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Temporal trends in mammal responses to fire reveals the complex effects of fire regime attributes

Mammal responses to fire over time

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Abstract. Fire is a major ecological process in many ecosystems worldwide. We sought to identify which attributes of fire regimes affect temporal change in the presence and abundance of Australian native mammals. Our detailed study was underpinned by time series data on 11 mammal species at 97 long-term sites in southeastern Australia between 2003 and 2013. We explored how temporal aspects of fire regimes influenced the presence and conditional abundance of species. The key fire regime components examined were: (1) severity of a major

fire in 2003, (2) interval between the last major fire (2003) and the fire prior to that, and (3) number of past fires. Our long-term data set enabled quantification of the interactions between survey year and each fire regime variable: an ecological relationship missing from temporally restricted studies. We found no evidence of any appreciable departures from the assumption of independence of the sites. Multiple aspects of fire regimes influenced temporal variation in the presence and abundance of mammals. The best models indicated that six of the 11 species responded to two or more fire regime variables, with two species influenced by all three fire regime attributes. Almost all species responded to time since fire, either as an interaction with survey year or as a main effect. Fire severity or its interaction with survey year was important for most terrestrial rodents. The number of fires at a site was significant for terrestrial rodents and several other species. Our findings contain evidence of the effects on native mammals of heterogeneity in fire regimes. Temporal response patterns of mammal species were influenced by multiple fire regime attributes, often in conjunction with survey year. This underscores the critical importance of long-term studies of biota that are coupled with data sets characterized by carefully documented fire history, severity, and frequency. Long-term studies are essential to predict animal responses to fires and guide management of when and where (prescribed) fire or, conversely, long-unburned vegetation is needed. The complexity of observed responses highlights the need for large reserves in which patterns of heterogeneity in fire regimes can be sustained in space and over time.

Key words: fire regime variables; fire–time interaction; hurdle models; invisible mosaic; mammals; southeastern Australia; temporal responses to fire.

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INTRODUCTION

Fire is a major ecological process in many ecosystems globally (Bowman et al. 2009, Moritz et al. 2014). It can have significant impacts on the types and spatial patterns of vegetation cover (McKenzie et al. 2011, Wood et al. 2011), key ecological processes such as nutrient cycling and carbon storage (North and Hurteau 2011, Keith et al. 2014*b*), and on biodiversity (Andersen et al. 2003, Fontaine and Kennedy 2012, Banks et al. 2013, Lindenmayer et al. 2014*a*, Woinarski et al. 2015). Understanding the effects of fire on different ecosystem attributes is

therefore critical to improving land-management decisions, including how to best conserve biodiversity in fire-prone environments.

Quantifying the long-term impacts of fire regimes (sensu Gill 1975) on biodiversity is a critical part of improving land management. Such regimes are comprised of fire intensity, fire interval (frequency), severity, season of fire occurrence, and fire type (e.g. peat fire or aboveground fire). The fire regime is considered to become a property of a point in the landscape because repeated fires overlap so, eventually, each location may experience different combinations of these fire regime components (Gill and Allan 2008). Such fire regime factors are important because they are highly likely to influence various measures of biodiversity response such as temporal trends in populations of species over time (Bradstock et al. 2012, Di Stefano et al. 2013, Lindenmayer et al. 2014*a*). Indeed, this is the key premise of the "invisible mosaic hypothesis" developed by (Bradstock et al. 2005) in which, for example, species responses to contemporary habitat disturbances are dependent on the underlying historic spatial and temporal patterns of disturbance.

Despite the vast and rapidly expanding literature on the impacts of fire on biodiversity (e.g. Whelan 1995, Keeley 2009, Keeley et al. 2012, Berry et al. 2015*b*, DellaSala and Hanson 2015), it remains unclear which components of a fire regime are the most important ones influencing the temporal trajectories of biota in post-disturbance environments (Bradstock et al. 2012). This is a significant knowledge gap (Driscoll et al. 2010), as it prevents fire managers and biodiversity managers from determining which components of fire regimes are those to best manage as part of efforts to promote biodiversity conservation in fire-prone environments.

Knowledge gaps about the effects of fire regime components on biodiversity occur for several key reasons. A primary one is the relative rarity of long-term, time series studies that quantify the influence of multiple attributes of fire regimes on temporal changes in the occurrence of individual species and assemblages. For instance, several authors have proposed different temporal patterns of response following wildfire for populations of individual species, species richness, or assemblage composition (e.g. Gill et al. 1999, Whelan et al. 2002, Langlands et al. 2006, Nimmo et al. 2012, Pulsford et al. 2014). As examples, recent work on time-since-fire has proposed the existence of generalized response curves such as delayed, irruptive, and plateau-shaped curves (Nimmo et al. 2012, Watson et al. 2012). However, many of these projected temporal trends are based on cross-sectional or space-for-time information and not on

time series data. This is despite space-for-time studies having some shortcomings (Likens 1989, Lindenmayer et al. 2012) as such investigations often do not document long-term temporal changes in the presence and/or abundance of biota at the site, patch or other levels which makes it difficult to determine how such changes are influenced by covariates like key components of fire regimes.

A further shortcoming is that while there are many theories about species- and community-level responses to disturbance regimes (Farnsworth et al. 2014, Maravalhas and Vasconcelos 2014, Pulsford et al. 2014), these often use relatively simplistic representations of disturbance histories such as disturbance frequency or time since most recent fire. Indeed, many studies document temporal trends in change in response to just one factor; often time since the last fire (van der Ree and Loyn 2002, Saab et al. 2007), which is often considered the key descriptor in succession-based perspectives on disturbance ecology (Nimmo et al. 2012, Watson et al. 2012). However, as outlined previously, fire regimes are characterized by multiple factors in addition to the interval elapsed since the last conflagration, including timing (e.g. seasonality), and severity and frequency (Smucker et al. 2005, Keeley 2009, Fontaine and Kennedy 2012).

In the empirical investigation of Australian native mammals we report here, our primary objective was to answer the key question: Which fire regime attributes influence temporal changes in the abundance of individual mammal species? Our particular focus was on three key fire-related variables that have been found to be important in studies conducted elsewhere in different ecosystems. These were: (1) time since the last fire (e.g. van der Ree and Loyn 2002, Smucker et al. 2005, Saab et al. 2007, Watson et al. 2012), (2) fire severity (e.g. Kotliar et al. 2007, Fontaine and Kennedy 2012, Rush et al. 2012, Lindenmayer et al. 2014*a*), and (3) number of past fires: a reflection of the fire history at a site (e.g. Lindenmayer et al. 2008, Bradstock et al. 2012, DellaSala and Hanson 2015).

Our study occurred at Booderee National Park in southeastern Australia, and was underpinned by extensive data on long-term mammal abundance gathered for a wide range of species (from terrestrial rodents to arboreal marsupials) over more than a decade at 97 long-term monitoring sites. These detailed and long-term data sets on mammal abundance, coupled with detailed, fine-scaled, and relatively long-term fire history and severity data, make Booderee National Park an ideal ecosystem to quantify relationships between aspects of fire regimes and temporal patterns of change in mammal species richness and abundance.

We structured our study around three main fire variables. First, we examined interactions between three fire regime attributes and survey year. That is, interactions between: (1) fire severity × survey year, (2) number of fires × survey year, and, (3) time since last fire × survey year. We examined these interactions because the effects on biodiversity of fire-related variables also may change over time, for example, as the vegetation structure recovers and plant species composition changes (Pulsford et al. 2014). Second, we quantified the main effects of fire severity, number of fires, and time since last fire. Third, we explored non-fire effects on native mammals of vegetation type, spatial location of sites within the study area, and temporal effects.

Understanding and quantifying the temporal trajectories of biota is pivotal to developing well targeted conservation management interventions and in turn effective conservation programs (Caughley and Gunn 1996, Sodhi and Ehrlich 2010). Indeed, understanding long-term responses to disturbances is a fundamental part of determining how to best manage species and their habitats and ultimately to ensure that species, communities, and ecosystems are effectively conserved (Pulsford et al. 2014). The new insights from this study derived by examining the long-term effects of the different fire regime attributes should make it possible to better identify the mechanisms driving temporal changes in species responses and, in turn, develop better strategies to enhance biodiversity conservation in similar kinds of fire-prone landscapes in Australia (e.g. see Keith et al. 2014a) as well as other ecosystem around the world where fire is a major ecological process (Smith 2000, Keith et al. 2002, Friederici 2003, Pons and Clavero 2009, Swanson et al. 2011, Fontaine and Kennedy 2012, DellaSala and Hanson 2015).

METHODS

Study area

We conducted this study at Booderee National Park, a ~6500 ha area co-managed by the Wreck Bay Aboriginal Community and Parks Australia (a section of the Australian Federal Government's Department of the Environment). Booderee National Park is located 200 km south of Sydney and 20 km south of the city of Nowra on the south coast of New South Wales, southeastern Australia (approximate midpoint is 35.1489415° S, 150.6454625° E). The area has a temperate maritime climate with a mean annual rainfall of 1225 mm distributed relatively evenly over the year. Mean minimum and maximum air temperatures for January (summer) are 18–24°C and 9.5–15°C for July (winter). The geology of the study area is dominated by Permian (~260 million year old) sandstone sequences that form part of the southern boundary of the

extensive Sydney Basin. Pleistocene (<1.6 million year old) windblown sand dune systems cover the Permian sandstones in parts of Booderee National Park. Other geological formations include silt stones and Tertiary-aged alluvial deposits (Cho 1995, Lindenmayer et al. 2014*b*).

Booderee National Park has had a diverse history of human land use. There is evidence of long-term indigenous occupation in the park. Over the past century parts of the park (before it was gazetted as a reserve) were partially cleared for grazing by domestic livestock, exotic softwood plantation establishment, and the construction of infrastructure such as roads and (a now derelict) lighthouse (Lindenmayer et al. 2014*b*). The largest and most intensively disturbed areas are in the western section of the park, although significant natural regeneration as well as vegetation restoration efforts have occurred in this part of the reserve (Lindenmayer et al. 2014*b*).

Survey site design

To complete this study, we established 110 permanent long-term sites across the seven key vegetation types in our study area; warm temperate rainforests, forests, woodlands, heathlands, shrublands, swamps, and sedgelands (Appendix A). Of these vegetation types, two (sedgelands and swamps) were comparatively rare and the 13 sites supporting these kinds of vegetation were excluded from the study reported here.

We employed a stratified randomized and replicated process to distribute our 97 survey sites widely throughout Booderee National Park to limit the potential for geographic bias in our results (Fig. 1). We replicated sites within each vegetation type with a focus on replication of the most common classes (see Appendix A). In general, the number of samples was generally proportional to the total area occupied by each vegetation type.

We established a permanent 100 m long transect at each of our 97 sites. The choice of transect length was influenced by the substantial heterogeneity in vegetation cover at Booderee National Park where major changes in vegetation type often occur over a short distance. Transect lengths in excess of 100 m would have resulted in many transects spanning two vegetation types. We ensured that not only the length but also the location of survey transects were confined to a single vegetation type.

Fire in Booderee National Park

Booderee National Park has a well-documented fire history dating back several decades (Ingwersen 1977, Taws 1998) and this indicates that there have been 198 fires since 1968 with

two major large-scale (>1000 ha) conflagrations in that time, in 1973 and 2003. We focused this study on the effects of three fire regime variables: (1) Number of fires at a site from 1968 to 2003. Notably, no fires have occurred at any of our sites since 2003. These data were derived from extensive on-the-ground fire mapping of the location and size of each of the 198 fires known to have occurred in Booderee National Park since 1968 (Westgate et al. 2012). The majority of fires since 1968 have been small scale, low-intensity prescribed burns, but small uncontrolled (wild) fires also have been common. The median size of fires is 4.95 ha (Westgate et al. 2012). Some of our sites have remained unburned, whereas others have experienced up to five different fires since 1968 (Lindenmayer et al. 2014*b*; see Table 1A). (2) Fire interval corresponded to the time elapsed between the 2003 fire and the preceding fire at a site (Table 1B). (3) The severity of the 2003 fire. For the purposes of this study, our fire severity variable was based on a fire severity category assigned to each one of our 97 long-term sites using on-the-ground field observations of the direct effects of the 2003 fire on vegetation cover and completed within 10 d of the conflagration: (1) no fire (43 sites), (2) moderate-severity fire (36 sites) in which > 75% of the understory and midstory were burned but not killed and > 75% of the overstory remained unburned, and, (3) high-severity fire (18 sites) in which > 75% of the midstory was killed and > 75% of the overstory was burned. For the six sites where there was a mix of fire severities, we chose the one that was dominant. Table 1 contains summary statistics of the data on fire severity, number of fires at a site and the time since fire at a site prior to 2003.

Field surveys of terrestrial and scansorial mammals

Each of the 97 sites in our study consisted of star picket markers set at 0, 20, 40, 60, 80, and 100 m points along the transect. We recorded the coordinates of each transect using a global positioning system facilitating the recording of these location data in a GIS database constructed for Booderee National Park. The trapping infrastructure we established at each site was as follows: We placed an Elliott aluminum box trap ($10 \times 10 \times 30$ cm; Elliott Scientific Equipment, Upwey, Victoria, Australia) at 10-m intervals along the transect. We placed a small wire cage trap ($20 \times 20 \times 50$ cm) at 20-m intervals along the transect. We placed a large wire cage trap ($30 \times 30 \times 60$ cm) at the 0 and 100 m points of the transect.

Our trapping protocols at each site involved opening Elliott traps and cage traps for four consecutive days in 2003 and three consecutive days in subsequent surveys years. We baited all traps with a mixture of peanut butter and rolled oats. Elliott traps and cage traps in which an

animal had been captured were wiped clean, re-baited, and re-positioned where the initial capture had taken place. We completed trapping surveys of our 97 sites in the summer of all years between late 2003 (immediately after the fire in that year) and 2013. Not all sites were surveyed in all years due to logistical issues associated with trapping effort (see Appendix C: Table C1).

Field surveys of arboreal marsupials

We counted arboreal marsupials by repeated spotlighting along each permanent transect established at each of the 97 sites in our study. In any given survey year, each transect was surveyed twice by a different observer on a different night. We did not undertake spotlighting on nights of poor weather (rain, high wind, fog, or heavy cloud cover). We completed spotlighting surveys in each of eight years over a 10-year period: 2003, 2004, 2005, 2006, 2007, 2009, 2011, and 2013.

Species targeted for detailed analysis

Our study included a suite of native mammal species in five broadly different groups characterized by marked differences in life history and other attributes (Hume 1999, Tyndale-Biscoe 2005, Breed and Ford 2007; see Appendix B) including body size, diet, mating system, fecundity, longevity, social organization, habitat requirements, and other characteristics. We focused this study on 11 of the more commonly recorded species of mammals that were representative of six broad groups of taxa. These were: terrestrial rodents (bush rat *Rattus fuscipes*, swamp rat *R. lutreolus*, and eastern chestnut mouse *Pseudomys gracilicaudatus*), terrestrial marsupial omnivores (long-nosed bandicoot, *Perameles nasuta*), terrestrial herbivorous macropods (eastern grey kangaroo *Macropus giganteus* and black wallaby *Wallabia bicolor*), scansorial marsupial carnivores (brown antechinus *Antechinus stuartii*), arboreal marsupial omnivores (sugar glider *Petaurus breviceps*, common ringtail possum *Pseudocheirus peregrinus*, and common brushtail possum *Trichosurus vulpecula*), and arboreal marsupial folivores (greater glider *Petauroides volans*).

Notably, invasive mammals such as the house mouse (*Mus musculus*), black rat (*R. rattus*), and the feral cat (*Felis cattus*) and the red fox (*Vulpes vulpes*) are extremely uncommon in Booderee National Park. The latter species in particular is targeted by an intensive poison baiting program that has been conducted throughout Booderee National Park for more than a decade (Lindenmayer et al. 2014*b*).

Statistical analyses

We used data on the number of species recorded at a given site in a given survey year to construct an aggregate measure of overall mammal species richness. Given the different sampling years for trapping and spotlighting (see previous section), we computed species richness separately for each method of data collection. We modeled mammal species richness based on trapping surveys using a Poisson distribution. For spotlighting data, we analyzed mammal species richness data obtained using a hurdle model due to an excess of zero counts (Welsh et al. 1996; see following section). We then constructed hurdle models, again due to excess zeros, for the presence/absence and the conditional abundance (i.e. the abundance of a given species at a site given its presence at a site) of 11 species for which we had sufficient data (>30 detections overall) to complete statistical modeling.

A potential issue in our analyses was spatial dependence in animal responses. We completed formal analyses to test for such effects using the variog function from the R package geoR (Ribeiro and Diggle 2001, Diggle and Ribeiro 2007) to construct empirical estimates of the variogram to assess the spatial dependence of the residuals from each of our final models. We assessed the spatial dependence for each year separately. Examination of the empirical variograms showed no evidence of any appreciable departures from the assumption of independence of the sites beyond sampling fluctuations.

We modeled the effects of three fire regime variables. These were: (1) the last inter-fire interval (the time between the 2003 fire and the preceding fire at that site); (2) the number of fires that have occurred at a given site over the past 35 years (prior to December 2003); and (3) the severity of the 2003 fire. We also modeled interactions between these three fire regime variables and survey year. In addition, we modeled the effects of vegetation type as a categorical variable with four levels (one for each vegetation type; see Appendix A). Finally, we analyzed the effects of a variable corresponding to the spatial location of a site within Booderee National Park (which we have termed "easting"). This variable attempted to account for a spatial gradient in human modification in which areas subject to the most intensive past human disturbances are those located in the western section of Booderee National Park.

We used Akaike Information Criterion (AIC) to guide model selection on the logistic regression and conditional abundance parts of the hurdle models separately. We chose AIC over the Bayesian Information Criterion (BIC) at this preliminary stage to allow the inclusion of more

potential predictors in the model. Due to the more stringent inclusion criteria with larger sample sizes, BIC tends to favor simple models compared to AIC. We used the glmer function from the lme4 package (Bates et al. 2014) to model the logistic (presence/absence) component. We employed the glmmadmb function from the glmmADMB package (Fournier et al. 2012, Skaug et al. 2013) to fit the conditional abundance model. We modeled the conditional abundance part of the model using a zero-truncated negative binomial distribution where possible and where convergence was an issue, we used Poisson distribution. Both models included site as a random effect.

We employed the package MuMIn (Barton 2014) to explore all possible subsets of a model with the following terms: vegetation type (warm temperate rainforest, forest, heathland, shrubland, and woodland), fire severity (unburned, moderate, and severe), a linear effect of: survey year, time since fire prior to 2003, the number of fires prior to the 2003 fire, easting, and a quadratic effect of survey year and time since fire prior to 2003. We included interactions between survey year and the following variables: fire severity, time since fire prior to 2003, and number of fires prior to 2003. Only the best model component was retained for each model component (presence and conditional abundance), to avoid having too many potential models in the second stage of the analysis.

To account for potential correlation between the random effects from the presence/absence and conditional abundance model components, we used the MCMCglmm function from the MCMCglmm package (Hadfield 2010). Both components had random effects for site and both components allowed for over-dispersion relative to the binomial and Poisson distribution via an individual-level random effect. The MCMCglmm package fits the hurdle model via Markov Chain Monte Carlo (MCMC) techniques and gives samples from the posterior distribution. We chose uninformative but proper priors for the fixed effects components and minimally informative but proper priors for the variance components. Specifically, we used multivariate normal priors for the regression parameters and inverse Wishart distributions for the variance components. The combined model consisted of the best AIC from the presence and conditional abundance portions of the model.

The hurdle model parameters are summarized by the posterior mean, 95% credible intervals, and Btail, which gives the fraction of the posterior distribution that is to the left or the right of zero if the posterior mean was greater or less than zero, respectively. Small values of

Btail indicate support for nonzero parameter values, that is, posterior distributions that are shifted away from zero. The parameters from the presence and conditional abundance components of the hurdle more are reported on the log odds ratio and log scale respectively.

We also assessed the residuals from each component of the hurdle models for evidence of nonlinearities over and above specified by our models using generalized additive models (Wood 2006). In all cases there was no evidence of any need to move to a more complicated functional form.

<div align="center">RESULTS</div>

We recorded 13 species of native mammals in our repeated trapping surveys and 15 species of mammals in our repeated spotlighting surveys between 2003 and 2013, including eight species which were observed using both detection methods (see Appendix C). In this section, we first present results for interactions between fire regime variables and survey year. We then outline results for main effects of fire regime variables (i.e. where there was no significant interactions between fire regime variables and survey year). We conclude with a brief description of findings for those response variables where there was no evidence of important effects of fire regime variables.

Interactive effects: fire severity × year

We found fire severity by year interactions for the presence component of the hurdle model for four species and one species also had a fire severity by year interaction for the conditional abundance component of the model. The presence component of the hurdle model for the bush rat contained strong evidence of an interaction of fire severity and survey year (unburned vs. moderate, Btail < 0.001, unburned vs. severe, Btail < 0.001, moderate vs. severe, Btail = 0.048; see Fig. 2A; Appendix D, and Appendix E: Table E1). The presence of the bush rat decreased gradually on the unburned sites over time, while the occurrence of individuals at sites that were burned at moderate and high severity by the 2003 fire exhibited a period of rapid decline followed by later recovery. The moderately burned sites reached their minimum occurrence rate in 2009 and the severely burned sites reach theirs in 2010.

We found that both presence/absence and conditional abundance model components for the brown antechinus (see Fig. 2B; Appendix D, Appendix E: Table E2) contained strong evidence of a fire severity by survey year interaction. Both components have strong evidence of a difference between moderately burned and unburned sites (presence, Btail < 0.001; conditional

abundance, Btail = 0.001). They also contained evidence of a difference between severely burned and unburned sites (presence, Btail = 0.018; conditional abundance, Btail < 0.001). The difference between moderate and severely burned sites was mixed (presence, Btail = 0.310), conditional abundance, Btail = 0.030). Populations of the brown antechinus on moderate and severely burned sites exhibited a stable presence trajectory, while on unburned sites there was a decline in animal presence over time. The conditional abundance of the brown antechinus (see Fig. 2C; Appendix D, and Appendix E: Table E2) also appeared to be decreasing on unburned sites over time. By contrast, the abundance of the brown antechinus on burned sites appeared to be increasing with time (though sites subject to moderate- and high-severity fire in 2003 have slightly different trajectories).

The model for the presence component of the model for the long-nosed bandicoot (see Fig. 2D; Appendix D, and Appendix E: Table E3) contained evidence of an interaction between fire severity and survey year (unburned vs. moderate, Btail = 0.126, unburned vs. severe, Btail = 0.019, moderate vs. severe, Btail = 0.001). Populations on sites subject to either moderate severity fire or which remained unburned in 2003 exhibited a monotonically decreasing probability of presence, while the severely burned sites experience an increased occupancy 3–4 years post the 2003 fire followed by a subsequent decline.

The presence component of the hurdle model for the swamp rat (see Fig. 2E; Appendix D, and Appendix E: Table E4) contained evidence of an interaction between fire severity and survey year (unburned vs. moderate, Btail = 0.052; unburned vs. severe, Btail < 0.001; moderate vs. severe, Btail = 0.036). The probability of presence of the swamp rat on unburned sites was characterized by a slightly decreasing trend. On sites subject to moderate-severity fire, there was evidence of an increase in the probability of presence of the species until ca. 2007 before declining thereafter. In the case of sites subject to high fire severity, the presence of the Swamp Rat peaked in ca. 2011 and declined thereafter.

Interactive effects: number of fires × year

We found a number of fires by year interaction for the presence component of the hurdle model for three species and another species experienced an interaction for the conditional abundance portion of the model. The conditional abundance component of the hurdle model for the bush rat (see Fig. 3A; Appendix D, and Appendix E: Table E1) contained evidence of a marginal effect of an interaction between the number of fires prior to 2003 and survey year (Btail

= 0.028). There was a quadratic effect of survey year for bush rat. However, the interaction with number of fires affects the linear component, hence the relationships remain quadrate (see Fig. 3A). Sites experiencing fewer fires were characterized by a higher initial conditional abundance of the species compared to the sites experiencing more fires. However, this pattern was reversed by the end of our study.

We identified strong evidence of an interaction between the number of fires prior to 2003 and survey year for the probability of presence of the long-nosed bandicoot (see Fig. 3B; Appendix D, and Appendix E: Table E3; Btail = 0.003). The presence of the species was not initially influenced by the number of fires at a site, but the effect of this fire regime variable became apparent after 2005. There was a higher probability of presence of the long-nosed bandicoot on sites that experienced more fires prior to 2003.

The presence component of the hurdle model for the swamp rat (see Fig. 3C; Appendix D, and Appendix E: Table E4) was characterized by marginal evidence of an interaction between number of fires and survey year (Btail = 0.036). The interaction indicated that the presence of the species was initially influenced by the number of past fires at a site but this effect had disappeared after 2010. There was a higher probability of presence of the swamp rat on sites that experienced more fires prior to 2003.

The conditional abundance component of the hurdle model for the eastern chestnut mouse (see Fig. 3D; Appendix D, and Appendix E: Table E5) contained a marginal evidence of an interaction between the number of fires and survey year (Btail = 0.023). The peak in conditional abundance occurred earlier on sites that experienced a larger number of fires (third quartile of fires) compared to the peak in abundance observed on sites experiencing a smaller number of fires (first quartile).

The model for the probability of presence of the common ringtail possum (see Fig. 3E; Appendix D, and Appendix E: Table E6) contained strong evidence of an interaction between the number of fires prior to 2003 and survey year (Btail = 0.002). Initially, there was a positive association between the number of fires experienced at a site and the probability of presence of common ringtail possum, but this effect diminished after ca. 2006.

Interactive effects: time since fire × year

We found a time since fire by year interaction for the presence component of the hurdle model for two species and a model for another species contained an interaction for the

conditional abundance portion of the model. The presence component of the hurdle model for the common brushtail possum (see Fig. 4A; Appendix D, and Appendix E: Table E7) contained marginal evidence of an interaction between time since fire and year (Btail = 0.062). Initially, the probability of presence of the species was highest on sites characterized by a relatively recent last fire. However, this effect had lessened by the end of the study (2013).

We found strong evidence of a time since fire by survey year interaction for the eastern chestnut mouse (Btail = 0.002; see Fig. 4B; Appendix D, and Appendix E: Table E5). The peak in conditional abundance occurred earlier on sites that experienced a longer time since fire (third quartile of fires) compared to the peak in abundance observed on sites experiencing a shorter time since fire (first quartile).

The presence component of the hurdle model for the common ringtail possum (see Fig. 4C; Appendix D, and Appendix E: Table E6) contained evidence of an interaction between time since fire and survey year (Btail = 0.006). Initially, the species was less likely to occur on those sites that had burned relatively recently. However, this pattern was reversed after 2005.

Main effects: fire severity

Two species experienced a main effect of fire severity for the presence component of the model, and two different species had a main effect for the conditional abundance portion of the model. We identified a marginal effect of fire severity on the conditional abundance of the bush rat. Sites subject to moderate severity fire supported a lower conditional abundance of the species than unburned sites (Btail = 0.023), but there were no differences between severely burned and unburned sites (Btail = 0.131) and between moderate and severely burned sites (Btail = 0.342). In the case of the swamp rat, the conditional abundance of the species was higher on severely burned sites than moderately burned sites (Btail = 0.049), although there were no significant differences in conditional abundance between moderate and severely burned sites and unburned sites (Btail = 0.202 and Btail = 0.184 respectively). There was a higher probability of presence of the eastern chestnut mouse on severely burned sites compared to moderately burned sites (Btail = 0.044). Notably, we excluded unburned sites from the analysis of eastern chestnut mouse as the species was virtually absent from areas that had been unburned in the 2003 fires. Finally, the probability of occurrence of the common ringtail possum was lower on sites subject to moderate-severity fire (Btail = 0.002) and high-severity fire (Btail = 0.006) than unburned

sites, however, there was no significant difference in conditional abundance between sites subject to moderate- and high-severity burns (Btail = 0.274).

Main effects: number of fires

Four species had a main effect of the number of fires for the conditional abundance portion of the model. We identified marginal negative effects of the number of fires over the 35 years prior to 2003 at a site on the conditional abundance of the swamp rat (Btail = 0.042) and the common ringtail possum (Btail = 0.017). By contrast, there was a weak positive relationship between the number of fires prior to 2003 at a site and the conditional abundance of the eastern grey kangaroo (Btail = 0.152).

Main effects: time since fire

Four species experienced a quadratic effect of time since fire on the presence component of the hurdle model, and three species experienced a linear effect of time since fire on the presence component. One species experienced a quadratic effect of time since fire on the conditional abundance component of the hurdle model and three species had linear effect of time since fire.

There was a marginally positive association between time since fire and the presence of both the long-nosed bandicoot (Btail = 0.054) and the conditional abundance of the species (Btail = 0.023). By contrast, time since fire had a strong negative effect on both the presence of swamp rat (Btail = 0.002) and the conditional abundance of the species (Btail = 0.002). We also identified marginally negative relationships between the time since fire prior to 2003 and the conditional abundance of common ringtail possum (Btail = 0.030) and the presence of eastern grey kangaroo (Btail = 0.065).

We characterized the quadratic effects of time since fire by the quadratic coefficient as its sign determines whether or not the quadratic reaches a maximum (negative coefficient) or minimum (positive coefficient). We termed these two response patterns concave downward and upward, respectively. We also provide a rough estimate as how long ago minimum or maximum occurs.

Time since fire has a concave downward relationship with the presence of bush rat reaching a maximum for sites that burned ~38 years ago, prior to the final year of our study (2013; Btail < 0.001). Time since fire also has a concave downward relationship with the conditional abundance of bush rat reaching a peak abundance for sites burned ~34 years ago

(Btail = 0.048). Time since fire as a concave downward relationship with the presence of eastern chestnut mouse reached a peak on sites burned ~30 years ago (Btail = 0.150. Time since fire has a concave upward relationship with the presence of sugar glider and attained a minimum presence for sites burned ~27 years ago (Btail = 0.114). There was a concave downward relationship between time since fire and the presence of greater glider, reaching a maximum for sites that were burned ~42 years ago (Btail = 0.002). Finally, there was a concave upward relationship between time since fire and trapping species richness, reaching a minimum for sites burned in 1968 (Btail = 0.134).

Other effects: vegetation type

The models for nine of the 11 species we analyzed contained evidence of broad vegetation type effects on one or both components of the hurdle model with the exception of the long-nosed bandicoot and sugar glider. Also of note was that there was an absence of vegetation effects for species richness derived from trapping. More details can be found in the model summary tables given in Appendix E.

Other effects: spatial location

We identified spatial location effects within Booderee National Park for almost all of the species analyzed in this study; as reflected by evidence of relationships with the covariate "easting" in presence and/or conditional abundance components of the hurdle models (see Appendices D and E).

Seven species were characterized by an association with the easterly location within Booderee National Park. The presence of the bush rat (Btail < 0.001), brown antechinus (Btail < 0.001), long-nosed bandicoot (Btail < 0.001), swamp rat (Btail < 0.001), eastern chestnut mouse (Btail < 0.001), and common ringtail possum (Btail = 0.078) were all lower on sites located in the easterly part of Booderee National Park compared to the westerly section of the reserve. The conditional abundance of the bush rat (Btail < 0.001), brown antechinus (Btail < 0.001) and eastern grey kangaroo (Btail = 0.008) also were negatively associated with the variable easting. We also identified similar negative relationships between easting and trapping derived mammal species richness (Btail = 0.010) and spotlighting derived mammal species richness (Btail = 0.070). Only the presence of the common brushtail possum at a site was positively associated (Btail < 0.001) with easterly location within Booderee National Park.

Other effects: temporal trends

Five species experienced a quadratic effect year on the presence component of the hurdle model. Three species experienced a quadratic effect of year on the conditional abundance component of the hurdle model and three species had a linear effect of year. We found strong evidence of a decrease in conditional abundance over time of the common ringtail possum (Btail = 0.015) and greater glider (Btail = 0.010). We also identified a similar trend for the common brushtail possum although the evidence for this relationship was weak (Btail = 0.170). The models for species richness derived from trapping and spotlighting both contained strong evidence of a decreasing trend with survey year (Btail = 0.020; Btail = 0.001).

We identified quadratic relationships between survey year and several mammal species for both of the hurdle models. We report roughly when the peak occurs and give an indication of how important the quadratic term is for that given species.

We found evidence of a concave downward relationship between survey year and conditional abundance for the long-nosed bandicoot (peak 2005, Btail=0.001) and the swamp wallaby (peak 2011, Btail = 0.026). In addition, the probability of occurrence of five species was characterized by a concave downward relationship with survey year: eastern chestnut mouse (peak 2009, Btail < 0.001), swamp wallaby (peak 2009, Btail = 0.007), eastern grey kangaroo (peak 2007, Btail < 0.001), sugar glider (peak 2009, Btail = 0.002), and greater glider (peak 2003, Btail = 0.007).

DISCUSSION

Fire is a key ecological process in many ecosystems worldwide (Bowman et al. 2009, Keeley et al. 2012) and it can have profound impacts on biodiversity (Smith 2000, Fontaine and Kennedy 2012, Berry et al. 2015*b*, DellaSala and Hanson 2015, Woinarski et al. 2015). Numerous studies have documented the impacts of a single fire event on biota, but much remains to be learned about the impacts of a sequence of fires and hence the importance of key fire regime attributes (Bradstock et al. 2005, 2012, Driscoll et al. 2010). We used long-term data on mammal occurrence together with fine-scaled fire history and severity information to address the question: Which fire regime attributes influence temporal changes in the abundance of suite of individual mammal species? We found evidence of interspecific differences in temporal responses to both the main effects of the fire regime variables, as well as interactions between these variables and time (viz: survey year). This suggests the answer to our key question is

complex and multi-faceted. Our key findings were: (1) Multiple fire regime attributes were important for several species. For example, six of the 11 species responded to more than one fire regime attribute. In addition, all three fire regime attributes featured in models for most terrestrial rodents as well as the long-nosed bandicoot (Table 2). (2) Each fire regime attribute was important but their effects manifested differently for each species (Table 2). Further complexity emerged through differences in the presence/absence versus the conditional abundance components of the hurdle models constructed for each mammal species analyzed in this study (see Appendices D and E). (3) The effects of the fire regime attributes also varied over time, as illustrated by the interaction between fire attributes and survey year for many species (Table 2). Thus, for example, a species response to a particular fire variable observed early in our study either dissipated later in the investigation or the initial trend pattern was later entirely reversed (e.g. Fig. 3). (4) Fire severity and its interaction with survey year or as a main effect was important for most terrestrial rodents, the long-nosed bandicoot and the common ringtail possum. (5) The number of fires at a site was significant in models for most species of small terrestrial mammals (except the eastern chestnut mouse) as well as the long-nosed bandicoot and the common ringtail possum, with a marginal (main) effect for the eastern grey kangaroo (see Appendices D and E). (6) Almost all species responded to time since fire prior to 2003, either as an interaction with survey year (Fig. 4) or as a main effect (see Appendices D and E). (7) There were effects on the probability of presence or conditional abundance of many species associated with underlying vegetation type and the spatial location of sites within the study area. (8) There were marked changes in temporal patterns in probability of presence or conditional abundance of many species that did not appear to be directly related to fire.

Taken together, our findings underscore a level of complexity of mammal responses to fire regimes that have rarely been quantified. They also suggest that heterogeneity of fire regimes per se may be important and indicate that fire and biodiversity management in fire-prone environments has particular challenges that must be met to adequately address the complexity of biotic responses to fire. More in-depth discussion of fire regime effects and their implications for management are given in the remainder of this study.

Fire effects

We identified a wide range of fire-associated temporal response patterns (see Figs. 3–5). Indeed, many species exhibited either or both linear and/or quadratic temporal change patterns

for the presence/absence and/or the conditional abundance components of the hurdle models (Appendix E). It also highlighted a greater range of temporal patterns than hypothesized to occur in earlier studies of fire effects on biodiversity (e.g. Gill et al. 1999) and those following fire in Mallee-dominated environments in inland southern Australia (Nimmo et al. 2012, Watson et al. 2012).

An unexpected outcome of our work was that many species responded to two or more key fire regime variables, with the models for some species featuring all three fire regime variables (Table 2). Moreover, these responses to different multiple fire regime variables were often in different (positive or negative) directions for different species (summarized in Table 2) suggesting that the heterogeneity of fire regimes per se may be important for landscape-level species richness, beyond for example, heterogeneity in other factors (like the spatial patchiness of fire events) that have been identified in the past (Parr and Andersen 2006, Farnsworth et al. 2014, Maravalhas and Vasconcelos 2014). Previous research at Booderee National park has indicated that the likely underlying drivers of heterogeneity of fire regimes in Booderee National Park include topography, topographic wetness and aspect (Stirnemann et al., *in press*).

Our analyses contained evidence of linear and/or quadratic effects of time since fire prior to 2003 and its interaction with survey year (Fig. 5). The inter-fire interval between the last fire and the preceding one influences the biological legacies (sensu Franklin et al. 2000) left after the most recent fire. This, in turn, can affect habitat quality for particular species. As an example, (Pereoglou et al. 2011) showed burned old growth heathland supported many collapsed shrubs that provided suitable nest sites for the eastern chestnut mouse but such structures were largely absent from recently burned young heathland.

Our study contained evidence of the effects of fire severity on many individual mammal species but its impacts changed over the 10+ year duration of our study. Thus, temporal trajectories of a species on a site between 2003 and 2013 were often affected by the severity of the fire that occurred on that site in 2003. The reasons for these key findings remain unclear but they may be relate to either the recovery of vegetation following the fire, and hence the suitability of post-fire habitats for occupancy by particular species. They also may be linked with the time required for species to recolonize a site after the 2003 fire if it had been locally extirpated by the conflagration a decade earlier.

Our analyses contained evidence of prolonged fire history effects on the temporal trajectories of a number of species. For example, the conditional abundance of bush rat peaked on sites burned ~34 years ago. In another example, the probability of presence of the greater glider reached a maximum value on sites that were burned ~42 years previous to the 2003 fire. These findings suggest a high level of potential sensitivity of such species to fire and, in turn, underscore the value of areas that have been long unburned areas as suitable habitat. The importance of long-unburned areas for biodiversity have been underscored in a range of other studies in a number of studies in other ecosystems around the world (e.g. (Woinarski et al. 2004, Nimmo et al. 2012, Berry et al. 2015*b*). At the individual species level, work by other researchers (e.g. Lunney et al. 1987, Berry et al. 2015*a*) on species such as the bush rat and the greater glider suggest that they are potentially sensitive to the effects of fire and areas of long unburned vegetation can be important for the species.

Our investigation was characterized by an array of often highly contrasting temporal patterns among species, even among closely related taxa such as the bush rat and swamp rat. This suggested there were no clear links between fire responses and life history attributes. Conversely, the eastern chestnut mouse and the black wallaby exhibited similar linear and quadratic temporal effects, but are characterized by few common life history attributes (Appendix B).

A key part of the methodology underpinning this study was to employ hurdle models to explore a suite of factors influencing both the presence/absence of species at a particular site and then the conditional abundance of a species at site given its presence. In essence, the two components of the hurdle models therefore contain information corresponding to species occurrence (distribution) and species abundance. Typically, the presence/absence and abundance components of the models were characterized by a different set of significant explanatory variables, suggesting that different factors and processes may affect species distribution and species abundance. One plausible ecological explanation for these differences is that more or different site attributes may be required to support pairs, groups or colonies of interacting animals (such as those that are breeding) than sites where single individuals of the same species occur (Zanette et al. 2000, Morrison et al. 2006).

We note that the majority of the 198 fires recorded in our study site area since 1968 have been small-scale conflagrations (median size of 4.95 ha; Westgate et al. 2012). Different results than those reported here may occur if the frequency of larger fires is increased. Indeed, other

studies have indicated that the frequency of large fires can have a significant impact on biodiversity, including groups such as small mammals (Lawes et al. 2015).

Vegetation, spatial, and temporal effects

We found that several species responded strongly to the type of vegetation at a site with arboreal marsupials like the greater glider and the common brushtail possum more likely to occupy sites in rainforests, forests, and woodlands than heathland or shrubland. This result was unsurprising given their requirements for large trees that provide hollows in which to nest (Gibbons and Lindenmayer 2002) and foraging sites; especially for the greater glider which is a specialist arboreal folivore with a diet comprised almost entirely of eucalypt leaves (Hume 1999). Neither species exhibited conditional abundance responses to vegetation type, likely because they do not occur in treeless habitats such as those dominated by shrubland and heathland. Consistent with the known habitat requirements of the eastern chestnut mouse (Fox 1982, Pereoglou et al. 2011), we found that the species was more likely to occupy heathland and woodland sites than our survey sites dominated by rainforest, forest, and shrubland. One of our target species (the brown antechinus) was ubiquitous across BNP as reflected by a paucity of vegetation type effects for the presence/absence component of the hurdle model for this animal (see Appendix C). However, the conditional abundance of the brown antechinus was highest in heathland, possibly a reflection of the high levels of vegetation cover typical of environments preferred by this species (Catling and Burt 1995).

We identified spatial location effects for several species, as reflected by evidence for the importance of the variable "easting" in the hurdle models. Species richness and either species occupancy of sites or conditional abundance at sites was depressed further east in Booderee National Park. The reasons for these results remain unclear and were counter to patterns anticipated at the outset of this investigation as areas in the west of Booderee National Park are characterized by considerable past human disturbance as a result of land clearing, intensive domestic livestock grazing, and exotic softwood plantation establishment (Lindenmayer et al. 2014*b*). Our findings are not an artifact of vegetation type as our site selection process ensured that the different broad classes of vegetation are represented spatially across Booderee National Park.

Many species of native mammals we studied exhibited temporal trends for declining probability of presence or conditional abundance beyond patterns associated with the effects of

fire regime variables (Fig. 5). These patterns are suggestive of the influence of other (unmeasured) factors operating within Booderee National Park. Other species in our study such as the greater glider also may be responding to factors beyond those associated with fire and which were not measured in this investigation. For example, the greater glider appears to be regionally extinct in Booderee National Park (Lindenmayer et al. 2011), and has been lost both from sites that were burned in 2003 and those that were not. In previous work, we postulated that the removal of exotic predators like the red fox from Booderee National Park has triggered an increase in the abundance of the Powerful Owl (*Ninox strenua*) and other nocturnal predators. These predatory birds may have, in turn, depressed populations of the greater glider (Dexter et al. 2012). Similar processes might be affecting the reserve-wide pattern of temporal decline in the common ringtail possum, a closely related species to the greater glider and also a prey species for large predatory owls (Lavazanian et al. 1994). Changes in the abundance of exotic predators also may have influenced the temporal patterns of occurrence and/or abundance of macropods like the black wallaby and eastern grey kangaroo. Both species have been characterized by a temporal increase in probability of occurrence and/or conditional abundance, although these patterns have tapered in recent years (see Fig. 5).

We did not examine the potential effects of one species on another (e.g. through competitive exclusion) that can sometimes occur as part of post-disturbance animal successional dynamics (reviewed by Pulsford et al. 2014). This was beyond the scope of this study and requires, for example, careful analyses of co-occurrence patterns linked with vegetation succession and other kinds of change (e.g. see Lindenmayer et al. 2014*c*). We also are aware that some species may exhibit inherent and intrinsic patterns of change over time (Forsyth and Caley 2006), such as the cyclical patterns exhibited by an array of species of northern boreal mammals (Krebs et al. 2001). However, much longer time series data than were available to us would be required to document such kinds of patterns (Forsyth and Caley 2006).

Finally, this study was a multi-point-based examination of temporal responses of mammals on 97 long-term sites and we did not explore the effects of spatial attributes of fire regimes (such as fire size). Such spatial attributes may interact with temporal variables with subsequent impacts on mammal responses. Analyses of spatiotemporal changes in fire area (and other spatial variables) in relation to temporal changes in biodiversity are very challenging and

complex, and are beyond the scope of the work reported here. That work will be the subject of subsequent investigation.

Management implications

This investigation has several implications for fire management and biodiversity conservation. First, responses to multiple fire regime attributes coupled with the prevalence of interactions between fire regime variables and survey year underscore the critical importance of long-term studies of biodiversity and fire (Pons and Clavero 2009, Recher et al. 2009). Indeed, we argue that the complex array of temporal and other responses, including marked heterogeneity in the effects of fire regime attributes observed in this investigation would not have been identified with traditional cross-sectional (space-for-time) that are generally the norm in ecological studies of fire and biodiversity. Overlooking such long-term effects would be a significant oversight as our findings strongly suggest that the invisible mosaic of historical disturbance by fire (sensu Bradstock et al. 2005) will have a large influence on the responses of species to the next fire at a given site. Hence, we suggest that the history of past fire in an area needs to be documented as thoroughly and as far back in time as possible to help determine when and where more fires are needed or, conversely, where and when long-unburned vegetation is required. Our results demonstrating the effects of the number of past fires and the time since the last fire, indicate that simple fire management recommendations to burn a certain proportion of the landscape (e.g. 5% of a vegetated estate per annum; see Teague et al. 2010) are inappropriate for biodiversity conservation and do not address the requirements of different species. A second implication of our study is that managers may need to focus their attention on particular species, such as those of conservation concern and which are range-limited and/or sensitive to particular fire regime-related attributes. An example taxon from our empirical investigation is the eastern chestnut mouse. Populations in Booderee National Park are the most southerly known in the species' distribution and very isolated from the next nearest population (Pereoglou et al. 2011). The long-term exclusion of fire could result in the loss of the eastern chestnut mouse from Booderee National Park. Conversely, our data analyses also suggest that some species respond to the number of past fires and/or the time elapsed since the last fire. In the cases of species where responses to these fire regime variables are negative, a key management action will be to strive to maintain at least some areas of long unburned habitat; a recommendation increasingly

recognized as being important in other environments around the world (e.g. Welsh et al. 1996, Franklin et al. 2002, Burton et al. 2003, Kirkpatrick et al. 2010, Berry et al. 2015*b*).

The unexpected interspecific complexity of different responses to a range of fire regime attributes highlights the complexity of managing fire-prone environments for an array of different species. Perhaps the most tractable solution to such complexity is to ensure that there are large areas available for conservation management within which there are areas that have been subject to different levels of fire severity in the past and different fire histories. Moreover, if an aim of management is to maintain habitat for the array of mammal species in a given area (e.g. a park or reserve), then it will be critically important not to do the same kind of management everywhere, otherwise the diversity of kinds of post-fire conditions needed by different species will fail to be created.

Finally, as important as fire is as a key ecological process in many environments, it is also clear that biodiversity in these places also respond to non-fire-related environmental factors. In the case of this investigation, there was a strong effect of the spatial position of sites across the study area on the probability of presence and/or the conditional abundance of many species. Such spatial effects can be important in reserve management as species that might be expected, for example, to be susceptible to the effects of fire, may nevertheless be absent from areas for other reasons that are not be directly related to fire.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–E are available online: http://dx.doi.org/10.1890/15-0575.1.sm

FIG. 1. The location of long-term field survey sites at Booderee National Park.

FIG. 2. Fire severity in 2003 by survey year interaction for each component of the hurdle model for those species where this interaction was retained in the final model. Species were bush rat (*Rattus fuscipes*), brown antechinus (*Antechinus stuartii*), long-nosed bandicoot (*Perameles nasuta*), and swamp rat (*Rattus lutreolus*). The posterior median and 95% credible intervals (CI) for probability of occurrence and conditional abundance are shown in each panel. Sites that were

unburned in 2003 are denoted by (u), moderately burned sites by (m), and severely burned sites by (s).

FIG. 3.   Number of fires prior to 2003 experienced at a site by survey year interaction for each component of the hurdle model for those species (as in Fig. 2, with the addition of eastern chestnut mouse (*Pseudomys gracilicaudatus*) and common ringtail possum (*Pseudocheirus peregrinus*) and not including brown antechinus) where this interaction was retained in the final model. The posterior median and 95% CI for probability of occurrence and conditional abundance are shown in each panel. To illustrate the interaction, we chose to depict three levels of number of fires: the first quartile, denoted by 1 (the median), denoted by m and the third quartile, denoted by 3.

FIG. 4.   Time since previous fire prior to 2003 experienced at the site by survey year interaction for each component of the hurdle model for those species were this interaction was retained in the final model. The posterior median and 95% CI for probability of occurrence and conditional abundance are shown in each panel. To illustrate the interaction, we chose to depict three levels of time since fire: the first quartile, denoted by 1; the median, denoted by m and the third quartile, denoted by 3.

FIG. 5.   Temporal trends for the hurdle model components that do not have fire regime interactions with survey year. Note that (D) species richness from trapping, is a Poisson model. The posterior median and 95% CI for probability of occurrence and conditional abundance are shown in each panel. Species are as in Figs. 2 and 3, with the addition of black (swamp) wallaby (*Wallabia bicolor*), eastern grey kangaroo (*Macropus giganteus*), sugar glider (*Petaurus breviceps*), and greater glider (*Petauroides volans*).

Table 1.   Summary statistics of the data on fire severity, number of fires at a site, and the time since fire at a site prior to 2003

	Unburned	Moderate	Severe	Total
(A) Number of fires at site prior to December 2003 by severity of fire in 2003.				
0	6	2	1	9
1	16	13	8	37
2	10	11	3	24
3	10	3	5	18
4	1	6	1	8

5	0	1	0	1
(B) Statistics of time since last fire (yr) by severity of fire in December 2003				
Mean	17.09	19.49	22.03	18.89
Median	12.22	21.31	22.65	20.31
Standard deviation	12.92	11.29	9.82	11.83
First quartile	3.1	8.96	13.35	7.56
Third quartile	31	31	31	31
Minimum	1.08	1.62	6.1	1.08
Maximum	35	35	35	35

Table 2.   Model summaries for species richness (generated from either spotlighting or trapping surveys) and the 11 species of mammals that we modeled (see *Methods* for more details).

Response variable	Yr × fire sev.	No. fires × yr	YSF × yr	Yr^2	Yr	Fire sev.	No. fires	YSF^2	YSF	Easting	Veg. class
Bush rat (*Rattus fuscipes*)	L			L, P	L, P	L,P	P	L, P	L, P	L, P	P
Brown antechinus (*Antechinus stuartii*)	L, P			P	L, P	L,P				L, P	L, P
Long-nosed bandicoot (*Perameles nasuta*)	L	L		L, P	L, P	L	L		L, P	L	
Common brushtail possum (*Trichosurus vulpecula*)			L		L, P				L	L	L, P
Swamp rat (*Rattus lutreolus*)	L	L		L	L	L, P	L, P		L, P	L	L, P
Eastern chestnut mouse (*Pseudomys gracilicaudatus*)		P	P	L, P	L, P	L	P	L	L, P	L	L, P
Black wallaby (*Wallabia bicolor*)				L, P	L, P						L
Common ringtail possum (*Pseudocheirus peregrinus*)		L	L		L, P	L	L, P	L	L, P	L	L
Eastern grey kangaroo (*Macropus giganteus*)				L	L		P		L	P	L, P

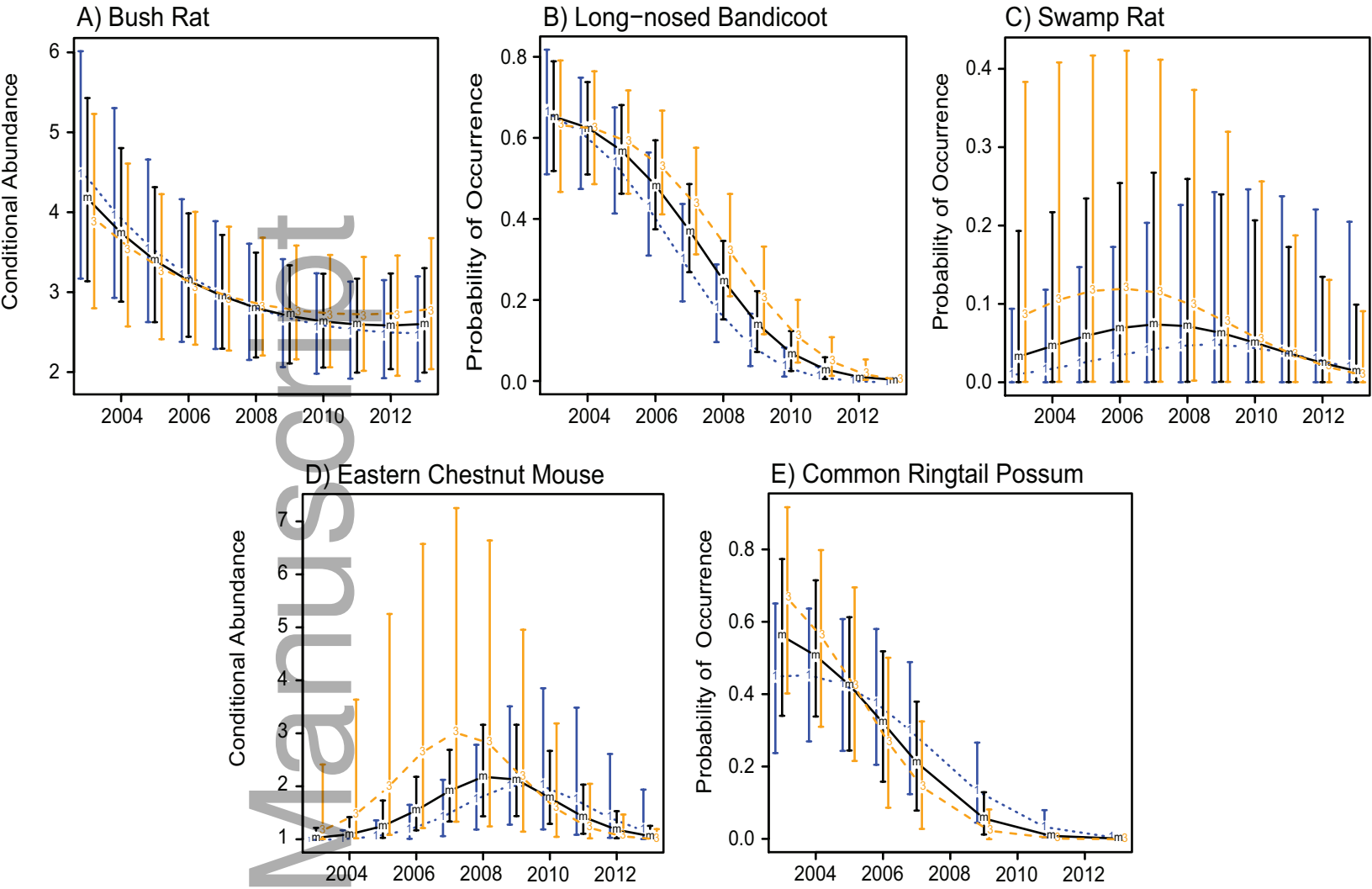|										
Sugar glider (*Petaurus breviceps*)				L	L			L	L		
Greater glider (*Petauroides volans*)				L	L, P			L	L		L, P
Species richness trapping					P			P	P	P	
Species richness spotlighting					L					P	L, P

Notes: For each response variable, we indicate whether a particular term was retained in the final model chosen via AIC. L indicates the term was important for the logistic component (presence/absence). P indicates the term was important for the Poisson component (conditional abundance). Note that the trapping species richness response did not require hurdle modeling and we therefore report results only for the Poisson model. Fire severity is indicated by fire sev. and it is modeled as a categorical variable with three levels: no fire, moderate fire, and severe fire. Veg class is a four-level categorical variable with levels: forest, heathland, scrubland, and woodland. We have followed the statistical convention in that lower-order terms were included in the model when they were involved in higher order terms; for example, if yr × fire was included, then year and fire were both included in the model.

BOODEREE NATIONAL PARK

New South Wales

Jervis Bay

Bowen Island

St. Georges Basin

Department
of Defence

JBT
leases

Department
of Defence

Wreck Bay
Aboriginal Land

Bherwerre Beach

St.Georges Head

● ANU fauna monitoring sites

N

0   1   2   3   4

Kilometres

Jervis
Bay

eap_1245_f1.eps

A) Bush Rat

B) Brown Antechinus

C) Brown Antechinus

D) Long−nosed Bandicoot

E) Swamp Rat

eap_1245_f2.eps

A) Bush Rat

B) Long-nosed Bandicoot

C) Swamp Rat

D) Eastern Chestnut Mouse

E) Common Ringtail Possum

eap_1245_f3.eps

A) Common Brushtail Possum B) Eastern Chestnut Mouse C) Common Ringtail Possum

eap_1245_f4.eps

A) Long-nosed Bandicoot
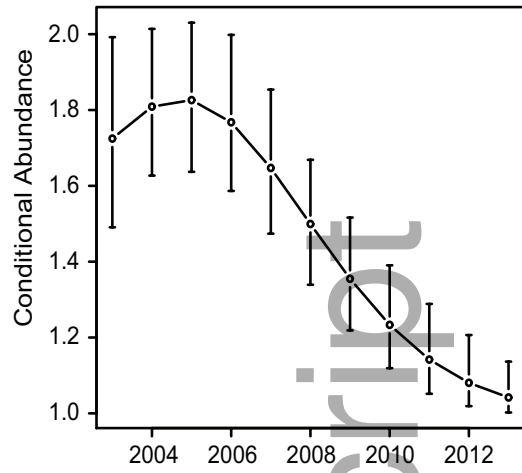
B) Common Brushtail Possum
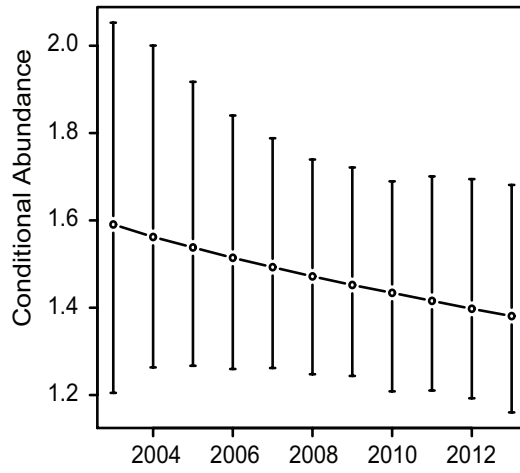
C) Eastern Chestnut Mouse
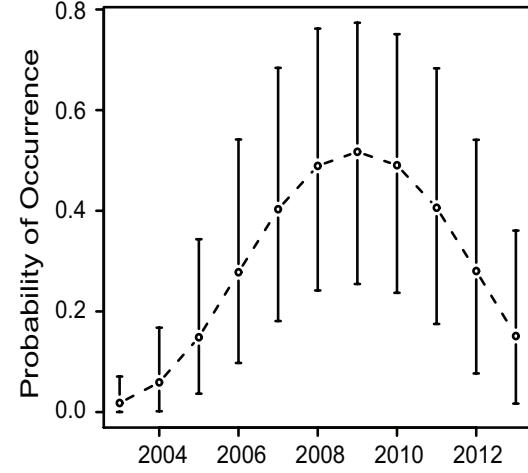
D) Trapping Species Richness
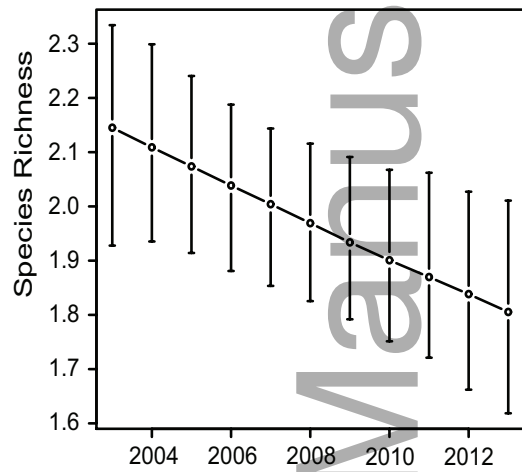
E) Black (Swamp) Wallaby
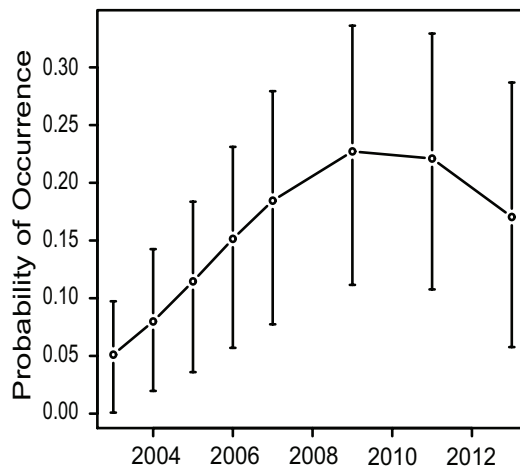
F) Black (Swamp) Wallaby
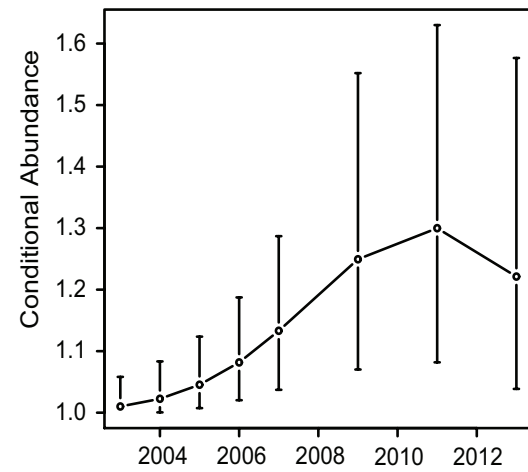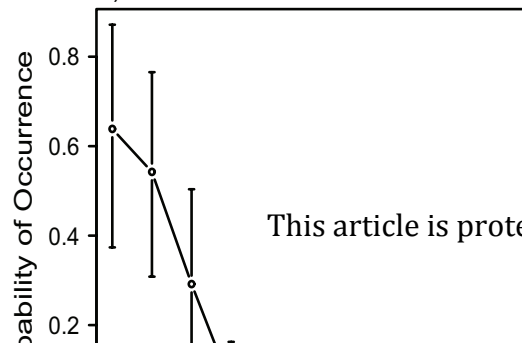
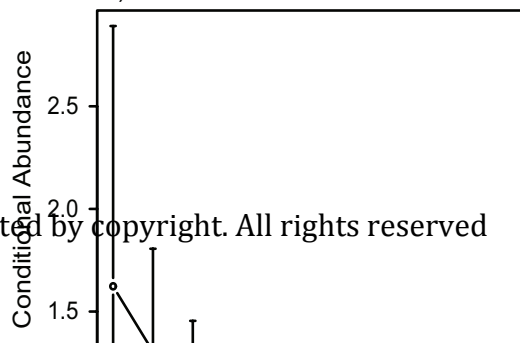G) Common Ringtail Possum
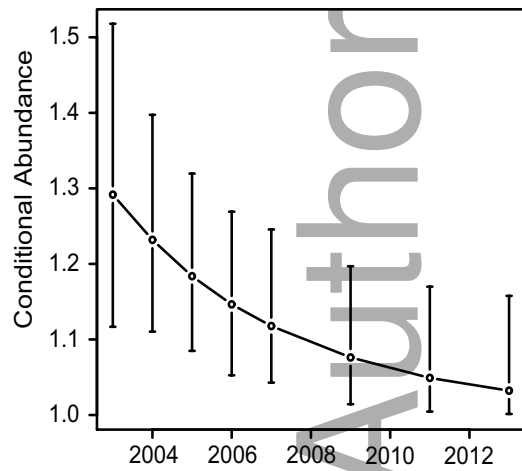
H) Eastern Grey Kangaroo
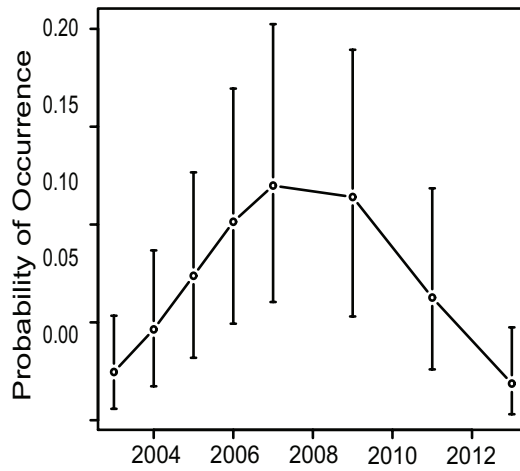
I) Sugar Glider
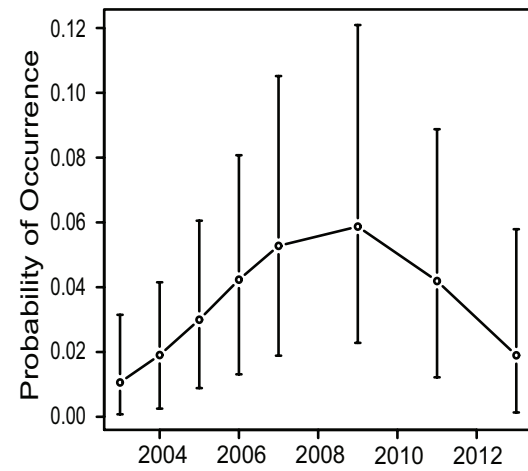
J) Greater Glider

K) Greater Glider

L) Spotlighting Species Richness