

Long-term mammal and nocturnal bird trends are influenced by vegetation type, weather and climate in temperate woodlands

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ABSTRACT

Many studies have documented the individual effects of variables such as vegetation, long-term climate and short-term weather on biodiversity. Few, however, have explicitly explored how interactions among these major drivers can influence species abundance. We used data from a 15-year study (2002-2017) in the endangered temperate woodlands of south-eastern Australia to test hypotheses associated with the effects of vegetation type, long-term climate, and short-term weather on population trajectories of seven species of (largely) nocturnal mammals and birds. Despite prolonged drought conditions, there was a significant increase in the abundance of some species over time (e.g. the Eastern Grey Kangaroo). It is possible that destocking of domestic livestock may have reduced competition with Kangaroos, thereby facilitating increases in abundance. The Common Brushtail Possum and Common Ringtail Possum were significantly less likely to occur in replanted woodlands, possibly because of the paucity of nesting sites. We found no evidence that replanted woodlands are refuges for exotic pest species like the European Rabbit and Red Fox. Short- and long-term rainfall and vegetation type had important independent and combined effects on animal abundance. That is, responses to periods of high short-term rainfall were dependent on vegetation type and whether sites occurred in long-term climatically-wet versus climatically-dry locations. For example, the Red Fox responded positively to high levels of short-term rainfall, but only at climatically-dry sites. Our results highlight the complementary value of different vegetation types across the landscape and the context-specific responses of animals to short-term fluctuations in moisture availability. They also underscore the value of long-term monitoring at a landscape scale for examining how multiple interacting factors influence trends in animal abundance.

INTRODUCTION

A large amount of the world's biodiversity is at risk of decline and extinction in the coming decades (Ceballos et al. 2017; Intergovernmental Science-policy Platform on Biodiversity and Ecosystem Services (IPBES) 2019). Documenting species declines is, in part, dependent on long-term studies to quantify population trajectories (Bayraktarov et al. 2019; Reinke et al. 2019; Scheele et al. 2019). Beyond quantifying patterns of temporal change in populations, however, it is also important to identify the factors influencing those changes. Such information is necessary to guide interventions to arrest declines (Garnett et al. 2018) or in the case of exotic species, help assess the efficacy of control measures (Braysher 2017).

In the study reported here, we used a 15-year dataset from the endangered temperate woodlands of south-eastern Australia to quantify patterns of temporal change in seven species of nocturnal and crepuscular animals; three native and two exotic mammal species and two native bird species. We modelled the main and interacting effects of three key factors on population trajectories. These were: **(1)** vegetation type (replanted woodland, old-growth woodland, natural regrowth woodland, and coppice regrowth woodland); **(2)** the amount of net rainfall (i.e. total precipitation minus pan evaporation) in the year prior to each survey; and **(3)** long-term average rainfall at each location.

Our study area is characterized by a strong wet-dry gradient in long-term average rainfall (see Figure S1.1 in Appendix 1). This enabled us to test whether animal abundance was highest in climatically-wet locations (productivity hypothesis, see Table 1). Likewise, short-term fluctuations in rainfall can have marked effects on resource availability (Barea and Watson 2007; Bateman et al. 2012). Because the temporal duration of our study spanned an extremely dry period (the Millennium Drought), as well as more mesic inter-drought periods (van Dijk et al. 2013), we were able to evaluate the hypothesis that periods of high rainfall drive resource pulses, which may in turn drive animal responses (Table 1).

Although the independent effects of vegetation type, long-term climate and short-term weather have previously received research attention, their interaction is not well understood. Indeed, statistical interactions between key variables are rarely quantified in ecological studies (Côté et al. 2016), despite their potentially profound effects on biodiversity (Crowther et al. 2018; Foster et al. 2016; Hansen and Turner 2019). Therefore, beyond the main effects of our three key variables, we also developed a series of hypotheses regarding the potential interactions between them (Table 1). These included a short-term weather by vegetation type interaction (a weather refuge hypothesis), in which we predicted that animal abundance would be highest in old growth woodlands during drought because such places contain large trees that can produce pulses of food such as flowers, seeds and fruit (reviewed by Lindenmayer and Laurance 2016). We also tested for two-way interactions between long-term climate and vegetation type (an environment-vegetation type hypothesis) and short-term weather and long-term climate (environment-weather pulse hypothesis). Finally, we tested for potential three-way interactions between vegetation type, long-term climate, and short-term weather, based on the expectation that the impacts of short-term rainfall would be mediated by the underlying long-term climatic conditions at a site and vegetation type. We predicted that the effects of short-term weather would be most pronounced on climatically-wet sites (where rates of growth are likely to be faster and overall levels of biomass are inherently higher (Soderquist and MacNally 2000) and especially in old-growth woodlands that are characterized by more larger and older trees than regrowth and restoration replantings (Ikin et al. 2015).

METHODS

Study area

Our study encompassed a 1.8 million hectare agricultural area within the South West Slopes region of New South Wales, south-eastern Australia (Figure 1). The region was formerly

dominated by temperate woodland (Lindenmayer et al. 2010), but has been cleared of an estimated 85% of its original cover to facilitate livestock grazing and cereal cropping. It is one of the most heavily modified agricultural regions worldwide (Fischer et al. 2009) and characterized by a range of land degradation problems such as soil erosion and secondary salinity (Stirzaker et al. 2002). Major restoration programs have been undertaken in an effort to tackle these problems (Lindenmayer et al. 2016a). There has also been substantial natural regeneration of temperate woodlands, particularly over the past 15 years (Geddes et al. 2011; Lindenmayer et al. 2012b), often as a result of changes in livestock grazing pressure (Fischer et al. 2009). Thus, woody vegetation in the South West Slopes region can be grouped in four broad categories.

1. Actively replanted woodlands that were at least seven years old at the start of this investigation (2002) but with many > 10-20 years old. These areas comprised planted understorey and overstorey native vegetation with a mix of native and exotic ground cover. Woody plants were typically spaced 2 m apart, but there was not a standard set of spacing and plant species composition protocols applied in revegetation efforts. A small number of plantings were established around large old (former paddock) trees. However, the vast majority were dominated by a single cohort of trees planted at the same time. We refer to these as ‘plantings’.
2. Naturally regenerated woodlands established from seeds germinating after being dropped by overstorey paddock trees. We refer to these as ‘regrowth’ sites.
3. Coppice regrowth woodlands that have regrown after fire or logging. We refer to these as ‘coppice’ sites.
4. Old-growth woodlands that were dominated by large scattered trees that were 200 or more years old (Lindenmayer et al. 2016b). We refer to these as ‘old-growth’ sites.

Our investigation was based on 203 long-term field sites, in each of which we positioned a 200 m long transect. We established permanent steel post markers at the 0, 50, 100, 150 and 200 m points along each transect. There were 65 plantings, 29 coppice sites, 37 regrowth sites, and 72 old-growth sites. Our sites were located on 46 farms and all but three farms supported at least two of our four site types, with 14 having three or four types. These farms were located across an west-east gradient of increasing rainfall (Figure S1).

We determined the size of patches of 203 sites from satellite data and it varied from 0.3–60.3 ha for plantings, 0.5–51.3 ha for regrowth and coppice, and 0.4–53.8 ha for old-growth.

Spotlighting surveys

We completed spotlighting surveys at our field sites in late winter of 2002, 2003, 2008, 2009, 2011, 2013, 2015 and 2017. In any given year, we surveyed the transect at each site by spotlighting using a 75W handheld spotlight. The vast majority of spotlighting surveys were undertaken by a core group of experienced field ecologists who have worked in woodland and other environments for five or more years. Each survey took 20 minutes to complete. We completed surveys at the same time each year (June –July) and did not undertake spotlighting on nights of poor weather (rain, high wind, fog or heavy cloud cover). We constrained our statistical analyses to detections of animals within 50 m either side of the 200 m transect.

We consider that eight repeated surveys at our 203 long-term sites is sufficient to sample responses of animals to vegetation type, climate and weather. Indeed, we know of no other studies that have sampled at a similar intensity to that completed in this investigation.

Climate and weather variables

We compiled information on rainfall over both short and long timescales to utilise in our analysis of animal responses to weather and climate. We chose to focus on rainfall because moisture is a key factor limiting productivity in many Australian ecosystems (Specht and

Morgan 1983; Specht and Specht 1999). We did not include temperature because it is highly correlated with rainfall in our study region, preventing its inclusion in the same statistical model (Lindenmayer et al. 2018a). Our long-term variable was the mean annual rainfall for each of our sites (1970-2014), divided by 12 to give an average value per month. Our sites spanned a gradient from climatically-wet to climatically-dry conditions (Figure S1.1). Our short-term variable was mean monthly rainfall minus mean monthly pan evaporation, which we averaged over the 12-month period prior to each survey. This measure – which we refer to as “net rainfall” – was nearly always negative for our study region, and captures relative moisture availability more effectively than rainfall alone.

Our investigation was conducted between 2002 and 2017 and spanned the Millennium Drought and a subsequently much wetter period (Nimmo et al. 2016; van Dijk et al. 2013; see Fig. S1.2). Both our long-term climate and short-term weather variables were extracted for each of our 203 field sites from monthly national grids (M. Hutchinson unpublished data), which were built using thin-plate smooth splines as described by (Hutchinson 1995). This method has been widely applied to estimate daily and monthly daily climate surfaces, as well as long-term climate averages (e.g. McKenney et al. 2011).

Statistical analyses

We detected five mammals and two birds with sufficient frequency to enable robust statistical analyses. These were the Eastern Grey Kangaroo (*Macropus giganteus*), Common Brushtail Possum (*Trichosurus vulpecula*), Common Ringtail Possum (*Pseudocheirus peregrinus*), European Rabbit (*Oryctolagus cuniculus*), Red Fox (*Vulpes vulpes*), Boobook Owl (*Ninox boobook*), and Tawny Frogmouth (*Podargus strigoides*). Of these, the Red Fox and European Rabbit are introduced species. We refer to these species from now on as kangaroos, brushtails, ringtails, rabbits, foxes, boobooks and frogmouths to avoid repetition.

We used a two-stage approach in our analysis. In Stage 1, we began by investigating individual species trajectories over time, and differences in abundance and trends of abundance with time between our four broad vegetation types and patch area. In Stage 2, we then added long-term and short-term rainfall effects and interactions into the model with time and vegetation type.

We used generalized linear mixed models (GLMMs) in GenStat (Release 20.1) for both sets of analyses. Our response variable for all analyses was the number of individuals of each species observed at a site in each survey year. We included random effects of farm and of sites within farms to account for the facts that sites were grouped within farms, and observations were repeated at the same sites year-on-year. The fixed effects were a quadratic effect (on the log scale) of time, linear effects of short-term weather, long-term climate, patch area (log), and categorical effects of broad vegetation type, together with interactions between these (excluding interactions of weather or climate with time). This can be summarized as follows:

$$\begin{aligned} \text{Log(abundance)} = & \text{Log(patch area)} + ((\text{time} + \text{time}^2) * \text{vegetation type}) + \\ & (\text{vegetation type} * \text{long-term climate} * \text{short-term weather}) \end{aligned}$$

We analysed our data using a Poisson distribution with over-dispersion (Wedderburn 1974) and the log link function. Using the Poisson distribution without over-dispersion corresponds to assuming that the number of animals seen at each visit to a site follows a Poisson distribution, with variance equal to the mean. Such a distribution would arise if individual animals occur independent of others. However, the location of individuals is often not independent of that of other individuals of the same species. The estimation of an over- or under- dispersion parameter is one way to deal with this statistical issue. In our dataset, kangaroos tended to occur together more often than expected by random occurrence. The

estimate of the dispersion parameter was 1.36(s.e. 0.05), meaning that the variance was about 1.4 times the mean (significantly larger than 1.0). All the other species tend to occur together less often than we would expect from random occurrence: brushtails (0.80, s.e. 0.03), ringtails (0.60 s.e. 0.02), rabbits (0.67, s.e.0.03), foxes (0.51, s.e. 0.02), boobooks (0.22, s.e.0.01), and frogmouths (0.39, s.e. 0.02).

For presentation purposes, we summarized the effects of interest using predictions adjusted for all the other variables in the model (Lane and Nelder 1982). Specifically, we calculated predictions at the mean values of continuous variables (such as long-term average rainfall), and averages over the predictions at each level of categorical variables (such as vegetation type), with equal weights for each level.

RESULTS

Stage 1: Patch area, vegetation type & time

Data on the occurrence and abundance of all species by year and by vegetation type are presented in Tables S1.1 and S1.2 in Appendix 1. Our first set of models focussed only on the effects on our seven species of patch area, time, vegetation type, and their interaction (Figure 2 and Tables S2.1, S2.2, S2.3). We found that the abundance of kangaroos, brushtails and rabbits increased strongly with patch area, and ringtails less strongly, while frogmouths decreased (Table S2.1). Doubling patch area corresponded to increasing kangaroo abundance by 80%, brushtails by 116%, rabbits by 293%, ringtails by 12%, and decreasing frogmouths by 21% (Table S2.2). There was no evidence of an interaction between abundance and vegetation type, except for a small effect for boobooks (Table S2.1).

The abundance of brushtails and ringtails was significantly different between vegetation types (Table S2.1), with highest levels of abundance in old-growth, and lower levels in

coppice and plantings (Table S2.3). Averaging over time, there was no evidence of association of the abundance of the other species with vegetation type.

The abundance of kangaroos and foxes increased significantly over time (Table S2.1), and for rabbits, boobooks and frogmouths there was evidence of non-linear changes over time (represented by the quadratic effect in our model) (Table S2.1, Figure 2). There also was a significant interaction between time and vegetation type for all species except brushtails and ringtails, but with different patterns exhibited by each species; there was no evidence of different non-linear effects of time in different vegetation types (Table S2.1). The abundance of kangaroos increased fastest in regrowth and coppice, while foxes increased fastest in old-growth and plantings (but there was little change in regrowth). There was no change in abundance over time for brushtails and ringtails (Table S2.1). The abundance of rabbits and boobooks increased initially in all vegetation types but then decreased, although the decrease was not as pronounced in old-growth and regrowth for rabbits, and coppice and regrowth for boobooks. Frogmouths exhibited no evidence of change over time in regrowth, but increased in the other three vegetation types.

Stage 2: Climate and weather in addition to vegetation type and time

Our second set of models tested for two- and three-way interactions between climate, weather, vegetation type and time (Figure 3), adjusting for the effects of patch area as before. Below we describe effects that were statistically significant in the analyses of deviance (Table S3.1 in Appendix 3).

We found that kangaroos were more than three times as abundant on sites with high long-term rainfall compared to low long-term rainfall (Table S4.1 in Appendix 4), but were almost half as abundant on sites with high short-term net rainfall compared to low short-term rainfall (Table S4.2). We used the 10 and 90 percentiles of the range of the rainfall variables to

represent “low” and “high” values here and in the subsequent results. The three-way interaction also was significant: there was much less association of abundance with long-term rainfall in old-growth or plantings during droughts, but there was a negative association in plantings that received high short-term net rainfall. There was little association between kangaroo abundance and short-term rainfall in coppice sites characterized by low long-term rainfall; but low net rainfall was associated with decreased kangaroo abundance in old-growth that received high long-term rainfall, and plantings that received low average rainfall (Table S4.3, Figure 3).

Brushtails and ringtails exhibited limited association with short-term average monthly net rainfall. The only significant effect was for brushtails, where there was an interaction between vegetation type and long-term rainfall: the abundance of this species was significantly lower in plantings with high long-term rainfall (Table S4.4).

The abundance of rabbits was strongly associated with rainfall patterns, particularly short-term net rainfall. The species was twice as abundant on sites with high short-term net rainfall than low short-term net rainfall (Table S4.5). This pattern was evident only on sites with low long-term rainfall (Table S4.7) and characterized all vegetation types, although the pattern was weakest in plantings (Table S4.7).

The model for foxes contained evidence of an interaction between short-term and long-term rainfall, with the pattern of higher abundance with high short-term net rainfall at sites with low long-term rainfall, reversed at sites with high long-term rainfall (Table S4.8).

The abundance of boobooks was strongly associated with rainfall. The species was more abundant on sites with low long-term rainfall than high long-term rainfall (Table S4.9), and on sites with high short-term net rainfall compared to low short-term net rainfall (Table S4.10). The three-way interaction also was significant, with the average effect of long-term

rainfall noted above being reversed on regrowth and plantings characterized by low short-term rainfall (Table S4.11). The average effect of short-term net rainfall was also reversed in coppice sites with low long-term rainfall, and also plantings with high long-term rainfall.

The abundance of frogmouths was not strongly associated with rainfall, although the three-way interaction between vegetation type, long-term rainfall and net short-term rainfall was statistically significant. However, the differences in abundance in response to these covariates were small (Table S4.12).

DISCUSSION

Long-term monitoring data are critical for quantifying the population dynamics of species (Krebs 1978; Lindenmayer et al. 2012a; Reinke et al. 2019; Scheele et al. 2019). Such data are also important to determine the effects of key drivers of change, ranging from abiotic factors like climate and weather, to biotic attributes such as vegetation cover (Lindenmayer et al. 2018a). We made a series of *a priori* predictions as part of testing eight hypotheses (see Table 1) associated with the main and interacting effects of climate (long-term rainfall), weather (short-term net rainfall), and vegetation type on temporal patterns of abundance in seven species of nocturnal mammals and birds in the endangered temperate woodlands of south-eastern Australia. We uncovered evidence for varying levels of support for these hypotheses, with marked inter-specific responses not only to the main effects of vegetation type, long-term climate, and short-term weather, but also interactions among these three key covariates. We found relatively few species responded to the vegetation structure hypothesis (see Table 1) in the way predicted at the outset of this investigation. Not surprisingly, we found strong evidence of positive patch area effects for several species, highlighting the need to account for the influence of this variable in quantifying other effects (such as long and short-term rainfall and vegetation type). We further discuss these findings as well as other key results from our study in the remainder of this paper.

Time hypothesis - patterns of temporal change

We found limited empirical support for the time hypothesis, with two species (kangaroos and foxes) exhibiting a temporal increase in abundance and therefore opposite to our predictions at the outset of this study (see Table 1). No species declined consistently over time, although two species first increased then declined. The reasons for these findings are unclear because much of our study encompassed severe drought periods when animal abundance would be expected to decline, as has been documented for many species of diurnal birds at the same sites that were the focus of this study (Lindenmayer et al. 2018b). It is possible that the patterns we observed were related to the outset of our field surveys coinciding with extremely depressed levels of rainfall during the height of the Millennium drought, which thereby reduced animal numbers, only for these to increase once more rainfall occurred following the break of the drought. However, this interpretation is not consistent with our findings from tests of the resource and weather pulse hypothesis (see below).

Our results showing temporal increases in occurrence for some species are unlikely to be linked to factors like observer proficiency because the same set of highly experienced observers were responsible for field data collection. We also note there has been limited change in overall farm or landscape-wide vegetation cover over the duration of the study, although there has been clearing in some regions. A possible explanation is that drought conditions may have served to concentrate animals in remaining areas of native vegetation. Such kinds of “concentration effects” may explain temporal increases in the abundance of animals often associated with open areas such as kangaroos. An additional or alternative explanation for increased abundance over time is widespread destocking of livestock (Sheep [*Ovis aries*] and Cattle [*Bos taurus*]) during drought periods (e.g. <http://www.agriculture.gov.au/abares/research-topics/agricultural-commodities/sept-2018/beef>). This may, in turn, favour species like kangaroos through limiting negative

impacts on habitat suitability, reducing competition for food, or both. Notably, previous studies have shown that changes in short-term weather can influence inter-specific competition (Bateman et al. 2012). Finally, as we did not survey each site annually, the increases in abundance that we documented under drier conditions may reflect recruitment that occurred in response to rainfall in non-surveyed years.

We recognize that some of the temporal responses we have documented may have been associated with management interventions such as pest control, including for rabbits and foxes. Unfortunately, detailed information on control measures employed for these species was not available. Landholders simply have not kept reliable records of such efforts.

Vegetation structure hypothesis and vegetation type stability hypothesis

We found partial support for the vegetation structure hypothesis with brushtails and ringtails most often recorded in old growth and rarely in plantings. The absence of large old trees with hollows in 10-25 year old restoration plantings (Vesk et al. 2008) is a likely reason for the paucity of detections of these obligate or facultative cavity-dependent mammal species in this kind of vegetation.

We found no evidence that plantings were refuges for pest species such as foxes and rabbits, nor for native species (like kangaroos) that can sometimes become over-abundant. This suggests that arguments against restoring woodlands because they are havens for pests cannot be sustained.

We tested for vegetation type x time interactions (termed the vegetation type stability hypothesis; see Table 1). At the outset of this study, we predicted that temporal changes in animal abundance would be greatest in plantings as these sites experience the fastest relative rate of change in vegetation structure (Lindenmayer et al. 2016a). Opposite to our initial predictions, we found that kangaroos and foxes increased fastest in old-growth woodland

relative to other vegetation types. It is possible this is an artefact of detectability by spotlighting in the more open old-growth woodland environment, despite restricting our counts to animals recorded within 50 metres of either side of the transect line at each site. We note that our data were not appropriate for conducting detection/occupancy analyses. We therefore cannot discount the possibility that differences in detectability between broad types of sites may have influenced our findings.

Long-term productivity hypothesis

Part of our test of the long-term productivity hypothesis entailed quantifying relationships between animal abundance and long-term rainfall. Kangaroos responded positively to this key climate variable as a main effect. Higher long-term rainfall can result in greater site productivity and hence potentially more resources such as food. Unexpectedly, the abundance of boobooks was negatively associated with sites that had higher long-term rainfall. One possible explanation for this relationship is that hollow formation is delayed in trees on sites subject to less water stress (Gibbons et al. 2000; Rayner et al. 2013) and hence such places may support fewer nesting sites for cavity-dependent species such as boobooks. However, there were no such long-term climate relationships for other cavity-using species (e.g. brushtails), suggesting that other, currently unknown factors may have influenced our results.

Resource and weather pulse hypothesis

We found support for the resource and weather pulse hypothesis for rabbits and boobooks. That is, the model for these species contained a significant positive effect of net short-term rainfall. Greater short-term rainfall may lead to greater quantities of food for these species.

Environment-vegetation type hypothesis

The response of only one species, brushtails, was characterized by an interaction between long-term rainfall and vegetation type. The abundance of the species was lowest in plantings

on climatically-wet sites. The underlying reasons for this effect remain unclear. Brushtails are an obligate hollow-using species (Gibbons and Lindenmayer 2002). Trees with hollows are generally rare in plantings (Vesk et al. 2008) and are most likely to develop in woodlands under physiological stress (Ikin et al. 2015). This may mean that hollow trees would be especially rare in plantings in wetter climates. An alternative explanation may be that the result is an artefact of the limited number of observations of this species in plantings. This suggests that further data gathered over a longer period than the 15 years of this study may be required to better determine the mechanisms leading to the patterns we observed.

Environment-weather pulse hypothesis

We found evidence of a significant interaction between long-term climate and short-term weather (and hence support for the environment-weather pulse hypothesis) for foxes. The species responded positively to high levels of short-term net rainfall, but only on climatically-dry sites. The abundance of this species may be relatively close to carrying capacity on climatically-wet sites and hence there may be limited potential for further increases in abundance in response to short-term rainfall.

Three-way interactions among vegetation type, long-term climate and short-term weather

Our analyses contained evidence of three-way interactions between vegetation type, long-term climate, and short-term weather for boobooks and frogmouths. The effects of additional rainfall on animal abundance varied dependent on whether it occurred in old-growth, plantings or regrowth or coppice in long-term wet versus dry locations (Figure 3, Figure S4.1). In the case of boobooks, a possible reason for such climate and weather effects may be associated with differences in vegetation structure. Old-growth is characterized by a greater abundance of larger and older trees than regrowth and plantings (Ikin et al. 2015), especially on climatically-wet sites (where rates of growth are likely to be faster and overall levels of

biomass are inherently higher (Soderquist and MacNally 2000). This may lead to old-growth located in wetter long-term climates being more productive after rain and supporting greater populations of prey.

Concluding comments

In our study, the abundance of different species was associated with vegetation type and varied in response to long-term climate conditions and fluctuations in net short-term rainfall. Our findings highlighted that multiple factors at multiple scales (e.g. local scale vegetation type and regional climate and short-term weather conditions), can together have an important influence on abundance. Finally, our results showed that interactions between key drivers can have important effects on temporal patterns of abundance (see Côté et al. 2016; Foster et al. 2016), including in regions subject to extensive land use change such as those dominated by agricultural production (Brodie 2016). Our study highlights the value of long-term monitoring at a landscape scale for examining how multiple interacting factors influence trends in animal abundance over time.

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Table 1. Hypotheses associated with response of mammals and birds to long-term climate, short-term weather, and vegetation type.

Hypothesis	Description	Prediction	Citation/s
Time hypothesis	Marked declines have been documented in a wide range of species in many ecosystems globally. However, many studies have shown a mix of increasing and declining species.	There will be a negative relationship between time and the abundance of native mammal and bird species	(Ceballos et al. 2017; Intergovernmental Science-policy Platform on Biodiversity and Ecosystem Services (IPBES) 2019).
Vegetation structure hypothesis	Stands of temperate woodland are characterized by marked differences in structure, particularly the presence of large old trees, stem density, and the amount of ground cover. Differences in structure can influence animal populations.	Hollow-dependent species will be most abundant in old-growth where large old trees are more common. Non-hollow dependent species will be more abundant in plantings.	(Ikin et al. 2015; Vesk et al. 2008)
Long-term productivity hypothesis	Long-term climatic regimes characterized by wetter conditions can underpin greater levels of plant growth and productivity, especially in temperate woodlands where rainfall can be a limiting factor. This can affect the availability of food resources for animal populations.	The abundance of target species will be highest in the wetter locations in our study region	(Barea and Watson 2007)
Resource and weather pulse hypothesis	Short-term weather can have profound impacts on populations of a wide range of animals, particularly through impacts on the availability of resources such as food and water.	The abundance of animals will be suppressed during drought conditions and greater during wet periods.	(Aranzamendi et al. 2019; Bayliss 1987; Greenville et al. 2012; Pople and Grigg 1999; Seabrook et al. 2011)

Vegetation type stability hypothesis	Temporal changes in vegetation structure and composition can influence habitat suitability for biodiversity. Rates of change in plantings are relatively rapid for attributes like stem density and canopy height but comparatively slow in old-growth woodland. The rates of change in vegetation structure may influence the rate of change in abundance of animal populations.	Temporal changes in the abundance of target species of animals will exhibit the least change in old-growth and greatest change in plantings.	(Lindenmayer et al. 2016a; Pulsford et al. 2016)
Weather refuge hypothesis	Differences in vegetation structure can result in differences in key resources with effects on biodiversity during weather extremes. For example, the greater abundance of flowers, nectar and pollen associated with large old trees may make old-growth woodlands key refuges during prolonged dry periods.	The highest abundance of target species during droughts will be in old growth relative to regrowth and plantings.	(Betts et al. 2017; Lindenmayer and Laurance 2016)
Environment-weather pulse hypothesis	Underlying long-term climate may influence the ability of the vegetation at a site to respond to short-term weather. For example, the impacts of increased short-term rainfall may be more muted in lower productivity environments characterized by long-term dry climate where there are inherently fewer resources.	Animal abundance in climatically drier areas will be suppressed relative to locations with wetter long-term climatic conditions.	(Nimmo et al. 2016)
Environment-vegetation type pulse hypothesis	The rate of growth and structural development of vegetation is strongly shaped by underlying long-term climatic conditions. A vegetation type x long-term climate interaction may manifest through, for example, the influence of rainfall on the relative levels of cover of overstorey and understorey layers. Such vegetation type differences in woodland structure may, in turn, affect habitat suitability for animals.	Animal abundance will be depressed in plantings in locations characterized by long-term dry climate.	(Huggett and Cheeseman 2002; Ikin et al. 2015; Specht and Morgan 1983; Specht and Specht 1999; Yamaura et al. 2019)

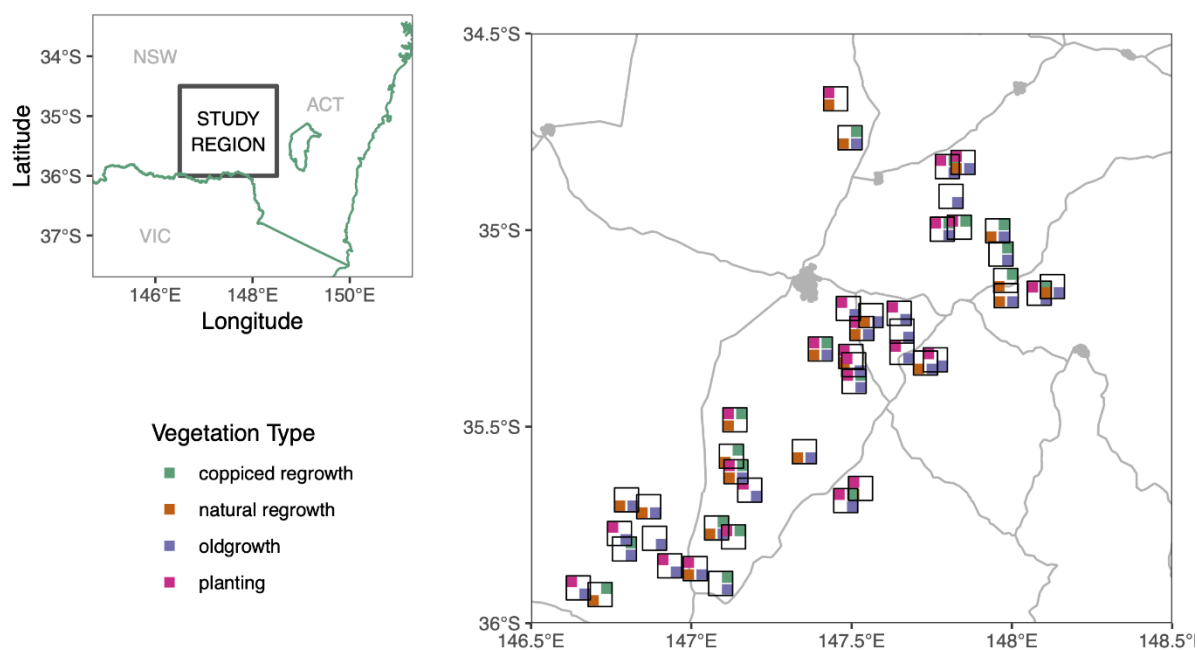
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540

FIGURE CAPTIONS

Figure 1. Location of the study area targeted for long-term surveys of nocturnal animals. Black squares designate surveyed farms, with internal squares showing the vegetation types that were surveyed on each farm.



547 **Figure 2. Estimated abundance of each species over time in each of four vegetation**
 548 **types, adjusted for average patch area (7.62 ha).**

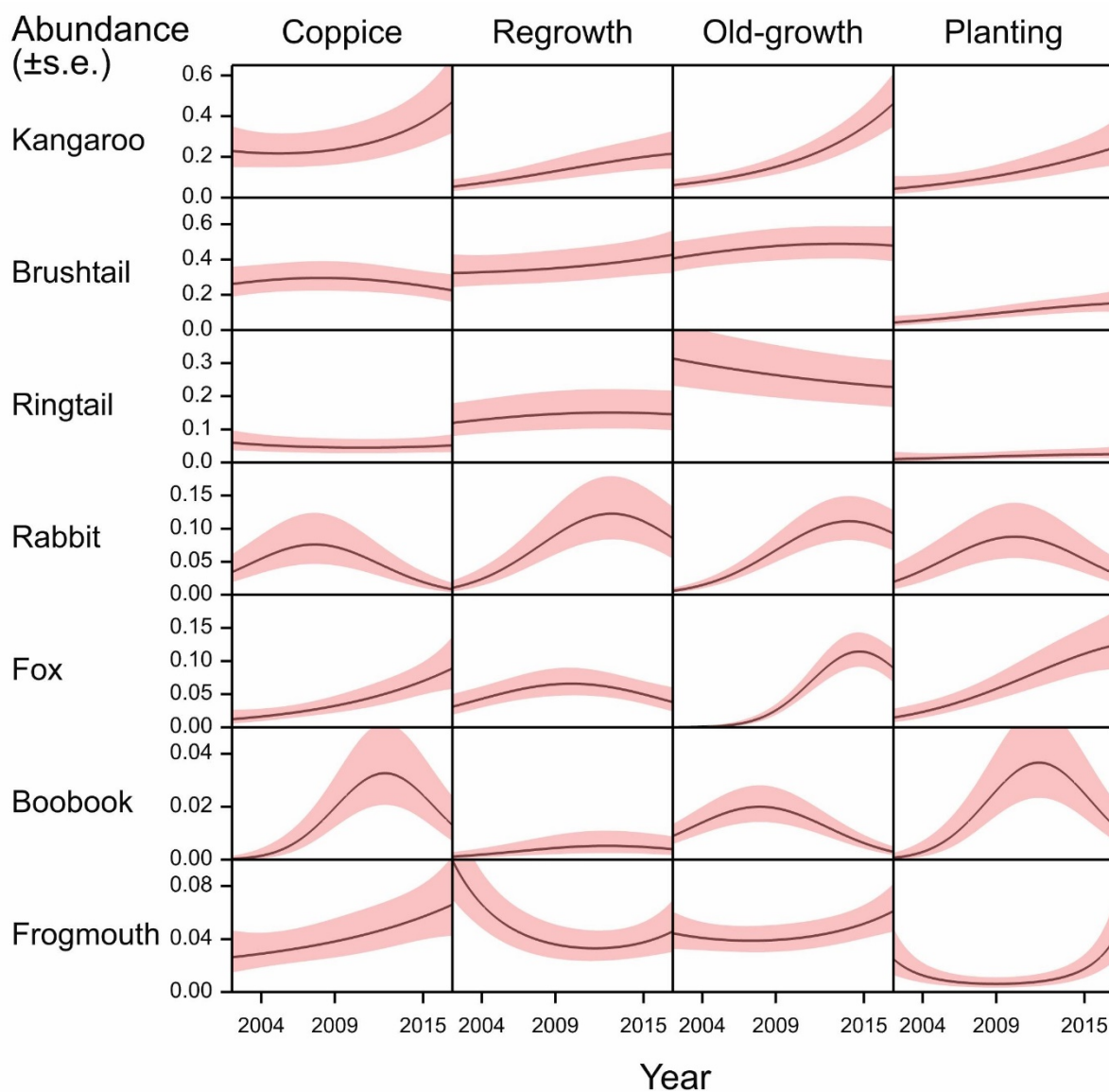


Figure 3. Effect of long-term average monthly rainfall on animal abundance, split by species and vegetation type, and showing predictions for both low (red lines) and high (blue lines) short-term average monthly net rainfall.

