also found evidence that wildfire overrode or erased the effects of previous fire history for some attributes of forest and woodland vegetation structure. In forest sites that were not burnt in 2003, high fire frequency sites had higher understorey cover and a lower density of woody stems, potentially due to a high cover of bracken (*Pteridium esculentum*), and low woody shrub density respectively. Bracken is an early successional species that responds positively to fire as it is able to regrow rapidly from underground rhizomes, compared with many shrub species that must regenerate from seed and so may be disadvantaged by frequent fire (Spencer and Baxter 2006, Foster et al. 2015). High bracken cover and low shrub density could also be maintained by macropod browsing in frequently burnt sites, as macropods have been found to preferentially feed on burnt forest sites, and to promote bracken dominance in our study area (Foster et al. 2015). In sites that burnt in the 2003 fire, we detected no association between fire frequency and understorey variables, a result that is not surprising given that the understorey strata would be most affected by the moderate intensity fire we recorded in this study. It is possible that the effects of fire frequency on understory cover would again become evident in burnt sites with increasing time-since fire, but our study did not include sufficient replication to test this three-way interaction (i.e. time*FS03*FF). High fire frequency sites in woodland vegetation also had a lower density of logs than rarely burnt sites, which is consistent with other studies from dry *Eucalyptus* forests (Spencer and Baxter 2006, Aponte et al. 2014) and elsewhere (Donato et al. 2016). This effect was evident only on unburnt sites, possibly because the 2003 fire temporarily increased the supply of logs on burnt sites by killing or injuring large shrubs and trees (Bassett et al. 2015).

Our finding that many aspects of the invisible mosaic influenced forest and woodland vegetation structure contrasts with the results of Haslem et al. (2016), who found the effects of long-term fire history on vegetation structure of foothills *Eucalyptus* forests was limited compared with the effects of the most recent fire (severity, time-since fire), and environmental variables (e.g. rainfall) (Haslem et al. 2016). The stronger effects of long-term fire history on forest vegetation structure that we recorded are likely related to the smaller spatial extent (limiting climatic influences) and lower fire severity of sites in our study, compared with Haslem et al. (2016). For example, no high severity fire was recorded in our forest sites, while much of the study area of Haslem et al. (2016) was forest that burnt in a very high severity fire. Biological legacies such as logs, dead trees and surviving plants are more likely to persist following moderate severity, than high severity fire (Collins et al. 2012, Lindenmayer et al. 2012, Bassett et al. 2015, Johnstone et al. 2016).

The strong influence of the invisible mosaic on vegetation structure that we detected is consistent with studies of fauna in our study area, which have found strong associations between long-term fire history (not just time-since fire) and the occurrence of many vertebrate species. For example, bird species richness was found to be negatively associated with high fire frequency (Lindenmayer et al. 2008b), while some species of small mammals have been positively associated with high fire frequency sites (Lindenmayer et al. 2016). Therefore, although many recent studies of vertebrate fauna from other Australian fire-prone ecosystems have emphasized the importance of retaining areas of long-unburnt vegetation (Kelly et al. 2015, Croft et al. 2016), our results suggest that this should not be done without reference to the invisible fire mosaic. Fire management decisions that maintain long-unburnt habitats, but reduce variation in fire intervals or fire frequency may consequently reduce variation in structural attributes such as ground cover (e.g. Fig 4c), and the cover of vegetation in the understorey (Fig 4b), midstorey (Figs. 5b, c), or overstorey (Fig. 5a), which can be important determinants of fauna species richness and composition (Stirnemann et al. 2015a, Stirnemann et al. 2015b)

Managing competing priorities following a large wildfire.

The occurrence of large, severe wildfires is both inevitable and unpredictable in many fire-prone vegetation types worldwide. While in some ecosystems, managers can have a substantial influence on the incidence and extent of wildfires (Finney et al. 2007, Boer et al. 2009), in other ecosystems (including our study system), fuel management techniques such as prescribed burning have only a very limited effect on wildfire occurrence (Price and Bradstock 2010, Price and Bradstock 2011, Price et al. 2015, Cary et al. 2016). In such areas, a key question for land managers is how to manage fire in the time between large wildfires to ensure that the overall fire regime promotes diverse plant and animal assemblages (Bradstock et al. 2005). The answer to this question will largely depend on the extent to which large wildfires alter patterns of vegetation and habitat structures established by the pre-existing fire mosaic. We found that while the 2003 wildfire had substantial effects on vegetation structures, both the long-term fire frequency, and the length of pre-wildfire fire interval (determined by the fire age of vegetation prior to the wildfire) also were strongly related to particular vegetation attributes. Therefore, to maintain a diversity of habitat structures for fauna, fire management following large wildfires should aim to both reinstate variability in the fire age of vegetation (which will also determine the fire intervals of the next large wildfire), and to retain variability in the long-term fire frequency across a landscape.

The occurrence of a single extreme fire event typically alters the scale of the spatial mosaic and substantially increases the proportion of vegetation in a recently burnt state. To retain variability in vegetation structures, post-wildfire management may become focused on the persistence of particular habitats, and especially mid-successional and long-unburnt patches (Robinson et al. 2014, Kelly et al. 2015, Croft et al. 2016). However, while ensuring that long-unburnt habitats are available both now and in the future is important, narrowing management to focus solely on an idealized fire-age mosaic is unlikely to provide the long-term ranges of structural variability necessary for diverse plant and animal assemblages (Clarke 2008). Identifying ways for long-unburnt vegetation patches to escape large wildfires, while promoting a landscape of spatially variable long-term fire history, should therefore be a top priority for applied ecologists and land managers alike.

Acknowledgements

Sachiko Okada, Geoffrey Kay, Darren Brown and Arthur McLeod assisted with floristic surveys. Wade Blanchard provided statistical advice. We thank Martin Fortescue, Nick Dexter, and Matt Hudson for assistance in many aspects of this project. We thank the Wreck Bay Aboriginal Community and Parks Australia (Booderee National Park) for supporting this project. This research was financially supported by the Australian Research Council, the Long Term Ecological Research Network and the National Environmental Science Program. P.S.B. was supported by an ARC DECRA Fellowship. D.B.L. was supported by an ARC Laureate Fellowship.

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/eap.xxxx/suppinfo

Data Availability

Data available from the Long-Term Ecological Research Network data portal: http://www.ltern.org.au/knb/metacat/ltern2.107.49/html

Tables

Table 1. Results of the linear mixed models testing how vegetation structural attributes were affected by the severity of the 2003 wildfire (FS03), their previous fire history (fire frequency – FF, pre-fire interval – FI), and their interaction over time. Shown is the top-ranked model, as well as ΔAICc between the base model (~FS03*time) and the top model (for models including fire frequency and / or fire interval). Overstorey cover and log density were not analyzed for heath vegetation due to zero values at most sites.

	Forest	Woodland	Heath
Overstorey cover	FS03*time	FS03*time + FI ΔAICc = 2.30	-
Midstorey cover	FS03*time	FS03*time + FF + FI ΔAICc = 3.70	FS03*time + FF ΔAICc = 1.09
Understorey cover	FS03*time + FS03*FF + FI ΔAICc = 2.33	FS03*time	FS03*time
Bare earth	FS03*time + FF ΔAICc = 6.96	FS03*time + FI ΔAICc = 1.51	FS03*time + FF ΔAICc = 0.24
Log density	FS03*time	FS03*time + FS03*FF ΔAICc = 8.85	-
Stem density	FS03*time + FS03*FF ΔAICc = 4.46	FS03*time	FS03*time + FS03*FI ΔAICc = 3.77

Figures

Figure 1. Map of Booderee National Park, showing (a) the distribution of major vegetation types, (b) the mosaic of fire frequencies (1957-2012) within the park, and (c) the mosaic of time-since fire prior to the 2003 wildfire (colored shading), overlaid with the 2003 fire extent (cross-hatching) and fires occurring between 2003 and 2012 (hatching).

Figure 2. Fire history in Booderee National Park, showing the proportion of the park area in each of five classes of time-since as of; 2003 (pre-wildfire), 2003 (post-wildfire), and 2012. Values are proportions of the total park area (excluding highly disturbed areas and lakes), as well as proportions of each of the three major vegetation types. Area calculations assume the full area within each fire perimeter was burnt.

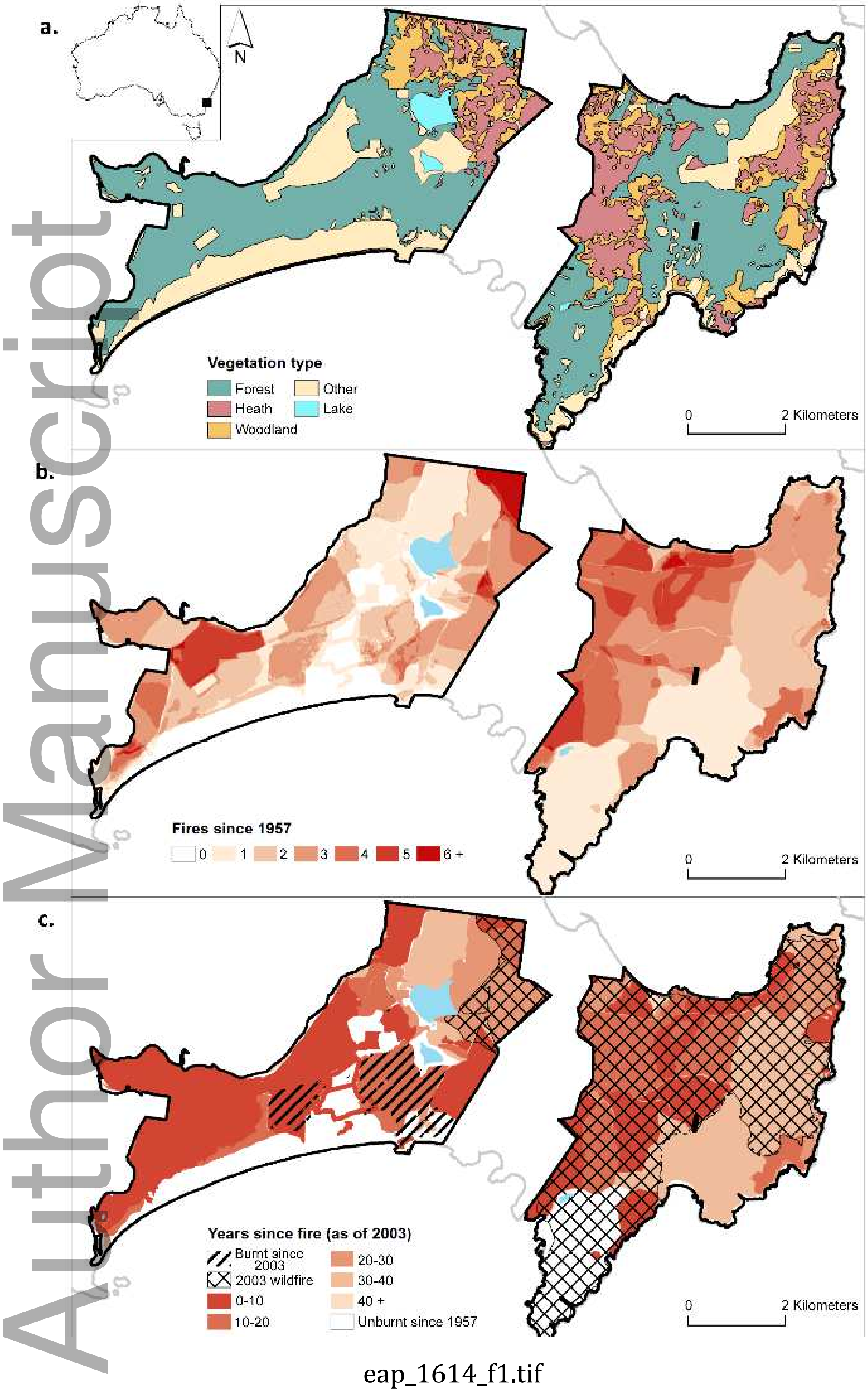
Figure. 3 Principal components analysis of structural variables for the three major vegetation types in Booderee National Park; (a) forest, (b) woodland and (c) heath. Sites (points) are grouped by year (one year post fire – 2004, and nine years post-fire – 2012), and the severity of the 2003 wildfire (unburnt, moderate [non-crowning or patchy fire], severe [crown fire]). Structure variable scores (blue text) are overlaid to illustrate group-variable associations (note variable scores have been plotted at a reduced scale for clarity). Axes show the proportion of variation in the structural variables explained by each principal component.

Figure 4. Prediction plots for top-ranked models for forest vegetation structure where the top model was at least two AICc lower than the base model. Plots show predicted values and 95% confidence bands for the minimum and maximum fire frequency (a, c, d), and the lower and upper quartiles for the length of the pre-wildfire fire interval (years since fire, panel b), for forest sites that were unburnt or moderately burnt in the 2003 wildfire (no forest sites burnt at high severity in the 2003 wildfire).

Figure 5. Prediction plots for top-ranked models for woodland vegetation structure where the top model was at least two AICc lower than the base model. Plots show predicted values and 95% confidence bands for the minimum and maximum fire frequency (b, d), and the lower and upper quartiles for the length of the pre-wildfire fire interval (years since fire, panels a, c), for woodland sites that were unburnt, moderately burnt or severely burnt in the 2003 wildfire.

Figure 6. Prediction plots for top-ranked models for heath vegetation structure where the top model was at least two AICc lower than the base model. Plots show predicted values and 95% confidence bands for the lower and upper quartiles for the length of the pre-wildfire fire interval (years since fire), for heath sites that were unburnt, moderately burnt or severely burnt in the 2003 wildfire.

[High resolution figure files are uploaded separately]



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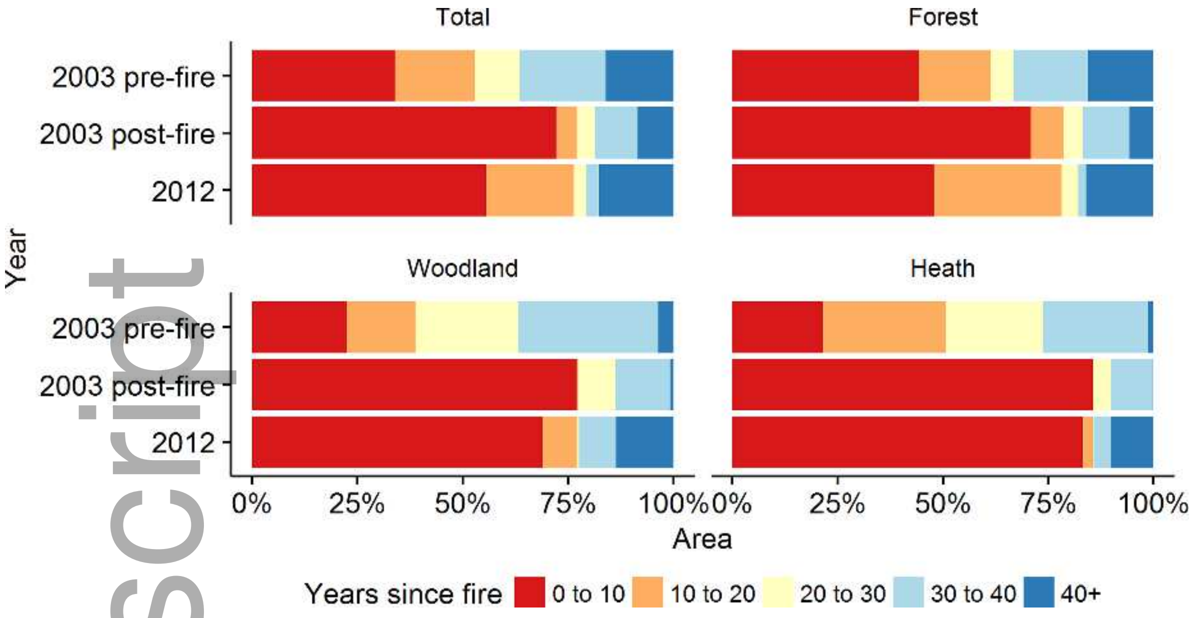

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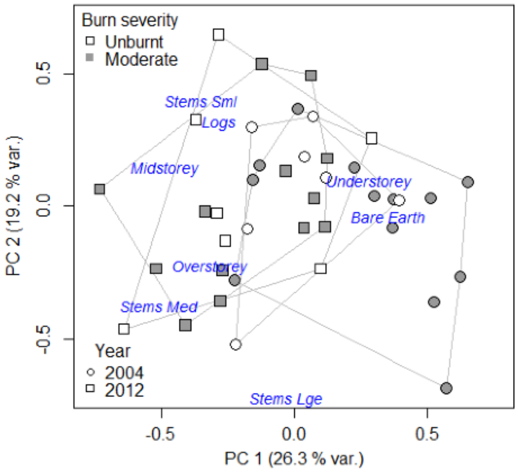
a. Forest



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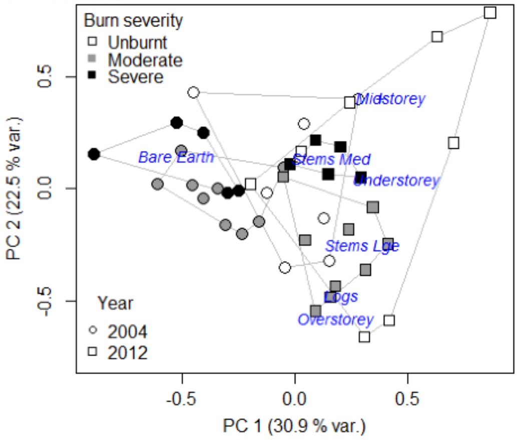
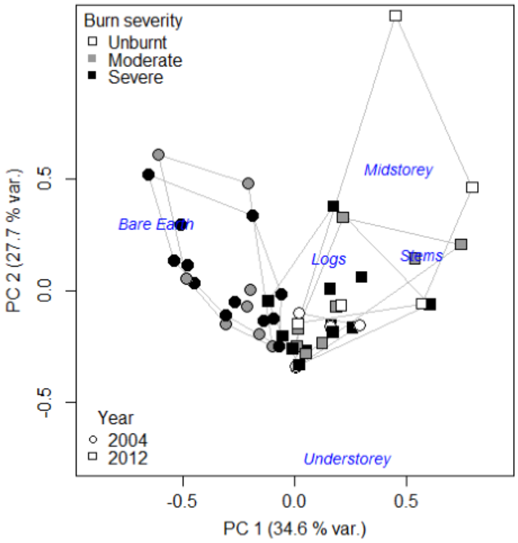


c. Heath



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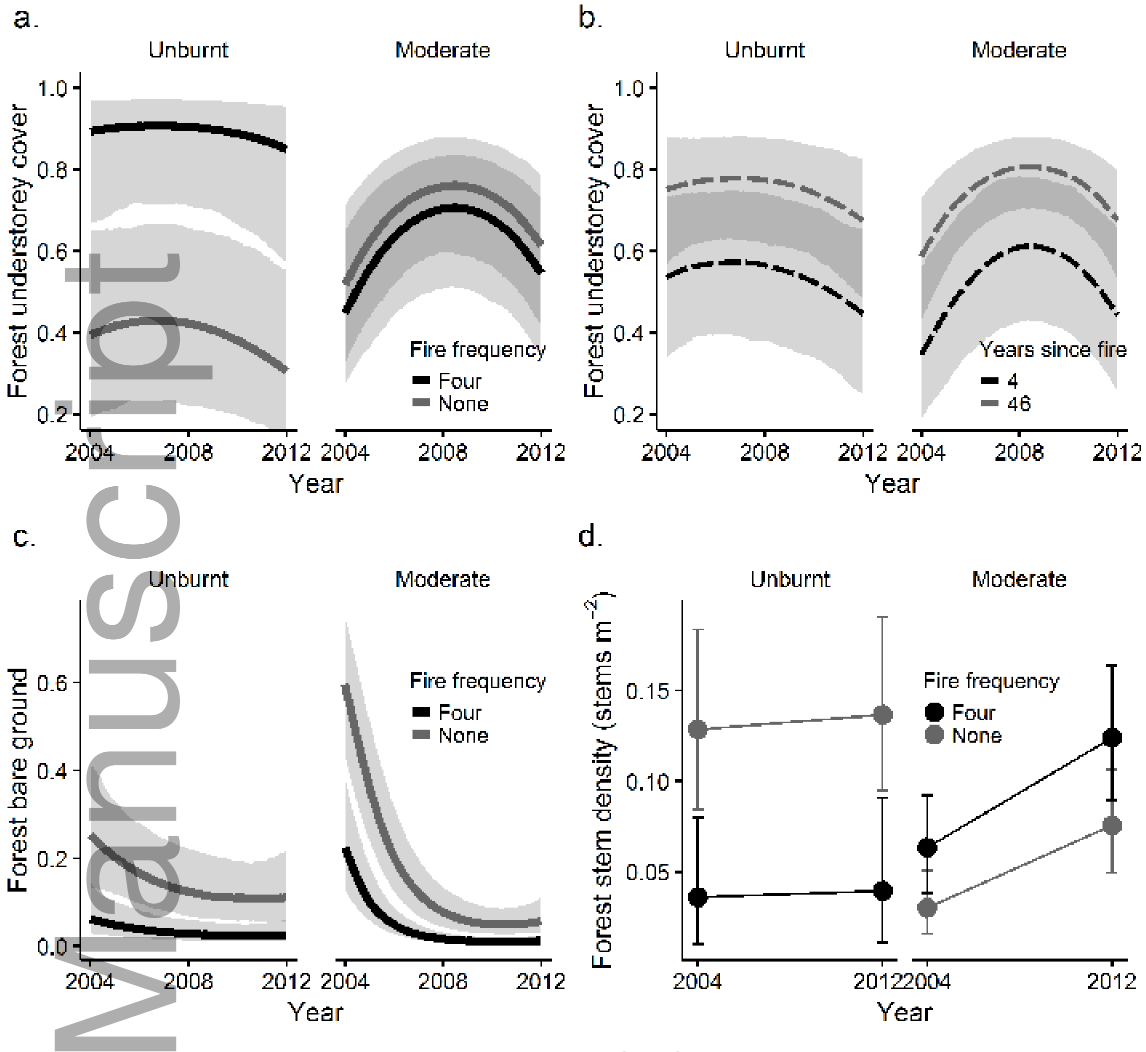

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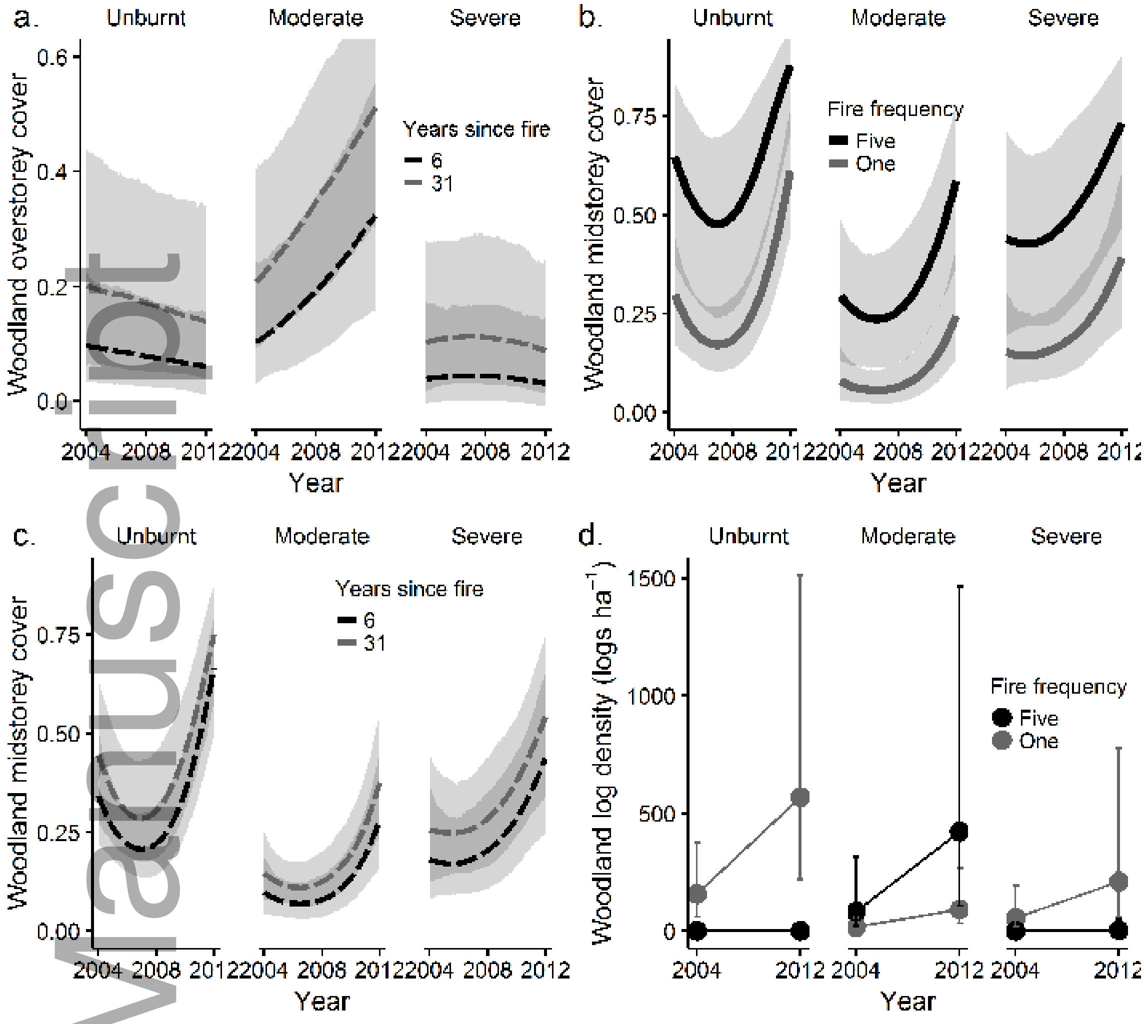

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