Factors influencing the occurrence of the Southern Long-nosed Bandicoot (*Perameles nasuta* Geoffroy) during a population irruption and decline

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ABSTRACT

Modelling the occupancy of species is a key part of the discipline of ecology, with particular efforts often focused on identifying which environmental, vegetation and other factors influence why a given species occurs where it does. Here, based on data gathered between 2003 and 2016, we developed models of the environmental, terrain, and vegetation factors associated with site occupancy of the Southern Long-nosed Bandicoot (*Perameles nasuta* Geoffroy) at Booderee National Park in the Jervis Bay Territory, south-eastern Australia. The Long-nosed Bandicoot is a nocturnal omnivorous marsupial which feeds primarily on subterranean invertebrates and fungi. The species has undergone a major reduction in abundance and site occupancy following a peak irruption in 2006 with the percentage of the sites at which the species was present declining from 74.3% of sites trapped in 2006 to 10.5% of sites trapped in 2016.

We found the Long-nosed Bandicoot was distributed widely across Booderee National Park and occurred in all six broad vegetation types in the reserve (forest, heathland, woodland, shrubland, sedgeland and rainforest). Detection-occupancy modelling revealed that the persistence and colonisation of sites by the species was negatively associated with the per cent cover of leaf litter, irrespective of broad vegetation type.

Occupancy models are an important tool in identifying parts of landscapes most likely to support populations of particular species, such as the Long-nosed Bandicoot over time and they may assist management of protected areas to prioritise resources to manage the habitat of those areas.

KEYWORDS: Statistical modelling, long-term data, serial site occupancy, temporal change in animal occupancy, environmental and vegetation covariates

INTRODUCTION

Quantifying the factors influencing the distribution and abundance of biodiversity has been a core part of ecology since the origins of the discipline (Elton 1927; Guillera-Arroita *et al.* 2015; Guisan and Thuiller 2005; Krebs 1978). Work to determine the factors influencing distribution patterns can be complicated by the fact that populations of species can vary temporally, for example in response to vegetation succession following disturbance (Pulsford *et al.* 2016) or pulses of resources such as those driven by climatic conditions (Barea and Watson 2007; Burrows *et al*. 2014; Dexter *et al.* 2011; Lindenmayer *et al.* 2019). In addition, the influence of key variables on species occupancy can change through time (Pierson et al. 2016), including as species move through different stages of their life cycles (e.g. Smith *et al.* 2016). Due to a paucity of data, such temporal changes in abundance can create substantial challenges for statistical modelling of factors affecting species occupancy, as models need to account for temporal changes in species abundance as well as possible temporal changes in habitat associations (Morrison *et al.* 2006).

In the investigation reported here, we quantified the factors influencing the occupancy of the Southern Long-nosed Bandicoot (*Perameles nasuta* Geoffroy) (hereafter referred to as the Long-nosed Bandicoot) in a protected area, Booderee National Park, in south-eastern Australia. The Long-nosed Bandicoot is a nocturnal marsupial endemic to south-eastern Australia (Hughes and Banks 2010). Previous studies of the species have been conducted at Booderee National Park. Lindenmayer et al. (2008) examined relationships between vegetation types, fire severity and capture rates. Dexter et al. (2011) reported on the habitat preferences and relative abundance of the Long-nosed Bandicoot during population irruption and decline up until 2008. Lindenmayer et al. (2016) explored how temporal aspects of fire regimes influenced the presence and conditional abundance of the species. MacGregor et al.

(2013) examined home range and habitat selection post-wildfire and MacGregor et al. (2015) examined the nest site selection by the Long-nosed Bandicoot following a fire.

In this paper, we used a multi-season occupancy model to quantify the factors which influenced the occupancy of the Long-nosed Bandicoot as the population irrupted and then declined in the ten years following the peak population in 2006. Modelling the occupancy of the species presented particular challenges because large parts of our study area have been subject to wildfires that have, in turn, affected the composition and structure of the vegetation (Foster *et al.* 2017) and therefore potential habitat suitability for the species. Specifically, our study was motivated by two key inter-related questions:

1. ***What combination of topographic and weather variables and attributes of vegetation structure influenced the initial occupancy, persistence and colonisation of the Long-nosed Bandicoot?***

   The Long-nosed Bandicoot is omnivorous, feeding on a variety of hypogeous fungi, soil invertebrates and plant roots (Scott *et al.* 1999) but the species is primarily insectivorous year-round (Thums *et al.* 2005). We hypothesised that bandicoots would persist in areas on flatter ground with deeper soils and higher moisture levels. We made these predictions because sites with higher rainfall would be wetter with deeper soils and would be expected to be more productive in terms of plant growth (Specht and Morgan 1983) as measured by understorey cover, fungal development and, in turn, invertebrate prey (Huggett and Cheeseman 2002). Hence, these places would have a higher probability of supporting animals in the medium to long term. Based on an examination of the distribution of bandicoot diggings, Hughes and Banks (2010) showed that the Long-nosed Bandicoot selected areas with moist, soft soils close to cover.

2. ***Is there evidence for temporal patterns of site occupancy in which the occupancy of the Long-nosed Bandicoot is related to past patterns of site occupancy?***

   That is, does the species exhibit serial site occupancy (persistence) and, if so, is this persistence related to environmental variables and vegetation attributes (including changes in the latter over time)? Dexter *et al.* (2011) found that individual adult bandicoots showed a high degree of philopatry. On this basis, we predicted that the occupancy of the Long-nosed Bandicoot at a site in any given year would be strongly positively related to whether the species inhabited that site in the previous years. Conversely, long unoccupied sites would likely remain unoccupied during the period of post-irruption decline.

Answers to the two questions outlined above are important to guide how to best manage areas of native vegetation within protected areas as well as identify parts of landscapes most likely to support populations of particular species, such as the Long-nosed Bandicoot, over time.

METHODS

Study area

Our work was focused within Booderee National Park in south-eastern Australia (Figure 1) which is a 6600 ha IUCN Category I reserve that supports more than 205 terrestrial vertebrate species, including threatened taxa and threatened ecological communities (Lindenmayer *et al.* 2014). Booderee National Park is located 200 km south of Sydney, south-eastern Australia (midpoint is 35°10'S, 150° 40'E). The region has a temperate climate with an average rainfall of approximately 1250 mm per annum spread relatively uniformly over the year. Average minimum and maximum air temperatures for February (summer) are 18-24°C and for July (winter) 9.2-15°C.

We employed a stratified, randomized, and replicated process to identify long-term monitoring sites throughout the study area. This limited the potential for geographic bias in our results. We established 109 permanent monitoring sites across six broad vegetation types – warm temperate rainforests, forests, woodlands, heathlands, shrublands, sedgelands – in Booderee National Park (Figure 1). We replicated sites within each vegetation type with a focus on the most common classes. The number of samples was generally proportional to the total area occupied by each vegetation class.

We established a permanent 100 m long transect at each of our 109 field sites. We used 100 metre transects because of high levels of heterogeneity in vegetation types at Booderee National Park (Stirnemann *et al.* 2014). This ensured that each transect was confined to a single vegetation type.

Field surveys for the Long-nosed Bandicoot

Each monitoring site started a minimum of 10 m from a track and consisted of star picket markers set at 0 m, 20 m, 40 m, 60 m, 80 m and 100 m points along a permanent transect running perpendicular to the track. Our trapping protocols for the Long-nosed Bandicoot involved deploying two large (30 x 30 x 60 cm) wire cage traps at the beginning and end of the transect and four small (20 x 20 x 50 cm) wire cage traps at 20 m intervals along each transect for three consecutive nights. We baited all traps with a mixture of peanut butter and rolled oats.

We determined the sex of each bandicoot captured and temporarily marked an ear with a spot of white paint. This enabled us to identify recaptures during any given trapping period. The maximum distance between adjacent sites was 1200 m and despite the minimum distance between adjacent sites being 30 m, no recaptures from adjacent sites were recorded. We completed trapping surveys in the summer (December – February) of all years between early

2004 and 2016. We surveyed all 109 sites annually between 2004 and 2010 and also in 2014. In 2011, 2012, 2013, 2015, and 2016, we surveyed sites bi-annually (with survey effort corresponding to approximately half the full set of sites in those years). Bi-annually surveyed sites were initially selected on the basis of vegetation type and geographic distribution across the park.

Vegetation Surveys

We established two 20 x 20 m vegetation monitoring plots at each of our 109 monitoring sites. We positioned these monitoring plots between the 20 m – 40 m points and between the 60 m – 80 m points on opposite sides of the transect. In 2004, 2006, 2007, 2009, 2012, 2017, we measured % leaf litter cover in the ground layer at each site by visual estimation in four 1 m x 1 m sub-plots within each 20 x 20 plot. We measured % cover of the understorey by visual estimation across each 20 m x 20 m plot. We defined understorey cover as the percentage cover of vegetation under 2 m in height in each vegetation plot. We completed surveys across multiple seasons within each survey year due to the large number of sites in our study. This data are summarised in Tables 1 and 2 of Appendix S1.

Environmental and other covariates used in statistical analyses

We generated Topographic Wetness Index (TWI) grids using GROCLIM (site productivity) (Xu and Hutchinson 2011) data for Booderee National Park at 10m resolution for use as covariates in subsequent statistical modelling of bandicoot occupancy. TWI is a relative measure of the position in the landscape derived by dividing the upstream contributing catchment area that drains through a particular point per unit contour length by the local slope (Beven and Kirkby 1979). We selected TWI as a variable of interest because it is likely to indicate areas of relatively high moisture and therefore relatively high productivity. Using ArcGIS, we created a 20m buffer around each 100m transect and then calculated the mean of the TWI for all grids within the buffer. We used rainfall to 9 am on the trapping day sourced from Bureau of Meteorology (2019) in the detection analysis. We used monthly rainfall data for each site from ANUClimate 1.0 (Hutchinson *et al.* 2014) for the Initial Occupancy, Persistence and Colonisation analysis.

We used a 'time-lagged' mean rainfall for the period 7 – 12 months prior to trapping for the Initial Occupancy, Persistence and Colonisation analysis as it would be more likely to have an influence on the breeding success of the Long-nosed Bandicoot than the mean annual rainfall. The amount of rainfall negatively influences fungal abundance and diversity (Hawkes et al. 2011), and we used 7 – 12 months as the time lag as this period occurs immediately before the winter period. This is the time when the abundance of invertebrates is at its lowest and also when subterranean foods including hypogeal fungi are more abundant in the diet of the Long-nosed bandicoot (Thums et al. 2005).

We recorded the lunar phase on a given trap night for use in subsequent detection analysis. We hypothesized that the Long-nosed Bandicoot would exhibit lunar phobia (*sensu* Price *et al.* 1984; Saldaña-Vázquez and Munguía-Rosas 2013) and therefore would be less active (and hence less likely to be trapped) on nights with bright moonlight to avoid predators.

Fire covariates

In late December 2003, a wildfire burned approximately 50% of the park, and 59 of our 109 long-term sites were burnt at varying levels of severity (Lindenmayer *et al.* 2008). There have been many other fires throughout Booderee National Park over the past 50 years and the location of past fires has been well documented (Foster et al. 2017). We modelled three fire variables. The variable 'Burn' indicated whether a site had been burnt in the 2003 wildfire. We also calculated the 'Time since last fire' (in years) at each site and the number of fires that had occurred at a site (since 1968). Foster et al. (2017) found that fire frequency and time since fire at 67 sites at Booderee National Park were not strongly correlated with TWI (r_s = 0.08 and -0.13 respectively).

STATISTICAL ANALYSIS

Vegetation analysis

To account for the timing of the vegetation surveys not coinciding with the timing of the trapping for the Long-nosed Bandicoot, we modelled vegetation variables through time with a multi-level Bayesian generalized linear regression model as follows. We modelled understory per cent cover with a zero-one inflated beta distribution and per cent leaf litter using a zero-inflated beta distribution (variables were scaled to the 0-1 interval). We used zero and zero-one inflated beta distributions to account for zero and 100 % cover which are not part of the support of the beta distribution when scaled at the 0-1 interval. These estimates were then used as predictors in the analysis of the occupancy of the Long-nosed Bandicoot (see Appendix S2 for a list of models and their corresponding Leave One Out cross validation Information Criteria values). The models were fitted with the R-package brms (Bürkner 2017) and we used the function bayes_R2 to compute a “pseudo-R2” for each of the measures (understory = 0.62, and leaf litter = 0.72).

Long-nosed Bandicoot occupancy

We modelled the presence/absence of the Long-nosed Bandicoot using a single species, multi-season occupancy model. As our sites are smaller than the typical home range of the Long-nosed Bandicoot, we infer that we are examining the probability of use rather than site occupancy (*sensu* MacKenzie 2006).

We first modelled detection of the Long-nosed Bandicoot. Then allowing for imperfect detection, we modelled: (1) ‘Initial Occupancy’ (that is, which factors if any, influenced whether animals first occur at a site [in 2004 at the outset of this investigation]). (2) ‘Persistence’ (defined as the probability that given a site is occupied in the previous trapping event that it is occupied in the current year). The previous trapping event was sometimes two years prior to the current year. And, (3) ‘Colonisation’ (considered to be whether a site is reoccupied after the species has been absent from a site).

We parameterized the initial occupancy status in 2004 and the subsequent persistence and colonisation of occupied and unoccupied sites, respectively. We followed the notation of (Royle and Kéry 2007).

Let *J* be the number of sites, *K* be the number of repeat surveys and *T* be the number of primary sampling periods (in our case years). Let the binary variable $y_{j,k,t}$denote whether or not Long-nosed Bandicoot was detected at site *j* during sampling occasion *k* in year *t*. We denote the true occupancy status of site *j* during the initial sampling period *t* by the binary variable: $z_{j,t}$ that indicates whether a site is occupied or not. We denote the probability of occupancy by $\psi_{j,t} = Pr(\ z_{j,t} = 1)$, which we allowed to vary due to site-level characteristics (see below for more details). Royle and Kéry (2007) define the survival/persistence probability $\phi_{j,t} = \Pr(\ z_{j,t+1} = 1 \mid z_{j,t} = 1)$ and the colonisation probability $\gamma_{j,t}$= Pr($z_{j,t+1} = 1 \mid z_{j,t} = 0)$.

Royle and Kéry (2007) used the state-space representation of the occupancy-detection model as follows. The state models for initial occupancy, persistence and colonisation are given by the following logistic regression models. Initial occupancy for species *i* at site *j*:

$$z_{j,1} \sim Bernoulli(\Psi_{j,1}), j = 1, \ldots, J$$

where we allowed the initial occupancy probability to depend on the following covariates via a logit link function:

$$logit(\Psi_{j,1}) = \theta_0 + \ \theta_1 Burn_{j,1} + \theta_2 TWI_{j,1} + \theta_3 FireFreq_{j,1} + \ \theta_4 TimeSinceFire_{j,1} \\ + \ \theta_5 LeafLitter_{j,1} + \ \theta_6 UnderStory_{j,1} + \ \theta_7 Rain712_{j,1}$$

where: $Burn_{j,1}$ is an indicator for whether or not the site was burned in 2003, $TWI_{j,1}$ is the topographic wetness index, $FireFreq_{j,1}$is the fire frequency at the site prior to 2003, $TimeSinceFire_{j,1}$is the time since fire prior to 2003, $LeafLitter_{j,1}$ is the amount of leaf litter at the site, $Understory_{j,1}$ is the amount of understory at the site and $Rain712_{j,1}$ is the amount of rainfall at the site in the 7 to 12 months prior to the survey. For subsequent years, we have the following relationships:

$$z_{j,t} |\ z_{j,t-1} \sim Bernoulli(z_{j,t-1}\phi_{j,t-1} + [1 - z_{j,t-1}]\gamma_{j,t-1})$$

and

$$\Psi_{j,t} = \ \Psi_{j,t}\ \phi_{j,t-1} + (1 - \Psi_{j,t})\gamma_{j,t-1}$$

with the following logistic models for persistence and colonisation:

$$logit(\phi_{j,t}) = \eta_0 + \ \eta_1 Burn_{j,t} + \eta_2 SY_{j,t} + + \eta_3 TWI_{j,t} + \eta_4 FireFreq_{j,t} \\ + \ \eta_5 TimeSinceFire_{j,t} + \ \eta_6 LeafLitter_{j,t} + \ \eta_7 UnderStory_{j,t} \\ + \ \eta_8 Rain712_{j,t}$$

and

$$logit(\gamma_{j,t}) = \lambda_0 + \ \lambda_1 Burn_{j,t} + \lambda_2 SY_{j,t} + + \lambda_3 TWI_{j,t} + \lambda_4 FireFreq_{j,t} \\ + \ \lambda_5 TimeSinceFire_{j,t} + \ \lambda_6 LeafLitter_{j,t} + \ \lambda_7 UnderStory_{j,t} \\ + \ \lambda_8 Rain712_{j,t}$$

where $SY_{j,t}$ is the survey year.

The observation equation, for $y_{j,k,t}$, is given by:

$$y_{j,k,t} \sim Bernoulli(z_{j,t}p_{j,k,t})$$

where $p_{j,k,t}$ is the probability of detecting and was modelled as follows:

$$logit(p_{j,k,t}) = \delta_0 + \delta_1 RainD_{j,k,t} + \delta_2 SeasonDay_{j,k,t} + \delta_3 SeasonDay^2_{j,k,t} \\ + \ \delta_4 sin(LunarCycle_{j,k,t}) \ + \ \delta_5 cos(LunarCycle_{j,k,t}) \ + \delta_6 LeafLitter_{j,k,t} \\ + \delta_7 SY_{j,k,t}$$

where $RainD_{j,k,t}$, $SeasonDay_{j,k,t}$, $LunarCycle_{j,k,t}$ are, the amount of rain until 9 am on the survey day, the number of days from the start of the survey season (November

30th), the lunar cycle in radians for the day of the survey (sin and cos are the usual trigonometric functions), respectively for the repeat surveys in the same primary sampling unit at *t*, and site *j*. Sites not observed in a given year were treated as missing values and were estimated as part of the Bayesian model.

We ran the model using the runjags (Denwood 2016) package in R (R Core Team, 2018) which provides an interface to the JAGS (Just Another Gibbs Sampler). We ran four chains with a burn-in of 20,000 iterations followed by 50,000 samples which were thinned by a factor of ten, leaving 4000 (4 chains by 1000) for posterior inference. The convergence of the chains was assessed via the Gelman-Rubin statistic ($\hat{R}$) (Gelman and Rubin 1992). All model parameters had $\hat{R}$ statistics less than 1.01, indicating adequate mixing of the chains. We assessed the residuals of both the detection and occupancy parts of the model using Dunn-Smyth residuals (Warton et al. 2017) and the Bayesian p-value (Royle and Kéry 2007). We constructed normal quantile-quantile plots, residuals vs fitted. We used variance inflation factors (Fox 2016) to assess the dependence between our predictors and they ranged from (1.27 to 2.38) which are deemed adequate. They were implemented using the car package (Fox and Weisberg 2018).

In general, there were no obvious patterns in the Dunn-Smyth residuals across 13 years with one or two exceptions when the species was not detected very frequently in a given year. The Bayesian p-value was 0.99 indicating no issues with model fit. We present posterior medians and 95% credible intervals.

RESULTS

We completed 1130 trapping events (i.e. the number of sites trapped over the 13 years of our study). We detected the Long-nosed Bandicoot in 375 of the 1130 trapping events (33.2%). We detected the Long-nosed Bandicoot in 190 of 299 trapping events up to and including 2006 (the peak of the irruption) and at 185 of 831 trapping events from 2007 to 2016. The presence of the species at a site declined from 74.3% of sites trapped in 2006 to 10.5% of sites trapped in 2016. We found that examples of ‘persistence’ occurred on 201 occasions at 80 sites in total and 53 occasions at 31 sites following the peak of the irruption in 2006. Over the 13 years of the study, we recorded the Long-nosed Bandicoot in all six broad vegetation types.

Detection

We were more likely to detect the Long-nosed Bandicoot later rather than earlier in a given season of trapping (Figure 2A, Figure 3A). We found strong negative effects of survey year with the Long-nosed Bandicoot being less likely to be detected in the later years of our study (Figure 2A, Figure 3B). There was no effect of rainfall in the 24 hours prior to capture on the probability of detection (Figure 2A). We also found no evidence of an effect of moon phase on the probability of detection (Figure 2A).

Initial occupancy

No topographic, climatic, vegetation or fire variables had influenced the probability of initial occupancy at a site (Figure 2B).

Persistence

Persistence has occurred at 31 sites since the peak of the irruption in 2006 and occurred more than once at 11 of these sites (with records of persistence in all six broad vegetation classes).

We found a negative linear effect of survey year on the probability of persistence of the Long-nosed Bandicoot at a site (Figure 2C, Figure 3C). We also found a negative effect of per cent cover of leaf litter on persistence (Figure 2C).

Colonisation

Instances of colonisation have occurred 73 times at 62 sites since 2006. We found a linear decrease in the probability of colonisation of a site over time (survey year) (Figure 2D, 3D). There also was evidence of a positive effect of fire frequency (Figure 2D) and a negative effect of leaf litter on the probability of colonisation (Figure 2D).

DISCUSSION

Studies of relationships between species occupancy and environmental and other factors are a key part of ecology (Elith and Leathwick 2009; Guillera-Arroita *et al.* 2015; Mackey and Lindenmayer 2001). However, models of such relationships can be challenging to construct for species undergoing rapid decline because of the low capture rates and the risk of imperfect detection. Here we used long-term site occupancy data to quantify the factors associated with occupancy of the Long-nosed Bandicoot which has undergone a marked decline in abundance over time (Figure 3B). We sought to identify the topographic, environmental and vegetation structure attributes associated with site occupancy.

What combination of topographic and weather variables and attributes of vegetation structure influenced the initial occupancy, persistence and colonisation of the Long-nosed Bandicoot.

Detection

We found that detections of the Long-nosed Bandicoot declined with time (Figure 3B). However, detections were influenced by the time within survey season that trapping occurred. The species was more likely to be detected on sites surveyed later in summer than those surveyed earlier. This result may be due to the breeding cycle of the Long-nosed Bandicoot at Booderee National Park which occurs from early spring through summer. Scott *et al*. (1999) found reproduction to be strongly seasonal with peak numbers of lactating females occurring between August and January. Such patterns, coupled with the ability of females of the Long-nosed Bandicoot to breed at about five months of age (Lyne 1964), may explain the higher probability of detection later in the trapping season.

The probability of detection of the Long-nosed Bandicoot declined over time. This is likely caused by the decline in the abundance of the Long-nosed Bandicoot at Booderee National Park since the peak of irruption in 2006. A population decline has been recorded in other studies at Booderee National Park. Dexter *et al*. (2011) reported an irruption from 2003 until 2006 then a subsequent decline until 2008. Lindenmayer *et al*. (2016) found a concave relationship between survey year and conditional abundance for the Long-nosed Bandicoot. Dexter *et al*. (2011) and Lindenmayer *et al*. (2019) suggest that the initial increase in the Long-nosed Bandicoot population may be due to the significant reduction in predation from the introduced red fox *Vulpes vulpes*. Baiting for the Red Fox was intensified in 2003 and has continued at the same rate throughout this study. There has been no evidence of increased predation by feral cats; feral cats have not been detected at Booderee National Park since the commencement of this study in 2004 (N.Dexter pers. com.). In the absence of feral cats, the subsequent decline in the population may be due to an overshoot of available resources often seen in irruptive dynamics and observed in a study parallel to ours (N. Dexter unpublished data).

Initial occupancy

We found that none of the variables we tested affected initial occupancy. This result may be linked with the fact that the Long-nosed Bandicoot was widely distributed across Booderee National Park and occurred in all broad vegetation types (see Dexter *et al*. 2011; Lindenmayer *et al.* 2008; Lindenmayer *et al.* 2018). Our findings for occupancy in a wide range of vegetation types were broadly consistent with the results of work that have been completed elsewhere in eastern Australia (Chambers and Dickman 2002; Opie *et al.* 1990; Stodart 1995; Swan *et al.* 2015).

Interestingly, the fire which affected 59 of our 109 study sites a few months before the 2004 survey did not influence the initial occupancy of a site. Foster *et al.* (2017) found the 2003 fire at Booderee National Park altered the vegetation structure in forest, woodland and heath by reducing the amount of understorey cover. We concur with the hypothesis of (Lindenmayer *et al.* 2008), it is likely that introduced predators such as the red fox influence the detection and therefore the initial occupancy of the Long-nosed Bandicoot. We suggest the irrupting population free from predation by the Red Fox was not constrained by the demands for refugia as provided by areas with high levels of understory cover.

Persistence and Colonisation

At the outset of this study, we hypothesized that the Long-nosed Bandicoot would persist at the wettest and most productive sites (as determined by GROCLIM indices such as rainfall and Terrain Wetness Index). Unexpectedly we found these variables did not affect the probability of persistence or colonisation. The reasons for the paucity of effects remain unclear, particularly as greater levels of rainfall and/or moisture availability might be expected to lead to greater plant growth and more resources such as insect prey.

The per cent cover of understorey also did not affect the probability of persistence or the probability colonisation. This result was surprising and differs from the findings of other investigations. Swan *et al.* (2015) found that the occurrence of the Long-nosed Bandicoot was positively related to understorey density at 1–2 m above the ground. Chambers and Dickman (2002) also found that suitable habitat for the Long-nosed Bandicoot often included a mosaic of dense undergrowth for shelter and open areas for foraging. MacGregor *et al.* (2013) concluded that dense understorey was vital for suitable nesting locations. We suggest that the results of this study should be treated with caution as per cent understorey was estimated visually over the 20m x 20m plots and maybe subject to measurement error.

Neither of the fire-related variables affected the persistence of bandicoots at a site, however, there was a positive effect of fire frequency on the colonisation of a site by the Long-nosed Bandicoot. Lindenmayer et al. (2016) also found there was a higher probability of detecting the Long-nosed Bandicoot at sites subject to more fires prior to 2003, although this effect was not evident until after 2005. Foster *et al.* (2017) found a high fire frequency was associated with low levels of bare earth cover in forest vegetation, irrespective of the 2003 wildfire severity. Sites that had burnt a greater number of times may support more grasses such as *Lomandra longifolia* or *Gahnia* sp. and therefore provide more cover and potential nesting sites.

We found the probability of site persistence by the Long-nosed Bandicoot was negatively affected by the per cent cover of leaf litter. Leaf litter also had a negative effect on colonisation. It is possible that animals avoid sites with high levels of leaf litter in an effort to reduce the chances of being detected by predators (Barnum *et al.* 1992). Movements in areas with high levels of leaf litter may be more easily heard by potential predators such as owls thereby making animals susceptible to capture (Goerlitz and Siemers 2007; Scobie *et al.* 2016). It is also possible that sites with high amounts of leaf litter do not support sufficient amounts of prey items such as the adults and larvae of Coleopterans which are known to be a key part of the diet of the Long-nosed Bandicoot (Thums *et al.* 2005). Finally, the presence of the Long-nosed Bandicoot may negatively influence the amount of leaf litter. Digging by other mammalian ecosystem engineers has been found to reduce the amount of leaf litter through turning over the soil and promoting the rate of litter break-down (Hayward *et al.* 2016; Valentine *et al.* 2016).

Is there evidence for temporal patterns of site occupancy in which the occurrence of the Long-nosed Bandicoot is related to past patterns of site occupancy?

We found a negative linear effect of survey year on persistence. The probability of persistence was high for the first two years but then declined steeply until about 2011 after which the rate of change of sites from occupied to unoccupied declined (Figure 3C). This suggests that when the Long-nosed Bandicoot was widespread in the initial years of trapping, animals were re-captured at multiple sites. As the population declined, however, animals were less likely to be trapped at a site in consecutive trapping sessions.

We found no evidence for temporal patterns of site occupancy over the thirteen years of this study. Long unoccupied sites remained unoccupied during the period of post-irruption decline with nineteen sites remaining unoccupied between 2006 and 2016. The decline in the probability of detection slowed from about 2013 (Figure 3B) while the decline in both the probability of persistence and probability of colonisation began to slow and 'plateau' (Figure 3C). We infer from this that the Long-nosed Bandicoot population started to stabilize in 2016, and if this pattern continues, the probability of colonisation of sites by the Long-nosed Bandicoot should remain stable.

There were insufficient instances of persistence and colonisation to determine which (if any) co-variates affected re-occupancy during the decline phase alone following the irruption. Nevertheless, our new understanding that animals are more likely to persist at sites that have lower amounts of leaf litter and colonise sites that have had more fires may be important for management. This is because it enables conservation actions to be spatially targeted in particular parts of the landscape where animals are most likely to persist and therefore where management is more likely to be effective. For example, for species such as the Long-nosed Bandicoot, which can be susceptible to predation by exotic carnivores (Burbidge and McKenzie 1989; Roberts *et al.* 2006), a simple understanding of the locations where animals have been recorded in the recent past may assist managers in focusing predator control programs where residual populations of at-risk prey species remain.

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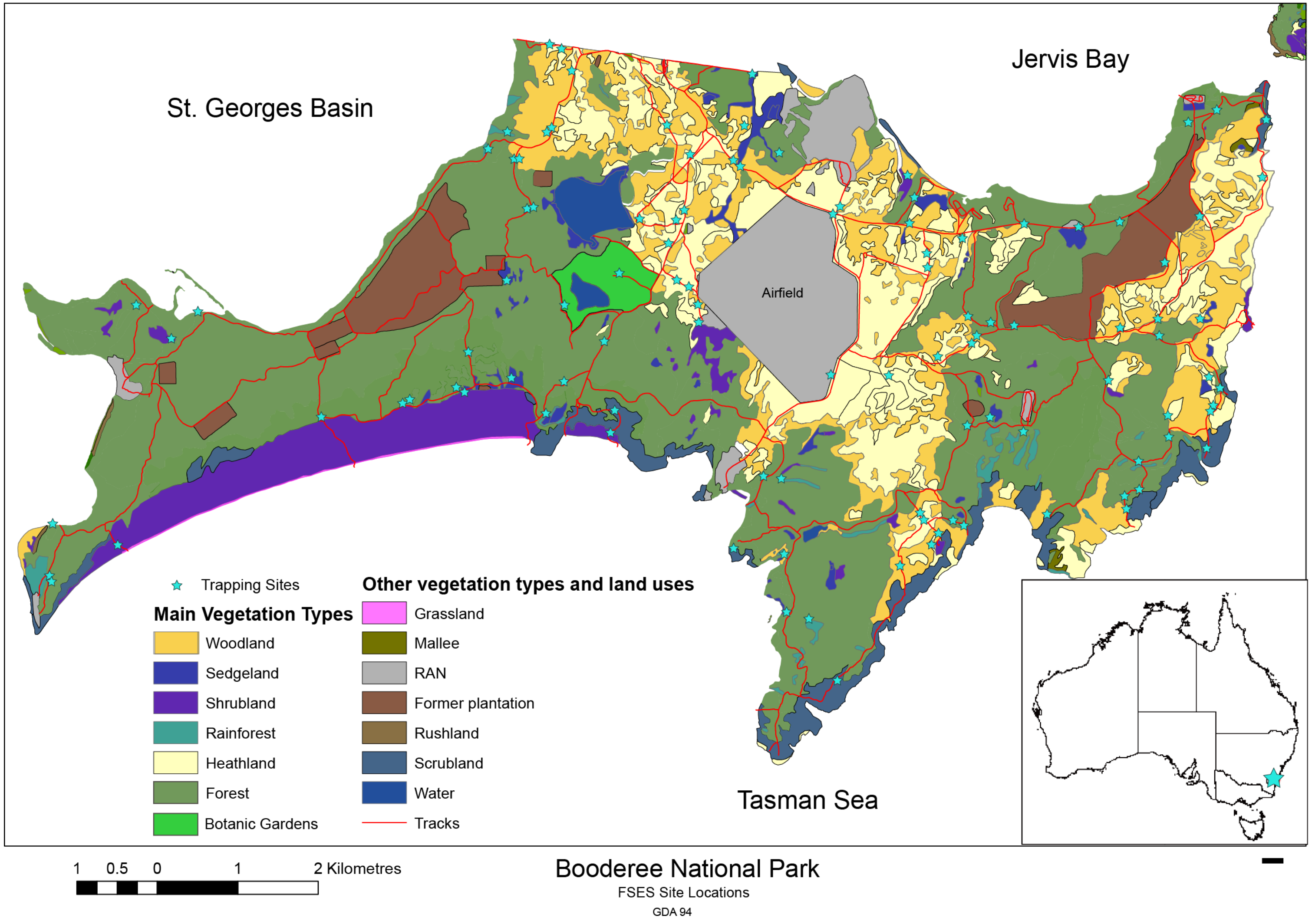
FIGURE LEGENDS

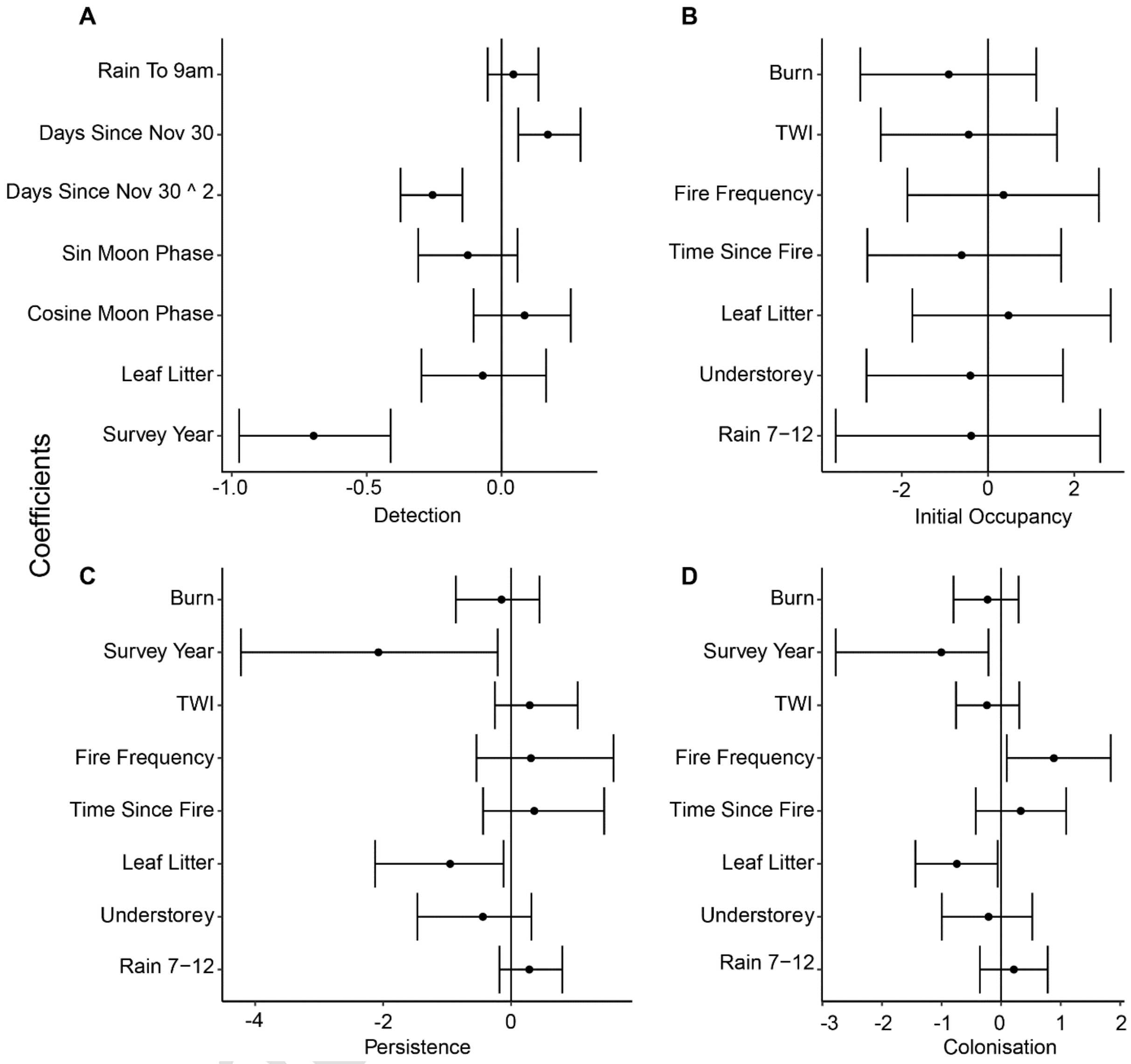
Figure 1. Map of Booderee National Park showing the main vegetation types and the location of permanent monitoring sites at Booderee National Park.

Figure 2: Multi-season Occupancy Model. A. Detection – the probability that a factor effects the detection of a Long-nosed Bandicoot B. Initial Occupancy – the probability that a factor influenced whether animals first occurred at a site in 2004. C. Persistence – the probability that a factor affects whether Long-nosed Bandicoot occupies a site in the current year given the site was occupied in the previous year. D. Colonisation – the probability that a factor affects whether a site is reoccupied after the Long-nosed Bandicoot has been absent from a site. Note that if the credible intervals of a term cross zero that term is not important.

Figure 3: Trend of factors with quadratic effects and their 95% credible intervals. A. Effects of days since November 30 and B. survey year on the probability of detecting the Long-nosed Bandicoot. C. Effect of survey year on the probability of persistence at a site and D. Effect of survey year on the probability of colonisation of a site by the Long-nosed Bandicoot.

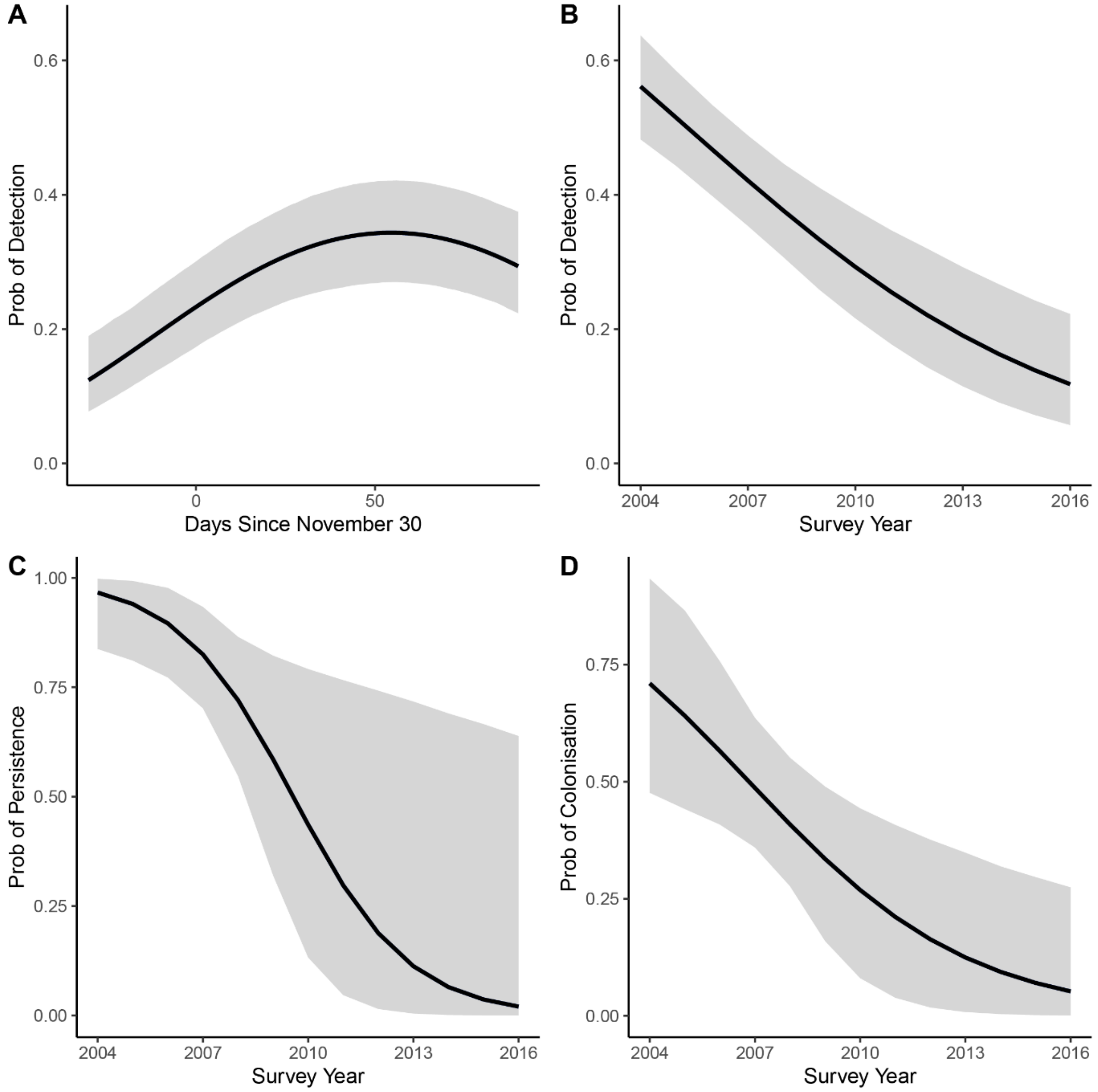

St. Georges Basin
Jervis Bay
Airfield
Tasman Sea
Trapping Sites
Main Vegetation Types
Woodland
Sedgeland
Shrubland
Rainforest
Heathland
Forest
Botanic Gardens
Other vegetation types and land uses
Grassland
Mallee
RAN
Former plantation
Rushland
Scrubland
Water
Tracks
1 0.5 0 1 2 Kilometres
Booderee National Park
FSES Site Locations
GDA 94

591


A
Rain To 9am
Days Since Nov 30
Days Since Nov 30 ^ 2
Sin Moon Phase
Cosine Moon Phase
Leaf Litter
Survey Year
-1.0
-0.5
0.0
Detection
B
Burn
TWI
Fire Frequency
Time Since Fire
Leaf Litter
Understorey
Rain 7−12
-2
0
2
Initial Occupancy
Coefficients
C
Burn
Survey Year
TWI
Fire Frequency
Time Since Fire
Leaf Litter
Understorey
Rain 7−12
-4
-2
0
Persistence
D
Burn
Survey Year
TWI
Fire Frequency
Time Since Fire
Leaf Litter
Understorey
Rain 7−12
-3
-2
-1
0
1
2
Colonisation

592

593


A
Prob of Detection
0.0
0.2
0.4
0.6
0
50
Days Since November 30
B
Prob of Detection
0.0
0.2
0.4
0.6
2004
2007
2010
2013
2016
Survey Year
C
Prob of Persistence
0.00
0.25
0.50
0.75
1.00
2004
2007
2010
2013
2016
Survey Year
D
Prob of Colonisation
0.00
0.25
0.50
0.75
2004
2007
2010
2013
2016
Survey Year

594

595

APPENDICES

Appendix S1: Summary of vegetation structure data collected at Booderee National Park

Table 1. Mean percentage cover of leaf litter per 20 m x 20 m plot in each vegetation type.

	2004		2006		2007		2009		2012		2017	
Broad Vegetation Type	**mean**	**SD**	**mean**	**SD**	**mean**	**SD**	**mean**	**SD**	**mean**	**SD**	**mean**	**SD**
Forest	51.17	21.16	54.08	23.85	59.30	26.06	58.33	23.29	67.31	26.61	61.62	27.22
Heathland	6.27	10.08	8.29	17.26	4.38	13.32	17.83	18.58	13.52	16.29	19.67	23.74
Rainforest	61.48	17.33	60.00	32.17	61.09	22.67	69.77	10.40	72.23	15.06	74.05	14.39
Sedgeland	12.16	17.52	12.80	20.14	13.13	19.24	18.18	19.11	23.59	19.47	21.39	17.92
Shrubland	45.16	25.70	39.09	25.99	38.13	28.37	49.09	23.25	42.61	25.46	48.09	25.53
Woodland	40.16	23.01	36.61	27.32	42.01	24.10	45.57	18.23	58.72	20.97	54.13	18.46

Table 2. Mean percentage cover of understorey per 20 m x 20 m plot in each vegetation type.

	2004		2006		2007		2009		2012		2017	
Broad Vegetation Type	**mean**	**SD**	**mean**	**SD**	**mean**	**SD**	**mean**	**SD**	**mean**	**SD**	**mean**	**SD**
Forest	49.48	23.50	51.04	21.73	64.79	20.93	68.13	22.89	56.63	22.10	46.71	34.48
Heathland	79.79	22.97	83.81	17.02	89.23	12.81	88.94	22.83	85.56	20.71	76.29	33.36
Rainforest	35.63	28.57	50.00	28.93	51.25	30.74	50.31	33.19	44.56	27.61	40.13	36.87
Sedgeland	41.06	29.16	58.13	31.56	54.38	29.88	80.31	19.19	65.81	25.98	66.00	39.94
Shrubland	44.88	32.12	52.50	27.94	51.75	31.45	59.15	35.75	45.70	35.10	43.73	34.38
Woodland	64.17	23.06	66.96	16.31	75.00	16.43	75.22	18.13	72.80	16.45	59.02	31.48

Appendix S2: List of models for vegetation modeling with their corresponding Leave one out cross validation information criteria (LOOIC). Note that models with lower LOOIC are preferred.

For each variable, we considered the following covariates: standardized survey year (YearS) and YearS^2, sin and cosine of the Julian day of the vegetation survey, broad vegetation type (forest, heathland, rainforest, sedgeland, shrubland, and woodland), aspect (divided into northerly and easterly components), amount of rainfall and time since fire, allowing for separate intercept and year effects (linear and quadratic where appropriate) for each site. We used the best fitting model to estimate the amount of each vegetation type (understory and leaf litter) present on December 15th of each survey year (the median bandicoot survey date). These estimates were then used as predictors in the analysis of bandicoot occurrence.

Model	LOOIC
Understory cover	
Y + Y^2 + sinJD + cosJD + (1+Y + Y^2|SiteNumber)	-204.12
Y + Y^2 + sinJD + cosJD + Vegtype + (1+Y + Y^2|SiteNumber)	**-209.59**
Y + Y^2 + sinJD + cosJD + Vegtype + TimeSinceFire03 + burnSev03 + burnSev03:TimeSinceFire03 (1+Y + Y^2|SiteNumber)	-205.42
Y + Y^2 + sinJD + cosJD + Vegtype + TimeSinceFire03 + burnSev03 + burnSev03:TimeSinceFire03 + aspectnorth + aspecteast + rain + TWI (1+Y + Y^2|SiteNumber)	-199.29
Leaf Litter	
Y + Y^2 + sinJD + cosJD + (1+Y |SiteNumber)	-306.70
Y + sinJD + cosJD + (1+Y |SiteNumber)	-308.64
Y + sinJD + cosJD + Vegtype + (1+Y |SiteNumber)	**-334.85**
Y + sinJD + cosJD + Vegtype + TimeSinceFire03 + burnSev03 + brunSev03:TimeSinceFire03 + (1+Y |SiteNumber)	-334.85
Y + sinJD + cosJD + Vegtype + TimeSinceFire03 + (1+Y |SiteNumber)	-332.7

Where:

sinJD = sin(2 * pi * JD /365.25), cosJD = sin(2* pi * JD/365.25), JD = is the Julian day of the year.

Best fitting models:

Understory:

	Estimate	Est.Error	Q2.5	Q97.5
Intercept	0.316	0.361	-0.381	1.03
Year	0.113	0.054	0.006	0.219
IYearSE2	-0.216	0.051	-0.317	-0.115
sinJD	0.156	0.053	0.053	0.26
cosJD	-0.193	0.055	-0.301	-0.088
Forest	0.242	0.4	-0.533	1.012
Heathland	1.438	0.394	0.677	2.216
Rainforest	-0.341	0.449	-1.239	0.517
Sedgeland	0.198	0.451	-0.672	1.11
Shrubland	-0.168	0.403	-0.973	0.606
Woodland	0.679	0.394	-0.079	1.452

Leaf Litter:

	Estimate	Est.Error	Q2.5	Q97.5
Intercept	-0.445	0.308	-1.043	0.136
Year	0.23	0.045	0.141	0.32
sinJD	-0.115	0.047	-0.209	-0.021
CosJD	-0.117	0.043	-0.201	-0.034
Forest	1.08	0.345	0.409	1.75
Heathland	-1.53	0.34	-2.18	-0.853
Rainforest	1.134	0.39	0.377	1.896
Sedgeland	-1.125	0.399	-1.919	-0.351
Shrubland	0.118	0.339	-0.531	0.784
Woodland	0.173	0.341	-0.487	0.842