



Do reptile responses to habitat structure and time since fire depend on landscape structure?

S.J. Mulhall^{a,*}, J. Di Stefano^a, A. Dorph^b, M. Swan^a, H. Sitters^{a,c}

^a School of Agriculture, Food and Ecosystem Sciences, University of Melbourne, 4 Water Street, Creswick, VIC 3363, Australia

^b School of Environmental and Rural Science, University of New England, Elm Avenue, Armidale, NSW 2351, Australia

^c Australian Wildlife Conservancy, P.O. Box 8070, Subiaco East, WA 6008, Australia

ARTICLE INFO

Keywords:

Habitat suitability
Land use change
Landscape modification
Fire management
Squamata
Heathy woodland

ABSTRACT

Land use changes, such as the development of agriculture and plantation forestry, and altered fire regimes, are major drivers of biodiversity loss worldwide, influencing the availability of suitable habitat for species. Reptiles are sensitive to both these processes as they are influenced by native vegetation extent and habitat structure. While much is known about the independent effects of fire and land use change on species distributions, few studies have investigated potential interactive effects; specifically, whether the influence of site-scale variables on reptiles depends on the properties of the surrounding landscape. We sampled reptiles at 107 sites in fire-prone heathy woodland, interspersed with plantation forestry and agriculture in south-west Victoria, Australia. We investigated the responses of seven reptile species to both site-scale variables (time since fire and several measures of habitat structure) and landscape-scale variables (extent of native vegetation and plantations and the presence of pasture within a 3.14 square km area) to 1) identify whether species' responses to fire and habitat depended on landscape structure, and 2) examine the relative influence of time since fire, habitat structure and landscape structure on reptile abundance. We predicted that responses to site-scale variables would vary with a key landscape structure variable: the amount of native vegetation cover. Further, we predicted that site-scale variables would be stronger predictors of species abundance than landscape-scale variables. Generalised linear models, accounting for imperfect detection, were used to estimate species responses to site and landscape-scale predictors. For two species (*Amphibolurus muricatus* and *Liopholis whitii*) there was evidence that their responses to site-scale variables depended on landscape structure. However, contrary to our first prediction, native vegetation cover was not the only landscape structure variable that influenced species' responses to site-scale variables. Three species (*Acrisoscincus duperreyi*, *A. muricatus*, and *Lerista bougainvillii*) responded to both habitat structure and landscape structure variables, though the relative influence of the variables at the different scales was varied among the species. One species (*Lampropholis guichenoti*) responded to fire and habitat structure variables at the site-scale but did not respond to landscape structure. One species (*Aprasia striolata*) responded to landscape structure variables but not to site-scale variables. Our second prediction, that site-scale variables would be the strongest predictors of abundance, was true for two species, but overall, our results were varied, with species responding at both scales. Examining species' responses to drivers at multiple spatial scales is essential for conservation management, as even species with low dispersal capacity such as reptiles can respond to processes occurring at large spatial scales.

1. Introduction

Biodiversity decline is occurring worldwide as suitable habitat for many species becomes depleted. Major drivers of habitat loss include disturbances from altered fire regimes and changes to land use (Haddad et al., 2015; Kelly et al., 2020). While much is known about the

independent effects of these processes on biodiversity, there is growing acknowledgement that they may also operate in combination, with the potential for interactive effects (Didham et al., 2007; Ewers and Didham, 2007; Geary et al., 2019; Driscoll et al., 2021). Understanding interactions between threatening processes is critical for conservation since some processes may have limited or no negative effects on

* Corresponding author.

E-mail address: sarah.mulhall@unimelb.edu.au (S.J. Mulhall).

<https://doi.org/10.1016/j.foreco.2023.121564>

Received 31 October 2023; Accepted 2 November 2023

Available online 15 December 2023

0378-1127/© 2023 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

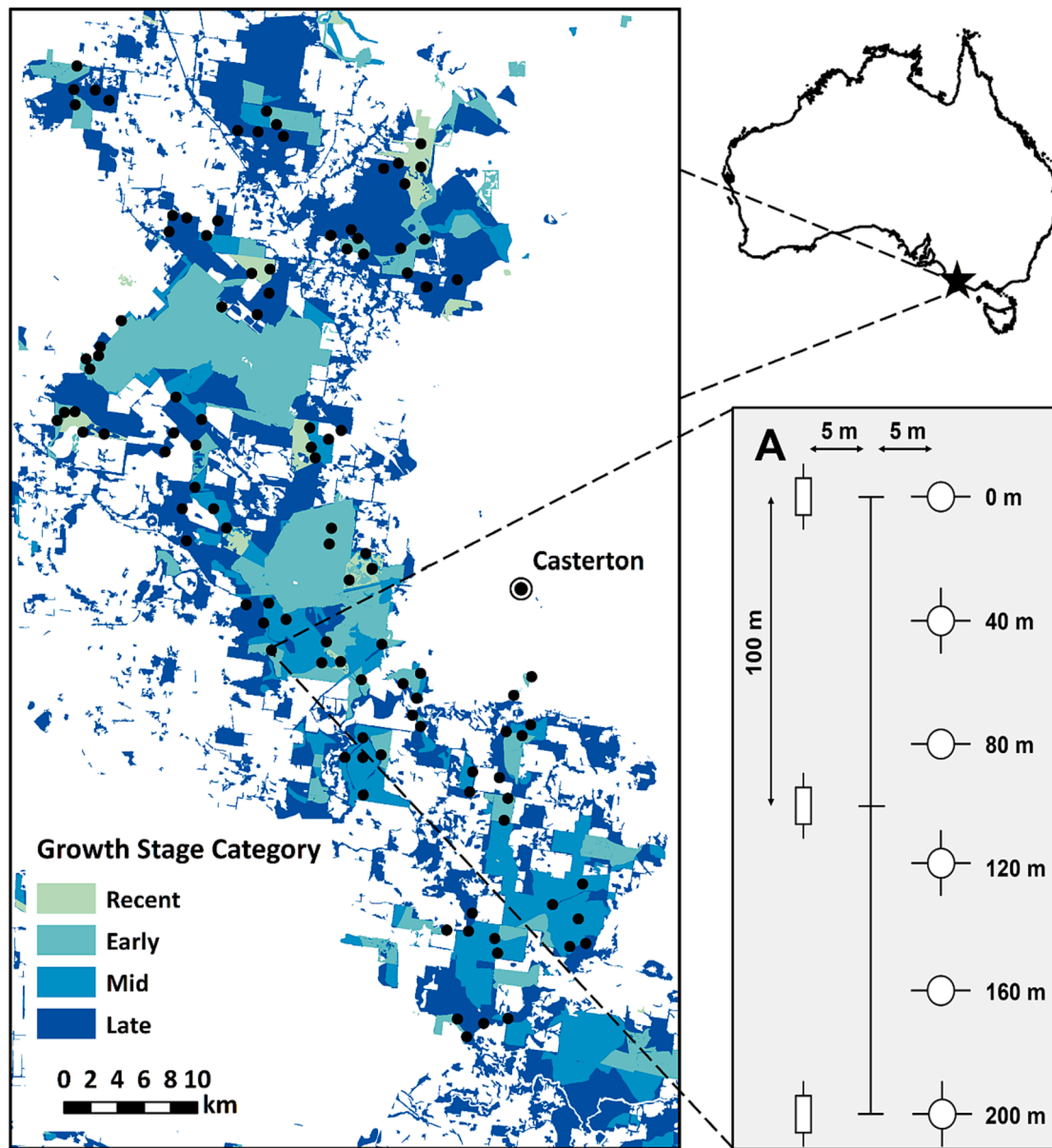


Fig. 1. Location of the study area and survey sites near Casterton, southeast Australia. Black dots indicate location of sites in native vegetation. Growth stage categories after Cheal (2010): recent (0–3 yrs); early (4–10 yrs); mid (11–34 yrs); and late (35 + yrs). White areas indicate pasture and plantations. Inset A shows the layout of pitfall and funnel traps along each 200 m transect. Circles represent pitfall traps (spaced 40 m apart), and rectangles represent pairs of funnel traps (spaced 100 m apart).

biodiversity when acting alone, but acting synergistically can drive populations to extinction (Doherty et al., 2015; Paterson et al., 2021). Models that specifically incorporate interactions are an important tool that allow us to test predictions about the response of species to interacting drivers and improve ecological management in these systems (Didham et al., 2007).

Fire is a natural process shaping the diversity of species and ecosystems across the globe (Bowman et al., 2009; Kelly et al., 2020). Fire is also known to increase the impact of other processes, including the spread of weeds (Brown et al., 2016), grazing (Raffaele et al., 2011; Legge et al., 2019) and predation (Doherty et al., 2015; Hradsky, 2020; Nalliah et al., 2022). Interactions between fire and other processes are likely to become more common in many parts of the world as climate change increases the size and frequency of fires, and fire begins to occur in ecosystems where it was previously rare or absent (Kelly et al., 2020). As such, further research is necessary to improve our understanding of interactions between fire and other processes, and their implications for

biodiversity, in order to develop effective conservation management strategies (Driscoll et al., 2010; Driscoll et al., 2021).

Globally, many landscapes are subject to change from land uses such as timber harvesting, agriculture, urbanization, and mining (Haddad et al., 2015; Potapov et al., 2017), with many regions influenced by multiple competing land uses (Gill and Williams, 1996; Triska et al., 2017). These activities result in altered landscape structure, defined as the composition and spatial configuration of different land use types (Bennett et al., 2006), and the influence of landscape structure on biodiversity is subject to substantial research (Fahrig, 2003; Bennett et al., 2006; Haddad et al., 2015). Fire (both prescribed fire and wildfire) often occurs in multi-use landscapes, and there is an extensive body of research investigating the response of plants and animals to fire metrics such as time since fire and fire frequency (Driscoll et al., 2010; He et al., 2019). However, the response of biodiversity to the interactive effects of fire and landscape structure remains a critical knowledge gap (Sitters and Di Stefano, 2020; Driscoll et al., 2021). Available research on

animals indicates that species' responses to fire may depend on the structure of the surrounding landscape (e.g. Hossack et al., 2013; Delaney et al., 2021; Santos et al., 2022; Zylinski et al., 2022). For instance, Zylinski et al. (2022) showed that a particular fire age-class (mid-successional vegetation) only had a positive influence on the richness of native woodland mammals when the extent of cleared land in the surrounding landscape was high.

Of concern is the potential for negative synergistic interactions between fire and landscape structure where the interacting effects result in worse conservation outcomes compared to the sum of the individual influences (Brook et al., 2002). This may occur when habitat loss and other changes to landscapes that cause habitat degradation, such as replacing native vegetation with plantations or urban settlements, exacerbates the effects of fire on already threatened species (Santos et al., 2022). For example, the abundance of Blue Mountains water skinks (*Eulamprus leuraensis*) is negatively correlated with recent fire and fire frequency as well as proximity to urbanization, indicating that effects of inappropriate fire management may be especially heightened in urban areas (Gorissen et al., 2015; Gorissen et al., 2018).

Australia is considered a reptile hotspot and has a rich diversity of squamate reptiles (lizards and snakes) with almost 1,100 species, most of which are endemic (ABRS, 2023; Uetz, 2023). Despite this diversity, there is limited knowledge of the ecology, distributions, and population trends for most species (Tingley et al., 2019; Chapple et al., 2021; Senior et al., 2021), and few studies have explicitly focused on heathy woodland communities (but see Friend, 1993; Lindenmayer et al., 2008; Ensbey et al., 2023). As ectotherms, reptiles have fundamentally different traits and life history strategies from other vertebrates, and therefore may also be expected to respond differently to disturbances (Doherty et al., 2020; Van Dyke et al., 2021). Reptiles are expected to be vulnerable to both fire and landscape structure due to their relatively low dispersal ability, small home ranges, energy use, and thermoregulatory strategies (Böhm et al., 2013; Tingley et al., 2019; Doherty et al., 2020; Mulhall et al., 2022). Furthermore, many reptiles are closely associated with elements of habitat structure that may be affected by fire, such as leaf litter, canopy cover, and understorey cover (Caughley, 1985; Driscoll and Henderson, 2008; Elzer et al., 2013; Infante et al., 2021). As such, various species have been found to respond to aspects of the fire regime, including time since fire, although substantial variability in responses has also been detected, including many null responses (Driscoll and Henderson, 2008; Smith et al., 2013; Hu et al., 2016; Nimmo et al., 2013; Santos and Cheylan, 2013). It is possible that considering fire and landscape structure concurrently may improve the capacity to predict fire responses in a wider range of species.

Preferences for particular fire regimes have often been linked to reptile species traits, and therefore inappropriate fire management is predicted to threaten certain species in fire-prone areas (Fenner and Bull, 2007; Nimmo et al., 2013; Shine et al., 2016). Indeed, a recent review found that fire is a threat to 43% of Australian squamates of conservation concern (Santos et al., 2022). Habitat loss and modification has been found to have a primarily negative effect on reptile abundance (Doherty et al., 2020), with agriculture amongst the most common sources of threat in Australia (Tingley et al., 2019) and worldwide (Böhm et al., 2013; Cox et al., 2022). Selective loss of habitats in south-eastern Australia, including native woodlands and grasslands, has disproportionately impacted certain taxa, including fossorial reptiles (Brown et al., 2008).

We conducted a multi-scale study to assess the responses of reptile species to time since fire, habitat structure, and landscape structure in a fire-prone, fragmented landscape in southeastern Australia. The aims of our study were to: 1) identify whether species' responses to time since fire and habitat structure were influenced by the structure of the surrounding landscape, and 2) examine the relative influence of site-scale variables (i.e. time since fire and habitat structure) and landscape structure variables on reptile abundance. We predicted that species responses to site-scale variables would vary with a key landscape structure

variable: the amount of native vegetation cover in the surrounding landscape. This is because native vegetation extent is likely to influence a range of processes, such as landscape connectivity, proximity to disturbance, and abiotic conditions, which are expected to influence species abundance (Wilson et al., 2016; Banks-Leite et al., 2020). Further, we predicted that site-scale variables would be stronger predictors of species than landscape-scale variables, owing to their reduced dispersal ability, small home range size and close association with habitat structure (Michael et al., 2016; Pinto et al., 2018).

2. Methods

2.1. Study area

The study was conducted in dry eucalypt woodlands across an area of ~320,000 ha in south-western Victoria, Australia (Fig. 1). The climate is mild with mean annual minimum and maximum temperatures of 8.3 °C and 20.1 °C respectively (Bureau of Meteorology, 2017). There is a rainfall gradient across the study area, with the mean annual rainfall ranging from 625 mm in the north to 735 mm in the south. Elevation above sea level ranges between 75 and 131 m.

This area was selected as an ideal location for studying the effects of both fire and landscape structure on reptiles as the native vegetation features a diverse fire history and is fragmented by agriculture and plantation forests. Native vegetation is primarily heathy woodland, which is characterised by a low canopy of desert stringybark (*Eucalyptus arenacea*) and brown stringybark (*Eucalyptus baxterii*), and a sparse understorey dominated by grass trees (*Xanthorrhoea australis* and *Xanthorrhoea caespitosa*), *Banksia* spp., *Leptospermum* spp., and a diverse range of heathy shrubs (Duff et al., 2013). Prescribed fire has been used as a tool for managing fuel loads and reducing bushfire risk to communities in the region since 1970 (Dess, 2016). Incidence of both prescribed fires and wildfires (including large wildfires in 1939 and 1983) have resulted in a range of post-fire growth stages (also known as age classes, seral stages or successional stages) in native vegetation patches. Fire severity has only been mapped routinely over the past decade, and was therefore not factored into this study. The area overlaps a major forestry region known as the 'Green Triangle'; plantation forests of pine (*Pinus radiata*) have been planted and harvested since the 1900s with eucalyptus (*Eucalyptus globulus*) plantations more recently established (URS Forestry, n.d.).

2.2. Survey design

We stratified native vegetation into four growth stage categories, representing major developmental stages in vegetation succession, following Cheal (2010): recently burnt (0–3 yrs); early successional (4–10 yrs); mid successional (11–34 yrs); and late successional (35 + yrs). We established 107 sites in the native vegetation using a restricted random protocol to sample the variability in both growth stages and landscape structure (Fig. 1). Sites were set up in loose clusters of five to increase survey efficiency. Potential sites were first identified in QGIS (version 2.18), followed by ground-truthing to ensure that patches of native vegetation were intact and had not experienced heavy disturbance (QGIS Development Team, 2016). Sites were positioned at between 50 and 200 m from roads to reduce edge effects and for ease of access, and at least 1 km apart to increase independence. Reptiles were surveyed at each site along a 200 m transect positioned at a random bearing.

2.3. Reptile survey protocol

Each 200 m transect consisted of six pitfall traps (20 L buckets buried level with the ground) and six funnel traps (18 × 18 × 79 cm), described in Thompson and Thompson (2007). The six pitfall traps were set along the transect at 40 m intervals, while the six funnel traps were set in pairs

Table 1

Site-scale, landscape-scale and interaction models used in abundance modelling of reptile species. There were 23 models in total.

Model type	Model
Site-scale variables	~ site-scale variable
bare ground	
canopy cover	
coarse woody debris	
leaf litter	
time since last fire (TSF)	
Landscape-scale variables	~ landscape-scale variable
native vegetation	
pasture	
plantation	
Interactions between site- and landscape-scale variables	~ site-scale variable × landscape-scale variable

at 100 m intervals. Drift fences, made from black polyethylene damp-course, were installed to improve detection rates (Fig. 1, insert A). To reduce the risk of heat stress and predation to animals caught in the pitfall traps, a short length of PVC pipe, a piece of cardboard carton, and a handful of leaf litter were placed at the bottom of each bucket. To reduce heat stress in funnel traps, covers made from 90% shade cloth were pinned down across the top of the pairs of traps (Thompson and Thompson, 2009).

Trapping was conducted for five consecutive nights at each site over the spring and summer of 2017/2018 (Nov – Apr). To increase trapping efficiency, clusters of 5–7 sites were surveyed during each trapping period. Traps were checked in the morning and late afternoon, and captured animals were identified and released on site. All animals except venomous snakes were marked with a marker pen to identify any individuals that were recaptured within the five-day trapping period. These data were used to define the number of unique individuals counted per day over the five-day trapping period. In subsequent analysis (described below) the total count was used as the response variable and the detection history (daily count) used to estimate and account for imperfect detection.

2.4. Site-scale predictors

At each site we used six 10 × 10 m plots spaced at 40 m intervals and centred on the pitfall traps (Fig. 1) to derive four habitat structure variables: leaf litter, bare ground, coarse woody debris, and canopy cover. Leaf litter was collected from two randomly selected points in each plot (12 samples per site) using a 0.1 m² fuel sampling ring. Samples were dried at 105° C for 48 h, and then their dry weights averaged to obtain the mean dry weight of the leaf litter at each site (Penman and York, 2010). Bare ground cover was visually estimated across a circular area with a two-metre radius from three random points within the plot. Canopy cover was calculated from the centre of the 10 m plot using photographs taken at ground level. To ensure only canopy cover was being captured in the photographs, any ground level vegetation was moved aside. Photographs were taken using a digital camera and analysed in Image J (Pérez and Pascau 2013) to provide a measure of percent canopy cover. Presence of logs > 5 cm in diameter and > 50 cm long were counted within each quarter of the plot. Site-level values for each habitat structure variable were calculated as means of the plot-level values. In addition to the habitat structure variables described above, we also measured the following: basal area, Xanthorrhoea cover, and under- and mid-storey cover at 0–50 cm, 50–100 cm, 100–150 cm, and 150 – 200 cm. However, as exploratory analysis showed that these variables were highly correlated with other variables (i.e. basal area) or generally less important predictors of reptile species in our study, they were not included in the final models.

We obtained a fire history map from the Victorian Department of Environment, Land, Water and Planning. Time since last fire (TSF) values, indicating the number of years since the last fire in 2017, were

extracted for each of the 107 sites where reptiles were surveyed.

2.5. Landscape-scale predictors

A map of vegetation cover at a scale of 1:25,000 was downloaded from the Victorian Government's open data platform, www.data.vic.gov.au. To quantify the structure of the surrounding landscape, we calculated the area of native vegetation, pasture, and timber plantations within a 1 km radius of each site centred on the mid-point of the transect using ArcMap 10.5 (ESRI, 1995). We selected 1 km as the length of the radius as this was shown to capture the variability in our focal landscape variables. Further, previous research on other fauna in the study area indicated that species responded most strongly to landscape structure in landscapes with radii between 500 and 1500 m (Delaney et al., 2021) and the midpoint of this range seemed reasonable for our study. While it would be informative to model the response of reptiles to a range of spatial scales that was beyond the scope of our work. Due to the relatively small range in the area of pasture, these figures were converted to binary values to indicate the presence or absence of pasture within a 1 km radius of each site. While land uses other than native vegetation, pasture and plantation were present in the region these were all of a negligible area; so, for example, properties surrounded by pasture were mapped as pasture.

2.6. Detection covariates

Since reptile activity is known to be influenced by weather and season, we recorded temperature and rainfall at a subset of 55 sites spread through the study area for the period of trapping (Spence-Bailey et al., 2010). Rainfall, which was very infrequent, was measured using rain gauges as the presence or absence of rain, and temperature was measured with HOBO U23 Pro V2 data loggers (Onset Computer Corporation, Bourne, MA, USA) placed at the beginning of the transect. Calendar date was used to represent the time of year between spring and summer.

2.7. Statistical analysis

All statistical analysis was conducted in R (version 4.2.0, R Core Team, 2020). We applied a negative binomial N -mixture model (Royle, 2004) via the `pcount` function in the `unmarked` package (Fiske and Chandler, 2011) to model the relative abundance (number of unique individuals per site) of seven species (eastern three-lined skink (*Acritoscincus duperreyi*), jacky dragon (*Amphibolurus muricatus*), lined worm-lizard (*Aprasia striolata*), garden skink (*Lampropholis guichenoti*), south-eastern slider (*Lerista bougainvillii*), southern grass skink (*Pseudemoia entrecasteauxii*) and White's skink (*Liopholis whitii*)) as a function site and landscape-scale predictor variables while accounting for imperfect detection and overdispersion. Only species that were detected at 10 or more sites were included (Table A1, Appendix) as we judged this necessary for robust results given our intention of including two variables and their interaction in our models (see below). Further, if a species was detected in a particular region of the study area (such as the southern grass skink, which was detected only at the southern end of the study area) then the data used in modelling was confined to the region where the species was detected and neighbouring sites within 5 km, so as to exclude areas outside the species' distribution.

Models were developed in two stages. Firstly, we modelled the probability of detection (p) using calendar date, maximum temperature, and rainfall as potential detection covariates. We built detection models using each of the three variables and their additive combinations and included a null model in this set. For each species, we chose the detection model that had the lowest values of Akaike's Information Criterion (AIC) for subsequent analysis (Table A2, Appendix).

In the second stage, we estimated the relative abundance of our seven focal species as a function of our site- and landscape-scale

Table 2

Responses of reptile abundance to time since fire, habitat structure and landscape structure. Top-ranked models ($\Delta\text{AIC} < 2$) and lower ranked ecologically important models for each species are displayed. Models are ranked by AIC. Number of parameters (nPars), R^2 , parameter estimates with lower and upper confidence limits (LCL, UCL), and P -values are also displayed. Time since fire (TSF), coarse woody debris (CWD).

Model and terms	nPars	ΔAIC	R^2	Estimate	LCL	UCL	P-value
Eastern three-line skink							
Canopy cover \times Pasture	8	0.00	0.19				
Canopy cover				-0.44	-0.71	-0.25	0.000
Pasture				-0.27	-0.16	0.23	0.009
Canopy cover \times Pasture				-0.13	-0.10	0.31	0.249
Canopy cover	6	3.34	0.14				
Canopy cover				-0.45	-0.67	-0.23	< 0.001
Pasture	6	12.90	0.06				
Pasture				-0.28	-0.49	-0.06	0.011
CWD	6	14.36	0.04				
CWD				-0.25	-0.47	-0.03	0.028
Native veg.	6	14.86	0.04				
Native veg.				0.23	0.01	0.45	0.036
Jacky dragon							
Canopy cover \times Plantation	8	0.00	0.10				
Canopy cover				-0.14	-0.48	0.21	0.439
Plantation				-0.46	-0.89	-0.04	0.032
Canopy cover \times Plantation				0.39	0.02	0.76	0.038
TSF \times Pasture	8	0.57	0.10				
TSF				-0.19	-0.59	0.22	0.370
Pasture				-0.14	-0.55	0.27	0.499
TSF \times Pasture				0.51	0.12	0.90	0.010
Bare ground	6	1.90	0.05				
Bare ground				0.30	0.03	0.57	0.027
Plantation	6	2.16	0.04				
Plantation				-0.37	-0.75	0.01	0.059
Lined worm-lizard							
Canopy cover \times Plantation	8	0.00	0.22				
Canopy cover				-0.64	-1.50	0.22	0.145
Plantation				-0.68	-1.60	0.25	0.153
Canopy cover \times Plantation				-0.92	-2.01	0.17	0.099
Native veg.	6	0.20	0.12				
Native veg.				0.62	0.00	1.23	0.048
Canopy cover \times Native veg.	8	0.24	0.21				
Canopy cover				-0.80	-1.88	0.28	0.146
Native veg.				0.62	-0.20	1.44	0.138
Canopy cover \times Native veg.				0.88	-0.20	1.97	0.111
Plantation	6	0.33	0.12				
Plantation				-0.61	-0.96	0.13	0.064
CWD \times Plantation	8	0.95	0.20				
CWD				-0.83	-2.17	0.50	0.221
Plantation				-1.03	-2.34	0.27	0.122
CWD \times Plantation				-0.98	-2.53	0.56	0.213
Garden skink							
Canopy cover	6	0.00	0.07				
Canopy cover				0.35	0.10	0.59	0.005
TSF	6	4.26	0.03				
TSF				0.23	-0.02	0.48	0.066
Bare ground	6	4.64	0.03				
Bare ground				-0.24	-0.51	0.03	0.079
Southeastern slider							
Bare ground \times Pasture	8	0.00	0.13				
Bare ground				0.22	0.04	0.39	0.014
Pasture				-0.29	-0.48	-0.09	0.004
Bare ground \times Pasture				-0.07	-0.24	0.11	0.464
Pasture	6	3.52	0.07				
Pasture				-0.28	-0.48	-0.08	0.006
Native veg.	6	3.93	0.06				
Native veg.				0.28	0.08	0.49	0.007
Plantation	6	6.05	0.05				
Plantation				-0.23	-0.44	-0.03	0.024
Bare ground	6	6.45	0.04				
Bare ground				0.20	0.02	0.39	0.028
White's skink							
CWD \times Native veg.	7	0.00	0.16				
CWD				-0.68	-1.52	0.15	0.109
Native veg.				1.14	0.12	2.16	0.029

(continued on next page)

Table 2 (continued)

Model and terms	nPars	Δ AIC	R ²	Estimate	LCL	UCL	P-value
CWD × Native veg.				1.34	0.47	2.21	0.003
Leaf litter × Native veg.	7	3.66	0.12				
Leaf litter				-1.04	-1.92	-0.16	0.021
Native veg.				-0.43	-0.97	0.12	0.125
Leaf litter × Native veg.				-0.75	-1.32	-0.18	0.010
Bare ground × Pasture	7	4.95	0.11				
Bare ground				0.78	0.07	1.50	0.032
Pasture				-0.52	-1.35	0.31	0.217
Bare ground × Pasture				0.69	-0.05	1.45	0.068
Bare ground	5	5.34	0.06				
Bare ground				0.65	0.05	1.24	0.034
Canopy cover × Native veg.	7	5.52	0.10				
Canopy cover				-0.54	-1.20	0.13	0.113
Native veg.				0.43	-0.32	1.19	0.258
Canopy cover × Native veg.				0.74	0.01	1.48	0.048
Canopy cover	5	5.79	0.05				
Canopy cover				-0.69	-1.38	0.00	0.051

predictors, including the best detection model derived in stage one. For each species we modelled their responses to 1) each of the five site-scale variables, 2) each of the three landscape-scale variables, and 3) 15 models representing the interaction between each site-scale variable and each landscape-scale variable (Table 1).

In both stage one and two variables were standardized prior to analysis. In stage two we checked for collinearity between each site-scale variable and each landscape-scale variable using the GGally package (Schloerke et al., 2021); the maximum Pearson's correlation between variables used in the same model was 0.37. In all models we used the default value of K, the upper bound of the summation over the possible values of abundance in the integrated likelihood (Royle, 2004), which is set to the maximum count for each species plus 100. Preliminary testing on datasets for each species showed that estimated parameters and AIC values changed very little when K was between 25 and 200. Finally, as our sites were clustered, we checked for positive spatial autocorrelation using of the residuals of the best model for each species. We used the ncf package to generate spline correlograms from 1000 permutations (Bjornstad, 2022) and did not detect positive spatial autocorrelation (Fig. A.1, Appendix).

2.8. Model comparison

The aim of the modelling was to 1) compare species responses to site-scale and landscape-scale variables and 2) determine if responses to site-scale variables depended on landscape-scale variables. To do this we performed model comparison for the full set of site-scale, landscape-scale, and interaction models (i.e. 23 models in total) (Table 1) and used AIC to rank the models for each species. Lower AIC values, where Δ AIC > 2, indicate models with greater parsimony. We used a weight of evidence approach (Muff et al., 2022) to identify noteworthy relationships between response and predictor variables where *P*-values < 0.001, ~ 0.001 – 0.01, ~ 0.01 – 0.05 and ~ 0.05 – 0.10 were considered to provide very strong, strong, moderate and weak evidence of a relationship. R² was used to measure goodness of fit.

3. Results

We recorded 1208 individual reptiles from 17 species in five families (Table A1, Appendix). Around 85% of the reptiles captured during this study belonged to one of three skink species (eastern three-lined skink,

southeastern slider, garden skink). Jacky dragons, lined worm-lizard, southern grass skink and White's skink were less abundant but detected at ≥ 10 sites and subjected to formal analysis. The remaining species (*Austrelaps superbus*, *Chelodina longicollis*, *Ctenotus robustus*, *Drysdalia coronoides*, *Eulamprus tympanum*, *Morethia obscura*, *Notechis scutatus*, *Pseudonaja textilis*, *Tiliqua nigrolutea*, *Tiliqua rugosa*) were detected at < 10 sites and were excluded from the analysis.

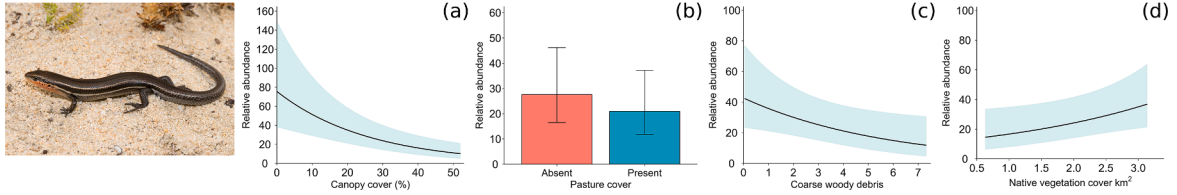
3.1. Responses to interactions between site- and landscape-scale variables

We found strong to moderate evidence that the responses of two species (jacky dragon and White's skink) to some site-scale variables depended on landscape structure. Abundance of jacky dragons increased with time since fire when pasture was present and decreased when pasture was absent (Table 2; Fig. 2f). Jacky dragons also responded differently to canopy cover depending on the amount of plantation cover, (Table 2; Fig. 2e). White's skink responded differently to coarse woody debris, leaf litter, and canopy cover, depending on the amount of native vegetation cover, although the uncertainty associated with the predicted responses was sometimes high (Table 2; Figs. 2r, s, v). Additionally, this species was found to respond differently to the percentage of bare ground depending on whether pasture was present or absent, although the uncertainty associated with the predicted response was also high (Table 2; Fig. 2t).

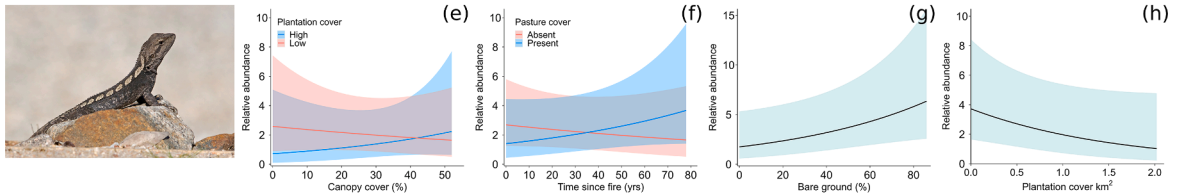
3.2. Responses to site-scale variables

Five out of the seven species responded to at least one site-scale habitat variable, and one species responded to time since fire. We found strong to moderate evidence for negative effects of canopy cover on the abundance of eastern three-lined skinks and White's skinks (Table 2; Figs. 2a, w), as well as a positive effect on the abundance of garden skinks (Table 2; Fig. 2k). We found evidence for positive effects of the percent of bare ground on the abundance of three species (jacky dragon, southeastern slider, White's skink) (Table 2; Figs. 2g, q, u), and negative effects on the abundance of one species (garden skink, Fig. 2m). There was moderate evidence of negative effects of coarse woody debris on the abundance of eastern three-lined skinks (Table 2; Fig. 2c). We found weak evidence of a positive effect of time since fire on the abundance of one species, the garden skink (Table 2; Fig. 2l).

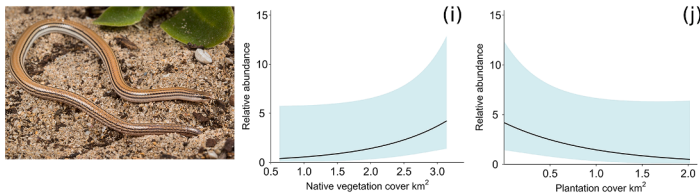
Eastern three-link skink (*Acritoscincus duperreyi*)



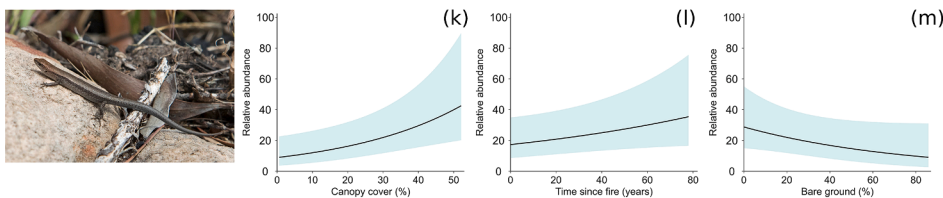
Jacky dragon (*Amphibolurus muricatus*)



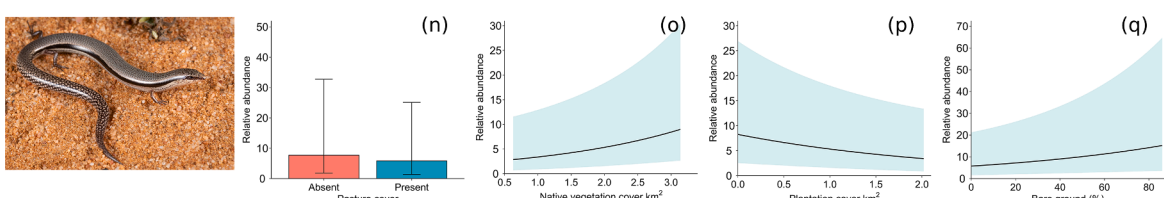
Lined worm-lizard (*Aprasia striolata*)



Garden skink (*Lampropholis guichenoti*)



Southeastern slider (*Lerista bougainvillii*)



White's skink (*Liopholis whitii*)

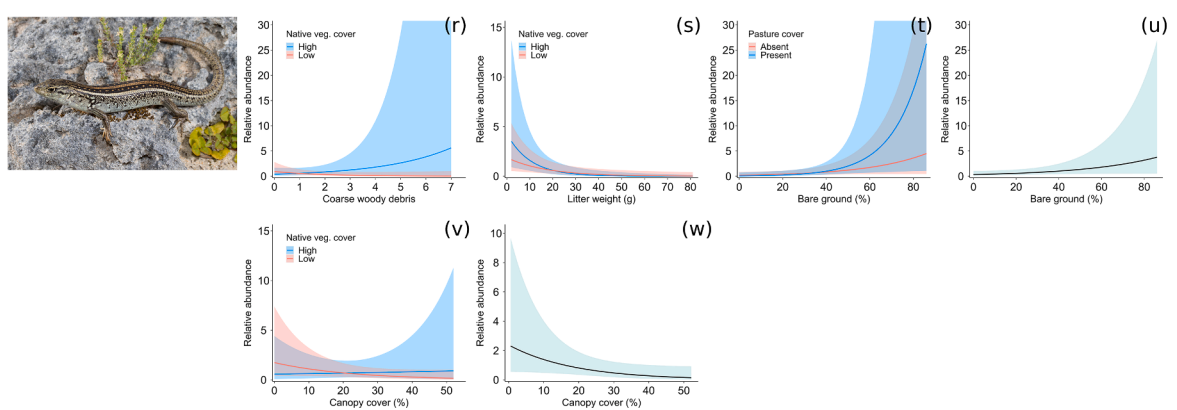


Fig. 2. Relationships between species abundance and key site-scale variables and landscape-scale variables. Shading represents 95% confidence limits. Black lines represent site-scale variables and landscape-scale variables. Red and blue bars represent the absence and presence of pasture, respectively. Red and blue lines represent different amounts of cover in the surrounding landscape: 'low' refers 20% cover, 'high' refers 80% cover.

3.3. Responses to landscape-scale variables

Four species were found to respond to landscape-scale variables. We found strong to moderate evidence of positive effects of native vegetation cover on the abundance of three species (eastern three-lined skink, lined worm-lizard, and southern-eastern slider) (Table 2; Figs. 2d, i, o). We found evidence of an effect of pasture on two species (eastern three-lined skink and southeastern slider) such that both species were found in higher abundance when pasture was absent in the surrounding landscape (Table 2; Figs. 2b, n). There was also moderate evidence of negative effects of plantation cover on the abundance of three species (Jacky dragon, lined worm-lizard, and southeastern slider) (Table 2; Figs. 2h, j, p).

3.4. Relative importance of site-scale and landscape-scale variables

Three of the seven species (eastern three-lined skink, jacky dragon, and southeastern slider) were found to respond to both site-scale and landscape-scale variables (Table 2). Two species (garden skink and White's skink) responded only to site-scale variables, while one species (lined worm-lizard) responded only to landscape-scale variables (Table 2). One species (southern grass skink) did not respond to any of the variables examined regardless of scale. Canopy cover was the best site-scale predictor of eastern three-lined skink abundance, and had a stronger effect than the amount of coarse woody debris at the site, or pasture and native vegetation in the surrounding landscape (Table 2). In contrast, landscape-scale variables were better predictors of southeastern slider abundance: models of pasture and native vegetation cover ranked higher than and bare ground (Table 2). No one variable at either scale was found to be the best predictor of jacky dragons (Table 2).

4. Discussion

We investigated the responses of seven reptile species in a fire-prone, fragmented landscape in southwest Victoria to identify whether species' responses to site-scale variables depend on landscape structure, and to compare the relative influence of variables measured at the site and landscape scale. The responses of two species to site-scale variables depended on the structure of the surrounding landscape, however contrary to our first prediction, native vegetation cover was not the only landscape structure variable that influenced species' responses to site-scale variables – plantation cover and the presence of pasture were also influential. Our second prediction, that site-scale variables would be the strongest predictors of abundance, was true for two species, but overall our results were varied, and most species responded to variables measured at both the site and landscape scale.

4.1. Do reptile responses to site-scale variables depend on landscape structure?

Our results indicate that landscape structure may influence species' responses to site-scale variables in fire-prone landscapes. To our knowledge this is the first time that reptile responses to the characteristics of their local environments have been shown to be influenced by the characteristics of the surrounding landscape. Interactions between processes can have important implications for animal populations and their management in fire-prone landscapes but are often both poorly

studied and difficult to predict (Delaney et al., 2021; Driscoll et al., 2021; Zylinski et al., 2022). Our findings provide initial insights into reptile responses to the interacting effects of processes operating at different spatial scales, as well as a basis for understanding geographically variable responses to fire that are sometimes observed (Nimmo et al., 2014).

Relationships between jacky dragon abundance and canopy cover and time since fire both appear to be influenced by landscape structure, indicating that landscape structure may impact habitat selection and post-fire recovery in this species. The differences in the responses to fire and canopy cover with changes in landscape structure may relate to the impacts of all these factors on thermoregulatory opportunities. Previous research has identified links between fire frequency, canopy cover and transmission of solar radiation and the thermal quality of habitat (Elzer et al., 2013). Indeed, removal of canopy cover in fire suppressed landscapes has been shown to improve habitat quality for some reptile species (Webb et al., 2005). Likewise, fragmentation can lead to greater temperatures and thermal variability in remnant vegetation as the ratio of edge-to-interior increases (Tuff et al., 2016). Furthermore, compared to native forests, pine plantations have a simpler vegetation structure, offer cooler temperatures, and receive less radiation (Mott et al., 2010) which is unlikely to represent suitable habitat for jacky dragons (Halstead and Schwanz, 2015). While we did not specifically measure fragmentation in this study, it seems likely that the variability in fire history, landscape structure, and degree of fragmentation in the study area creates a complex thermal environment that could influence reptile abundance.

Other evidence suggests that jacky dragons may have some capacity to adapt to modified landscapes. Jacky dragons in urban remnants have been observed moving between three different habitat types to perform different behaviours: dense native vegetation and exotic grass were used for foraging and cover, while open areas of lawn were used to bask (Burgin et al., 2011). The relationship observed in our study may indicate a similar pattern of behaviour, such that in landscapes where pasture is present, jacky dragons seek shelter in dense unburnt vegetation and use the open pasture for basking. In landscapes where pasture is absent, more recently burnt vegetation may provide the right level of cover to afford jacky dragons with opportunities for both basking and shelter. Alternatively, higher abundance at recently burnt sites when pasture is absent may be indicative of an increase in dispersal by jacky dragons post-fire. In the closely related mallee tree dragon (*Amphibolurus norrisi*), recently burnt patches were associated with an increase in genetic diversity, possibly due to increased male dispersal (Smith et al., 2014).

Landscape structure variables (native vegetation cover and pasture) were also demonstrated to influence the response of White's skink to several site-scale variables (coarse woody debris, leaf litter, canopy cover, and bare ground). The abundance of White's skinks increased with both coarse woody debris and canopy cover when native vegetation cover was high; however, when native vegetation was low, abundance decreased slightly in response to coarse woody debris and canopy cover. This response pattern indicates that this species is influenced by local resources when native vegetation cover is high, but responds to other factors when native vegetation cover is low. The positive response to coarse woody debris appears to be consistent with what is already known about this species' nesting and burrowing behaviours. White's skinks often live in family groups in burrows and crevices beneath rocks

and logs, and the availability and aggregation of habitat can have consequences for sociality and development of offspring (Chapple, 2003; Botterill-James et al., 2016). While we are unable to provide definitive explanations for the other interactions observed, they nevertheless have important implications for the management of this species, and more research is required to understand the underlying mechanisms.

4.2. Influence of habitat structure and fire on species abundance

Our results support our expectation that site-scale variables (fire and habitat structure) are important predictors of reptile species abundance: more than half of the species in this study responded to multiple site-scale variables. Changes to habitat structure have a range of consequences for reptiles, including the availability of food and nest sites, opportunities for thermoregulation, and predation risk (Santos et al., 2008).

Our results demonstrate that canopy cover is a key predictor of the abundance of three skink species (eastern three-lined skink, garden skink, and White's skink). As aforementioned, changes in canopy cover have been shown to influence the thermal quality of habitat for reptiles (Webb et al., 2005; Elzer et al., 2013), and the variation in responses observed among these species are likely to reflect their different thermoregulatory requirements and strategies (Avery, 1979; Pike et al., 2011). For example, eastern three-lined skinks responded negatively to canopy cover, a result that appears consistent with other studies. Exposure to higher incubation temperatures appears to benefit this species by increasing hatching success and influencing phenotypes of hatchlings (Shine and Elphick, 2001; Amiel and Shine, 2012). In other parts of their range, eastern three-lined skinks have also been found to prefer low levels of vegetation cover (Jellinek et al., 2004) and select nest sites with lower levels of canopy cover that receive increased solar radiation (Shine et al., 2002). Indeed, although eastern three-lined skinks nest under logs and rocks, they have been shown to actively select nests in cleared patches of forest where there is a higher availability of warm nest sites over the surrounding forest where logs and rocks are more abundant (Shine et al., 2002). This potentially also explains the negative response of eastern three-lined skinks to coarse woody debris observed in our study.

The area of bare ground was also found to be a key predictor of three species (jacky dragon, garden skink and southeastern slider). The preference for bare ground by southeastern sliders appears consistent with the hypothesis that burrowing reptiles are not dependent on understorey vegetation and therefore are able to exploit open areas produced by recent fire (Caughley, 1985). Burrowing appears to be an important strategy for reptiles and small mammals in fire-prone landscapes, as burrows provide shelter from the flame front during a fire event (Friend, 1993) and various studies have found support for a trend towards higher abundances of burrowing reptiles in recently burnt habitats (Caughley, 1985; Driscoll and Henderson, 2008; Smith et al., 2013). Though not explicitly measured in our study, southeastern sliders also appeared to be captured more commonly at sites with sandy substrates and were often observed burrowing into sand after being released (S. Mulhall *pers. obs.*). Like other *Lerista* species, southeastern sliders are known for their reduced limbs and elongated, snake-like bodies which are thought to be adapted for moving through 'fossorial or cluttered habitats' as they can fit through narrow gaps and their bodies experience less drag (Morinaga and Bergmann, 2020).

Time since fire was an important predictor of the abundance of one

species, the garden skink. Since fire influences the availability of resources over time, in some cases time since fire may be a useful surrogate for habitat structure variables, such as leaf litter and coarse woody debris (Swan et al., 2015). Nevertheless, fire-habitat relationships are often nonlinear (Haslem et al., 2011), and many studies indicate that time since fire is not necessarily a good predictor of fauna responses (e.g. Driscoll and Henderson, 2008; Nimmo et al., 2012; Swan et al., 2015). Our results for garden skinks, taken together with findings from other studies, suggest this species' response to fire may depend on a range of factors including vegetation type (Lindenmayer et al., 2008; Hu et al., 2016). This has also been demonstrated in a recent study of birds conducted in three different ecosystems (Rainsford et al., 2021). Although birds responded to habitat attributes related to time since fire, similar relationships between post-fire habitat found in one ecosystem were often not found in other ecosystems (Rainsford et al., 2021). While we detected a positive association between garden skink abundance and time since fire in the heathy woodland, investigation by Hu et al. (2016) found garden skinks responded negatively to time since fire in eucalypt forest, but detected no response in Banksia woodland. Meanwhile another study across a broad range of forest types found no relationship between this species and any fire associated measures including fire history and severity, but reported positive effects of leaf litter and negative effects of rock cover (Lindenmayer et al., 2008).

4.3. Influence of landscape structure on species abundance

Landscape structure variables were important predictors of the abundance of four lizard species (eastern three-lined skink, jacky dragon, lined worm-lizard, and southeastern slider). Of the four species that responded to landscape structure, three responded positively to native vegetation cover in the surrounding landscape and all species responded negatively to one or both other land use types (i.e. plantation and pasture). Sites with a low proportion of native vegetation in the surrounding landscape are likely to experience greater edge effects, potentially leading to increased negative influences such as predation risk (Hansen et al., 2019) and fluctuations in microclimate (Tuff et al., 2016). Reductions in the extent of native vegetation are more likely to disadvantage specialist species which depend on resources available in native vegetation, compared to generalist species that are often demonstrated to maintain higher populations in modified landscapes (Ewers and Didham, 2007). Additionally, generalist reptiles may have different thermoregulatory strategies and physiological tolerances that allow them to adapt to extreme climates (Carvajal-Cogollo and Urbina-Cardona, 2015; Mortelliti et al., 2015). While we did not find an effect of landscape structure on garden skinks (a widely distributed generalist), previous research conducted in eucalypt forest fragmented by pine plantations found that garden skinks were more abundant at sites with low amounts of eucalypt cover in the landscape (Fischer et al., 2005).

The impact of low quality habitat or non-habitat on species' abundance is also likely to depend on characteristics of the cover and whether they are able to compensate for reductions in native vegetation by using resources in the pasture and/or plantation (Ewers and Didham, 2007). Interestingly, one study found no difference in the abundance of eastern three-lined skinks between urban remnants and continuous bushland, but did find a negative effect of exotic plant cover and a positive effect of native vegetation community composition (Jellinek et al., 2004). Thus, our findings could reflect this species' preference for native over exotic plants, rather than an aversion to non-habitat per se. Management of

plantation and agricultural environments may also help to facilitate movement between habitat patches and reduce predation risk at habitat edges (Hansen et al., 2019). For example, retaining old logs may provide additional shelter within pine plantations (Fischer et al., 2005), while the presence of trees within areas of crops may allow animals to climb up and gain a vantage point to assist with navigation (Hansen et al., 2020). It should also be noted that although both pine and eucalypt plantations exist in our study area, the proportion of eucalypt plantation cover was not large enough to be analysed separately. Undoubtedly pine and eucalypt plantations have very different characteristics in terms of habitat structure and community composition, and seem likely to elicit different responses from fauna (Proença et al., 2010).

4.4. Relative importance of site-scale and landscape-scale variables

Overall, our results supported our hypothesis that site-scale variables would be stronger predictors of reptiles than landscape-scale variables. However, of the three species (eastern three-lined skink, jacky dragon, and southeastern slider) that responded to both site-scale and landscape-scale variables, the relative influence of the variables at the different scales was mixed. These differences may be attributed to trait differences among these species. Fossorial and semi-fossorial reptiles, such as southeastern sliders, may be especially sensitive to disturbance of the soil and understorey vegetation associated with agricultural and timber harvesting practices (e.g. grazing, ploughing, timber removal), and therefore less likely to move through these landscapes (Wong et al., 2020). Agricultural modification has previously been attributed to the decline of other fossorial species, including the pink-tailed worm-lizard (*Aprasia parapulchella*) (Wong et al., 2020) and striped legless lizard (*Delma impar*) (Dorrough and Ash, 1999). In comparison, in our study the eastern three-line skink (a terrestrial species) responded more to canopy cover than to any of the landscape structure variables. Potentially, terrestrial species may be somewhat less sensitive to these practices as they lack the burrowing behaviours exhibited by pygopodids or *Lerista* and are therefore less likely to be affected by disturbances to soil.

4.5. Management implications

Our results show that even species with relatively low capacities for dispersal compared to other organisms may respond to factors at both the site and landscape-scales (Doherty et al., 2020). Further, the range of different responses to fire, habitat structure, and landscape structure exhibited within this assemblage provides support for the need for multiscale approaches to ecological management (Fischer et al., 2004; Pastro et al., 2013; Fraga-Ramirez et al., 2017; Delaney et al., 2021). Identifying species-habitat relationships at the site-scale may be especially important for the persistence of reptiles with temperature-dependent sex determination, such as the eastern three-lined skink and jacky dragon. Maintaining critical habitat features which influence microclimate may help species to ameliorate nest temperatures, providing a buffer from the effects of climate change (Telemeco et al., 2009). Meanwhile, understanding how less mobile species respond to landscape structure is particularly pressing, due to their decreased capacity for range expansions necessary to keep pace with climate change (Araújo et al., 2006). We measured landscape structure in a 1 km radius around each site, however in the future it would be valuable to consider alternative scales, both smaller and larger, to determine the scale at which species respond most strongly to landscape structure (Delaney et al., 2021).

Our study of interactions between fire and landscape structure also highlights the need to identify how and if threatening processes interact to influence species' persistence. Ecological fire management strategies

aimed at promoting biodiversity may have unforeseen consequences if landscape structure is not accounted for (Lindenmayer et al., 2013; Delaney et al., 2021). Evidence from our study suggests that reptiles may respond differently to fire depending on the structure of the surrounding landscape. Consequently the specific strategies underlying conservation-focused fire management may need to be changed in different parts of the landscape (Zylinski et al., 2022).

CRediT authorship contribution statement

S.J. Mulhall: Conceptualization, Methodology, Formal analysis, Investigation, Visualization, Funding acquisition, Writing – original draft, Writing – review & editing. **J. Di Stefano:** Conceptualization, Investigation, Methodology, Supervision, Writing – review & editing. **A. Dorph:** Investigation, Methodology, Writing – review & editing. **M. Swan:** Investigation, Methodology, Writing – review & editing. **H. Sitters:** Conceptualization, Investigation, Methodology, Supervision, Funding acquisition, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

We acknowledge the Gunditjmarra people as the Traditional Owners of the lands on which this study was conducted and pay respects to their Elders. This work was part of an Australian Research Council Linkage Project, supported by Department of Energy, Environment and Climate Action, the Department for Environment and Water, Parks Victoria, and SA Water, and supported by the Holsworth Wildlife Research Endowment and the Ecological Society of Australia, and the Parks Victoria Applied Park Management Research Scholarship. Data collection was carried out under a scientific research permit issued by the Department of Energy, Environment and Climate Action (permit number 10008227). Faunal surveys were approved by the University of Melbourne Animal Ethics Committee (ID 1604071). Many thanks to: Zahlia Payne for assistance with reptile trapping; members of the Fire Ecology and Biodiversity Group (University of Melbourne) for assistance with habitat surveys; and Andrew Denham and Pam Mulhall for comments that helped improve the manuscript. Thanks also to the many volunteers who assisted with the site set-up and trapping, and all those who donated cardboard carton used in pitfalls.

Image credits

Eastern three-lined skink (*Acritoscincus duperreyi*): Stephen Zozaya.
Jacky dragon (*Amphibolurus muricatus*): Owen Lishmund.
Lined worm-lizard (*Aprasia striolata*): Stephen Zozaya.
Garden skink (*Lampropholis guichenoti*): Owen Lishmund.
Southeastern slider (*Lerista bougainvillii*): Stephen Zozaya.
White's skink (*Liopholis whitii*): Stephen Zozaya.

Appendix

Fig. A1

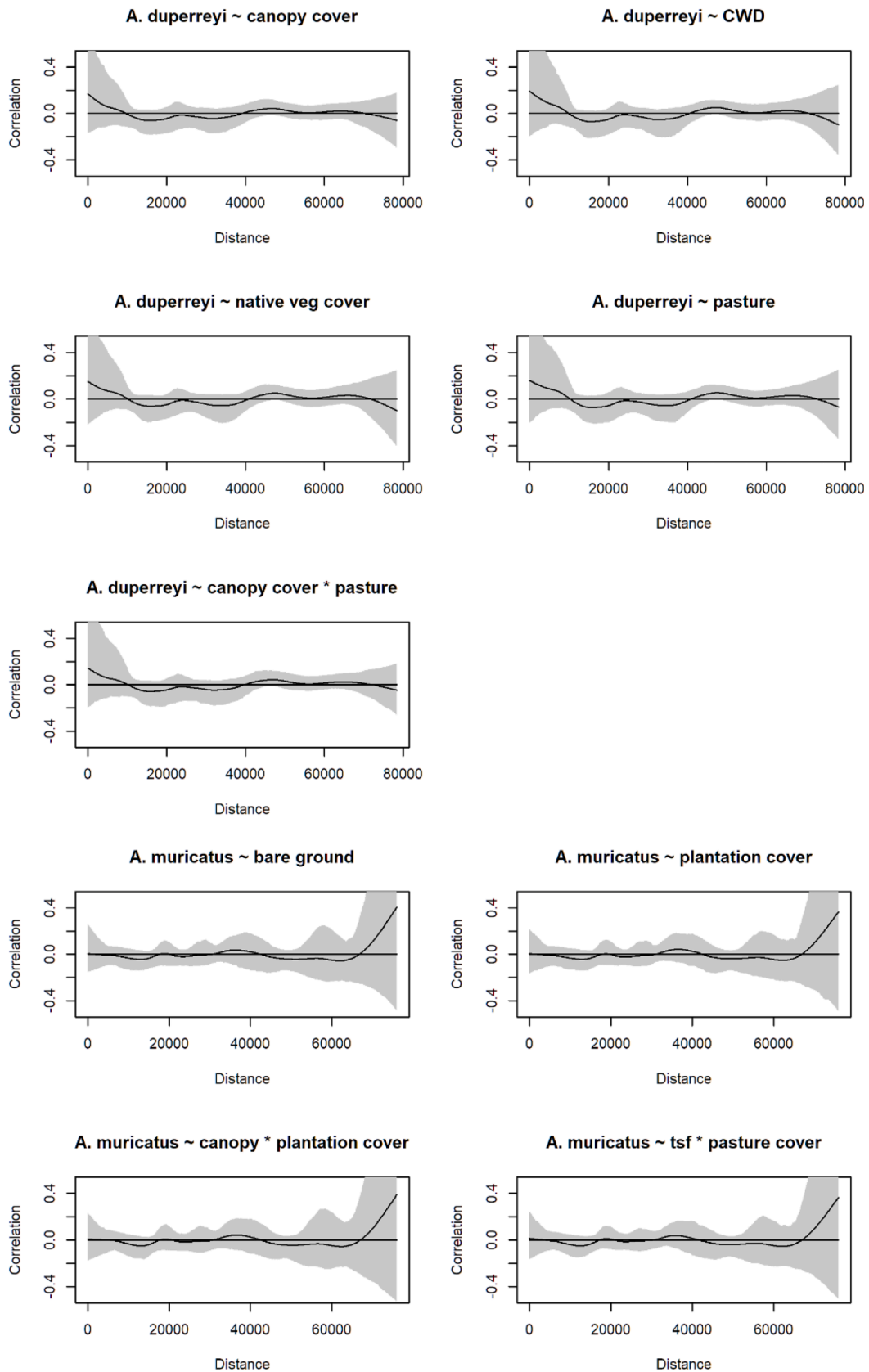


Fig. A1. Spline correlograms for top ranked models for eastern three-line skink (*A. duperreyi*), jacky dragon (*A. muricatus*), lined worm-lizard (*A. striolata*), garden skink (*L. guichenoti*), southeastern slider (*L. bougainvillii*), southern grass skink (*Pseudemoia entrecasteauxi*), and White's skink (*L. whitii*).

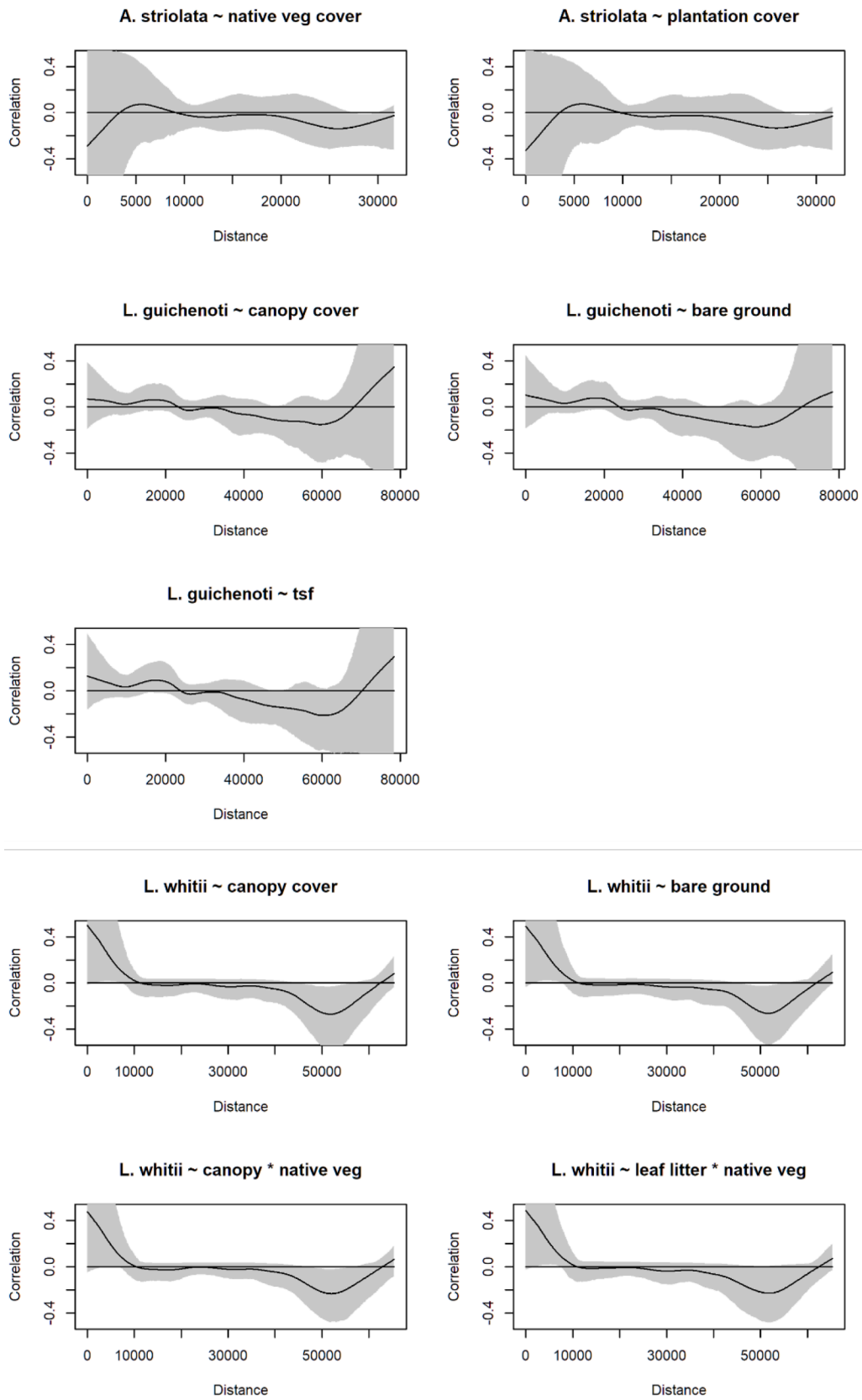


Fig. A1. (continued).

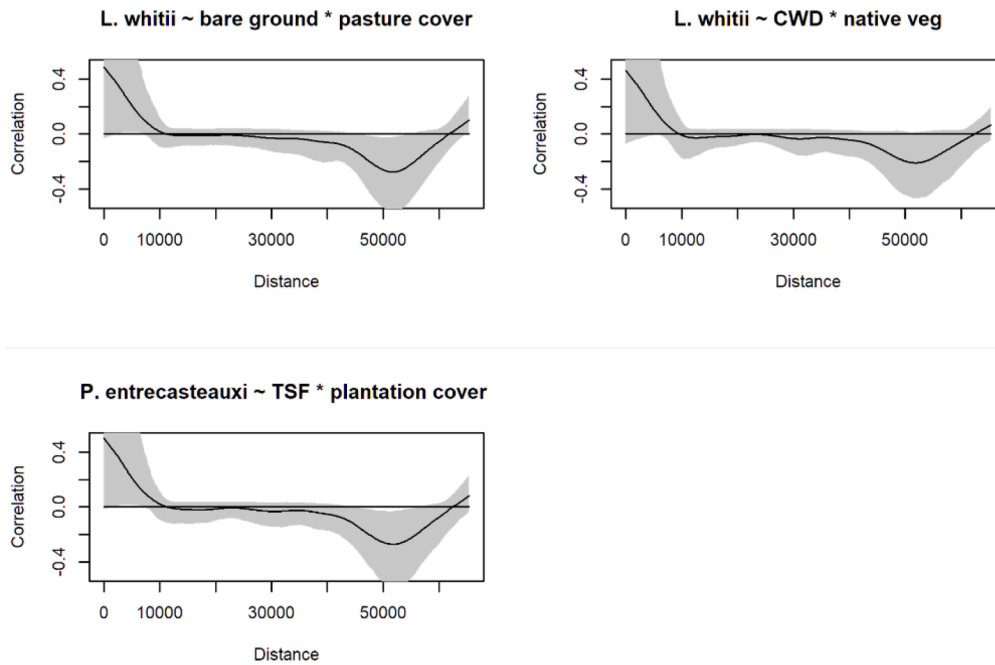


Fig. A1. (continued).

Tables A1 and A2

Table A1

Total number of individuals of the 17 species in five families caught in heathy woodlands in southwestern Victoria between Spring 2017 and Autumn 2018.

Species name	Common name	n	Sites detected
Agamidae			
<i>Amphibolurus muricatus</i>	Jacky dragon	44	35
Chelidae			
<i>Chelodina longicollis</i>	Eastern long necked turtle	1	1
Elapidae			
<i>Austrelaps superbus</i>	Lowlands copperhead	3	3
<i>Drysdalia coronoides</i>	White-lipped snake	1	1
<i>Notechis scutatus</i>	Tiger snake	4	4
<i>Pseudonaja textilis</i>	Eastern brown snake	2	2
Pygopodidae			
<i>Aprasia striolata</i>	Lined worm-lizard	25	14
Scincidae			
<i>Acritoscincus duperreyi</i>	Eastern three-lined skink	438	81
<i>Ctenotus robustus</i>	Robust ctenotus	3	2
<i>Eulamprus tympanum</i>	Southern water skink	8	4
<i>Lampropholis guichenoti</i>	Garden skink	303	72
<i>Lerista bougainvillii</i>	Southeastern slider	276	64
<i>Liopholis whitii</i>	White's skink	24	13
<i>Morethia obscura</i>	Shrubland morethia skink	18	8
<i>Pseudemoia entrecasteauxi</i>	Southern grass skink	39	18
<i>Tiliqua nigrolutea</i>	Blotched blue-tongue lizard	1	1
<i>Tiliqua rugosa</i>	Shingleback lizard	3	3
Unidentified skink	n/a	14	9
Unidentified snake	n/a	1	1
Total		1208	

Table A2

Best models of detection for each reptile species, used in abundance models.

Species	Detection covariates
Eastern three-lined skink	~ date + maximum temperature
Jacky dragon	~ date + maximum temperature
Lined worm-lizard	~ date + maximum temperature
Garden skink	~ date + maximum temperature
Southeastern slider	~ date + maximum temperature
Southern grass skink	~ maximum temperature
White's skink	~ rainfall

References

ABRS, 2023. Australian faunal directory. Squamata. Australian Biological Resources Study, Canberra.

Amiel, J.J., Shine, R., 2012. Hotter nests produce smarter young lizards. *Biol. Lett.* 8, 372–374. <https://doi.org/10.1098/rsbl.2011.1161>.

Araújo, M.B., Thuiller, W., Pearson, R.G., 2006. Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography* 33, 1712–1728. <https://doi.org/10.1111/j.1365-2699.2006.01482.x>.

Avery, R.A., 1979. *Lizards, A Study in Thermoregulation*. Edward Arnold, London.

Banks-Leite, C., Ewers, R.M., Folkard-Tapp, H., Fraser, A., 2020. Countering the effects of habitat loss, fragmentation, and degradation through habitat restoration. *One Earth* 3, 672–676. <https://doi.org/10.1016/j.oneear.2020.11.016>.

Bennett, A.F., Radford, J.Q., Haslem, A., 2006. Properties of land mosaics: implications for nature conservation in agricultural environments. *Biol. Conserv.* 133, 250–264. <https://doi.org/10.1016/j.biocon.2006.06.008>.

Bjornstad, O.N., ncf: Spatial Covariance Functions. R package version 1.3-2. <https://CRAN.R-project.org/package=ncf>.

Böhm, M., Collen, B., Baillie, J.E.M., Bowles, P., Chanson, J., Cox, N., et al., 2013. The conservation status of the world's reptiles. *Biol. Conserv.* 157, 372–385. <https://doi.org/10.1016/j.biocon.2012.07.015>.

- Botterill-James, T., Halliwell, B., Cooper-Scott, E., Uller, T., Wapstra, E., While, G.M., 2016. Habitat structure influences parent-offspring association in a social lizard. *Front. Ecol. Evol.* 4, 96. <https://doi.org/10.3389/fevo.2016.00096>.
- Bowman, D.M.J.S., Balch, J.K., Artaxo, P., Bond, W.J., Carlson, J.M., Cochrane, M.A., Pyne, S.J., 2009. Fire in the Earth system. *Science* 324, 481–484. <https://doi.org/10.1126/science.1163886>.
- Brook, B.W., Griffiths, A.D., Puckey, H.L., 2002. Modelling strategies for the management of the critically endangered Carpentarian rock-rat (*Zyzomys palatalis*) of northern Australia. *J. Environ. Manage.* 65, 355–368. <https://doi.org/10.1006/jema.2002.0561>.
- Brown, G.W., Bennett, A.F., Potts, J.M., 2008. Regional faunal decline - reptile occurrence in fragmented rural landscapes of south-eastern Australia. *Wildl. Res.* 35, 8–18. <https://doi.org/10.1071/WR07010>.
- Brown, K., Paczkowska, G., Gibson, N., 2016. Mitigating impacts of weeds and kangaroo grazing following prescribed fire in a Banksia woodland. *Ecol. Manag. Restor.* 17, 133–139. <https://doi.org/10.1111/emr.12208>.
- Bureau of Meteorology, 2017. Monthly climate statistics for 'CASTERTON' [090182]. http://www.bom.gov.au/climate/averages/tables/cw_090182.shtml (accessed 4 October 2017).
- Burgin, S., Wotherspoon, D., Hitchen, D.J., Ridgeway, P., 2011. Habitat use by the jacky lizard *Amphibolurus muricatus* in a highly degraded urban area. *Anim. Biol.* 61, 185–197. <https://doi.org/10.1163/157075511X566515>.
- Carvajal-Cogollo, J.E., Urbina-Cardona, J.N., 2015. Ecological grouping and edge effects in tropical dry forest: reptile-microenvironment relationships. *Biodivers. Conserv.* 24, 1109–1130. <https://doi.org/10.1007/s10531-014-0845-9>.
- Caughley, J., 1985. Effect of fire on the reptile fauna of mallee. In: Grigg, G., Shine, R., Ehmann, H. (Eds.), *Biology of Australasian Frogs and Reptiles*. Royal Zoological Society of New South Wales and Surrey Beatty & Sons, Chipping Norton, NSW, pp. 31–34.
- Chapple, D.G., 2003. Ecology, life-history, and behavior in the Australian scincid genus *Egernia*, with comments on the evolution of complex sociality in lizards. *Herpetol. Monogr.* 17, 145–180.
- Chapple, D.G., Roll, U., Böhm, M., Aguilar, R., Amey, A.P., Austin, C.C., Meiri, S., 2021. Conservation status of the world's skinks (Scincidae): taxonomic and geographic patterns in extinction risk. *Biol. Conserv.* 257, 109101. <https://doi.org/10.1016/j.biocon.2021.109101>.
- Cheal, D., 2010. Growth stages and tolerable fire intervals for Victoria's native vegetation data sets. Department of Sustainability and Environment, East Melbourne, Victoria, Australia. *Fire and adaptive management Report No. 84*.
- Cox, N., Young, B.E., Bowles, P., Fernandez, M., Marin, J., Rapacciolo, G., Xie, Y., 2022. A global reptile assessment highlights shared conservation needs of tetrapods. *Nature* 605, 285–290. <https://doi.org/10.1038/s41586-022-04664-7>.
- Delaney, L., Di Stefano, J., Sitters, H., 2021. Mammal responses to spatial pattern in fire history depend on landscape context. *Landsc. Ecol.* 36, 897–914. <https://doi.org/10.1007/s10980-020-01186-3>.
- Dess, T., 2016. Fire operations plan 2017/18. Barwon South West region. Department of Environment, Land, Water and Planning, Werribee, Victoria.
- Didham, R.K., Tylianakis, J.M., Gemmill, N.J., Rand, T.A., Ewers, R.M., 2007. Interactive effects of habitat modification and species invasion on native species decline. *Trends Ecol. Evol.* 22, 489–496. <https://doi.org/10.1016/j.tree.2007.07.001>.
- Doherty, T.S., Dickman, C.R., Nimmo, D.G., Ritchie, E.G., 2015. Multiple threats, or multiplying the threats? Interactions between invasive predators and other ecological disturbances. *Biol. Conserv.* 190, 60–68. <https://doi.org/10.1016/j.biocon.2015.05.013>.
- Doherty, T.S., Balouch, S., Bell, K., Burns, T.J., Feldman, A., Fist, C., Driscoll, D.A., 2020. Reptile responses to anthropogenic habitat modification: a global meta-analysis. *Glob. Ecol. Biogeogr.* 29, 1265–1279. <https://doi.org/10.1111/geb.13091>.
- Dorrrough, J., Ash, J.E., 1999. Using past and present habitat to predict the current distribution and abundance of a rare cryptic lizard, *Delma impar* (Pygopodidae). *Aust. J. Ecol.* 24, 614–624. <https://doi.org/10.1046/j.1442-9993.1999.00995.x>.
- Driscoll, D.A., Armenteras, D., Bennett, A.F., Brotons, L., Clarke, M.F., Doherty, T.S., Haslem, A., Kelly, L.T., Sato, C.F., Sitters, H., Aquilué, N., Bell, K., Chadid, M., Duane, A., Meza-Elizalde, M.C., Giljohann, K.M., González, T.M., Jambekar, R., Lazzari, J., Morán-Ordóñez, A., Wevill, T., 2021. How fire interacts with habitat loss and fragmentation. *Biol. Rev.* 96, 976–998. <https://doi.org/10.1111/brv.12687>.
- Driscoll, D.A., Henderson, M.K., 2008. How many common reptile species are fire specialists? A replicated natural experiment highlights the predictive weakness of a fire succession model. *Biol. Conserv.* 141, 460–471. <https://doi.org/10.1016/j.biocon.2007.10.016>.
- Driscoll, D.A., Lindenmayer, D.B., Bennett, A.F., Bode, M., Bradstock, R.A., Cary, G.J., York, A., 2010. Fire management for biodiversity conservation: key research questions and our capacity to answer them. *Biol. Conserv.* 143, 1928–1939. <https://doi.org/10.1016/j.biocon.2010.05.026>.
- Duff, T.J., Bell, T.L., York, A., 2013. Managing multiple species or communities? Considering variation in plant species abundances in response to fire interval, frequency and time since fire in a heathy *Eucalyptus* woodland. *For. Ecol. Manage.* 289, 393–403. <https://doi.org/10.1016/j.foreco.2012.10.032>.
- Elzer, A.L., Pike, D.A., Webb, J.K., Hammill, K., Bradstock, R.A., Shine, R., 2013. Forest-fire regimes affect thermoregulatory opportunities for terrestrial ectotherms. *Austral Ecol.* 38, 190–198. <https://doi.org/10.1111/j.1442-9993.2012.02391.x>.
- Ensbey, M., Legge, S., Jolly, C.J., Garnett, S.T., Gallagher, R.V., Lintermans, M., Zukowski, S., 2023. Animal population decline and recovery after severe fire: Relating ecological and life history traits with expert estimates of population impacts from the Australian 2019–20 megafires. *Biol. Conserv.* 283, 110021. <https://doi.org/10.1016/j.biocon.2023.110021>.
- ESRI, 1995–2022. ArcMap 10.5. <https://www.esri.com/>.
- Ewers, R.M., Didham, R.K., 2007. Confounding factors in the detection of species responses to habitat fragmentation. *Biol. Rev.* 81, 117–142. <https://doi.org/10.1017/s1464793105006949>.
- Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Syst.* 34, 487–515. <https://doi.org/10.1146/annurev.ecolsys.34.011802.132419>.
- Fenner, A.L., Bull, C.M., 2007. Short-term impact of grassland fire on the endangered pygmy bluetongue lizard. *J. Zool.* 272, 444–450. <https://doi.org/10.1111/j.1469-7998.2007.00287.x>.
- Fischer, J., Lindenmayer, D.B., Cowling, A., 2004. The challenge of managing multiple species at multiple scales: reptiles in an Australian grazing landscape. *J. Appl. Ecol.* 41, 32–44. <https://doi.org/10.1111/j.1365-2664.2004.00869.x>.
- Fischer, J., Lindenmayer, D.B., Barry, S., Flowers, E., 2005. Lizard distribution patterns in the Tumut fragmentation "Natural Experiment" in south-eastern Australia. *Biol. Conserv.* 123, 301–315. <https://doi.org/10.1016/j.biocon.2004.11.018>.
- Fiske, I., Chandler, R., 2011. unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. *J. Stat. Softw.* 43, 1–23. <https://doi.org/10.18637/jss.v043.i10>.
- Fraga-Ramirez, Y., Suazo-Ortuno, I., Avila-Caballada, L.D., Alvarez-Anorve, M., Alvarado-Diaz, J., 2017. Multiscale analysis of factors influencing herpetofaunal assemblages in early successional stages of a tropical dry forest in western Mexico. *Biol. Conserv.* 209, 196–210. <https://doi.org/10.1016/j.biocon.2017.02.021>.
- Friend, G.R., 1993. Impact of fire on small vertebrates in mallee woodlands and heathlands of temperate Australia - a review. *Biol. Conserv.* 65, 99–114. [https://doi.org/10.1016/0006-3207\(93\)90439-8](https://doi.org/10.1016/0006-3207(93)90439-8).
- Geary, W.L., Nimmo, D.G., Doherty, T.S., Ritchie, E.G., Tulloch, A.I.T., 2019. Threat webs: Reframing the co-occurrence and interactions of threats to biodiversity. *J. Appl. Ecol.* 56, 1992–1997. <https://doi.org/10.1111/1365-2664.13427>.
- Gill, A.M., Williams, J.E., 1996. Fire regimes and biodiversity: The effects of fragmentation of southeastern Australian eucalypt forests by urbanisation, agriculture and pine plantations. *For. Ecol. Manage.* 85, 261–278. [https://doi.org/10.1016/s0378-1127\(96\)03763-2](https://doi.org/10.1016/s0378-1127(96)03763-2).
- Gorissen, S., Mallinson, J., Greenlees, M., Shine, R., 2015. The impact of fire regimes on populations of an endangered lizard in montane south-eastern Australia. *Austral Ecol.* 40, 170–177. <https://doi.org/10.1111/aec.12190>.
- Gorissen, S., Greenlees, M., Shine, R., 2018. The impact of wildfire on an endangered reptile (*Eulamprus leuraensis*) in Australian montane swamps. *Int. J. Wildland Fire* 27, 447–456. <https://doi.org/10.1071/WF17048>.
- Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Townsend, J.R., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv.* 1, e1500052.
- Halstead, J.E., Schwanz, L.E., 2015. Impacts of thermal limitation on thermoregulatory behaviour and reproductive success in a lizard. *Aust. J. Zool.* 63, 225–232. <https://doi.org/10.1071/zo15012>.
- Hansen, N.A., Sato, C.F., Michael, D.R., Lindenmayer, D.B., Driscoll, D.A., 2019. Predation risk for reptiles is highest at remnant edges in agricultural landscapes. *J. Appl. Ecol.* 56, 31–43. <https://doi.org/10.1111/1365-2664.13269>.
- Hansen, N.A., Driscoll, D.A., Michael, D.R., Lindenmayer, D.B., 2020. Movement patterns of an arboreal gecko in fragmented agricultural landscapes reveal matrix avoidance. *Anim. Conserv.* 23, 48–59. <https://doi.org/10.1111/acv.12505>.
- Haslem, A., Kelly, L.T., Nimmo, D.G., Watson, S.J., Kenny, S.A., Taylor, R.S., Bennett, A.F., 2011. Habitat or fuel? Implications of long-term, post-fire dynamics for the development of key resources for fauna and fire. *J. Appl. Ecol.* 48, 247–256. <https://doi.org/10.1111/j.1365-2664.2010.01906.x>.
- He, T., Lamont, B.B., Pausas, J.G., 2019. Fire as a key driver of Earth's biodiversity. *Biol. Rev.* 94, 1983–2010. <https://doi.org/10.1111/brv.12544>.
- Hossack, B.R., Lowe, W.H., Honeycutt, R.K., Parks, S.A., Corn, P.S., 2013. Interactive effects of wildfire, forest management, and isolation on amphibian and parasite abundance. *Ecol. Appl.* 23, 479–492. <https://doi.org/10.1890/12-0316.1>.
- Hradsky, B.A., 2020. Conserving Australia's threatened native mammals in predator-invaded, fire-prone landscapes. *Wildl. Res.* 47, 1–15. <https://doi.org/10.1071/WR19027>.
- Hu, Y., Kelly, L.T., Gillespie, G.R., Jessop, T.S., 2016. Lizard responses to forest fire and timber harvesting: complementary insights from species and community approaches. *For. Ecol. Manage.* 379, 206–215. <https://doi.org/10.1016/j.foreco.2016.07.040>.
- Infante, J., Novoa, F.J., Ibarra, J.T., Melnick, D.J., Griffin, K.L., Bonacic, C., 2021. Altered fire regimes modify lizard communities in globally endangered Araucaria forests of the southern Andes. *Sci. Rep.* 11, 22709. <https://doi.org/10.1038/s41598-021-02169-3>.
- Jellinek, S., Driscoll, D.A., Kirkpatrick, J.B., 2004. Environmental and vegetation variables have a greater influence than habitat fragmentation in structuring lizard communities in remnant urban bushland. *Austral Ecol.* 29, 294–304. <https://doi.org/10.1111/j.1442-9993.2004.01366.x>.
- Kelly, L.T., Giljohann, K.M., Duane, A., Aquilué, N., Archibald, S., Battlori, E., Brotons, L., 2020. Fire and biodiversity in the Anthropocene. *Science* 370, eabb0355. <https://doi.org/10.1126/science.abb0355>.
- Legge, S., Smith, J.G., James, A., Tuft, K.D., Webb, T., Woinarski, J.C.Z., 2019. Interactions among threats affect conservation management outcomes: Livestock grazing removes the benefits of fire management for small mammals in Australian tropical savannas. *Conserv. Sci. Practice* 1, e52.
- Lindenmayer, D.B., Wood, J.T., MacGregor, C., Michael, D.R., Cunningham, R.B., Crane, M., Driscoll, D.A., 2008. How predictable are reptile responses to wildfire? *Oikos* 117, 1086–1097. <https://doi.org/10.1111/j.0030-1299.2008.16683.x>.
- Lindenmayer, D.B., Blanchard, W., McBurney, L., Blair, D., Banks, S.C., Driscoll, D., Gill, A.M., 2013. Fire severity and landscape context effects on arboreal marsupials. *Biol. Conserv.* 167, 137–148. <https://doi.org/10.1016/j.biocon.2013.07.028>.

- Michael, D.R., Ikin, K., Crane, M., Okada, S., Lindenmayer, D.B., 2016. Scale-dependent occupancy patterns in reptiles across topographically different landscapes. *Ecography* 40, 415–424. <https://doi.org/10.1111/ecog.02199>.
- Morinaga, G., Bergmann, P.J., 2020. Evolution of fossorial locomotion in the transition from tetrapod to snake-like in lizards. *Proc. R. Soc. B Biol. Sci.* 287, 20200192. <https://doi.org/10.1098/rspb.2020.0192>.
- Mortelliti, A., Michael, D.R., Lindenmayer, D.B., 2015. Contrasting effects of pine plantations on two skinks: results from a large-scale “natural experiment” in Australia. *Anim. Conserv.* 18, 433–441. <https://doi.org/10.1111/acv.12190>.
- Mott, B., Alford, R.A., Schwarzkopf, L., 2010. Tropical reptiles in pine forests: Assemblage responses to plantations and plantation management by burning. *For. Ecol. Manage.* 259, 916–925. <https://doi.org/10.1016/j.foreco.2009.11.031>.
- Muff, S., Nilsen, E.B., O'Hara, R.B., Nater, C.R., 2022. Rewriting results sections in the language of evidence. *Trends Ecol. Evol.* 37, 203–210. <https://doi.org/10.1016/j.tree.2021.10.009>.
- Mulhall, S.J., Sitters, H., Di Stefano, J., 2022. Vegetation cover and configuration drive reptile species distributions in a fragmented landscape. *Wildl. Res.* 50, 792–806. <https://doi.org/10.1071/WR21063>.
- Nalliah, R., Sitters, H., Smith, A., Di Stefano, J., 2022. Untangling the influences of fire, habitat and introduced predators on the endangered heath mouse. *Anim. Conserv.* 25, 208–220. <https://doi.org/10.1111/acv.12731>.
- Nimmo, D.G., Kelly, L.T., Spence-Bailey, L.M., Watson, S.J., Haslem, A., White, J.G., Bennett, A.F., 2012. Predicting the century-long post-fire responses of reptiles. *Glob. Ecol. Biogeogr.* 21, 1062–1073. <https://doi.org/10.1111/j.1466-8238.2011.00747.x>.
- Nimmo, D.G., Kelly, L.T., Spence-Bailey, L.M., Watson, S.J., Taylor, R.S., Clarke, M.F., Bennett, A.F., 2013. Fire mosaics and reptile conservation in a fire-prone region. *Conserv. Biol.* 27, 345–353. <https://doi.org/10.1111/j.1523-1739.2012.01958.x>.
- Nimmo, D.G., Kelly, L.T., Farnsworth, L.M., Watson, S.J., Bennett, A.F., 2014. Why do some species have geographically varying responses to fire history? *Ecography* 37, 805–813. <https://doi.org/10.1111/ecog.00684>.
- Pastro, L.A., Dickman, C.R., Letnic, M., 2013. Effects of wildfire, rainfall and region on desert lizard assemblages: the importance of multi-scale processes. *Oecologia* 173, 603–614. <https://doi.org/10.1007/s00442-013-2642-7>.
- Paterson, J.E., Pulfer, T., Horrigan, E., Sukumar, S., Vezina, B.I., Zimmerling, R., Davy, C. M., 2021. Individual and synergistic effects of habitat loss and roads on reptile occupancy. *Global Ecol. Conserv.* 31, e01865.
- Penman, T.D., York, A., 2010. Climate and recent fire history affect fuel loads in Eucalyptus forests: implications for fire management in a changing climate. *For. Ecol. Manage.* 260, 1791–1797. <https://doi.org/10.1016/j.foreco.2010.08.023>.
- Pike, D.A., Webb, J.K., Shine, R., 2011. Removing forest canopy cover restores a reptile assemblage. *Ecol. Appl.* 21, 274–280. <https://doi.org/10.1890/09-2394.1>.
- Pinto, T., Moreira, B., Freitas, H., Santos, X., 2018. The role of fire history, land-use, and vegetation structure on the response of Mediterranean lizards to fire. *For. Ecol. Manage.* 419–420, 139–145. <https://doi.org/10.1016/j.foreco.2018.03.029>.
- Potapov, P., Hansen, M.C., Laestadius, L., Turubanova, S., Yaroshenko, A., Thies, C., Esipova, E., 2017. The last frontiers of wilderness: tracking loss of intact forest landscapes from 2000 to 2013. *Sci. Adv.* 3, e1600821.
- Proença, V.M., Pereira, H.M., Guilherme, J., Vicente, L., 2010. Plant and bird diversity in natural forests and in native and exotic plantations in NW Portugal. *Acta Oecol.* 36, 219–226. <https://doi.org/10.1016/j.actao.2010.01.002>.
- QGIS Development Team, 2016. QGIS Geographic Information System (version 2.18). QGIS Association. <http://www.qgis.org>.
- R Core Team, 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- Raffaele, E., Veblen, T.T., Blackhall, M., Tercero-Bucardo, N., 2011. Synergistic influences of introduced herbivores and fire on vegetation change in northern Patagonia. *Argentina. J. Veg. Sci.* 22, 59–71. <https://doi.org/10.1111/j.1654-1103.2010.01233.x>.
- Rainsford, F.W., Kelly, L.T., Leonard, S.W.J., Bennett, A.F., 2021. Post-fire habitat relationships for birds differ among ecosystems. *Biol. Conserv.* 260, 109218 <https://doi.org/10.1016/j.biocon.2021.109218>.
- Royle, J.A., 2004. N-Mixture models for estimating population size from spatially replicated counts. *Biometrics* 60, 108–115. <https://doi.org/10.1111/j.0006-341X.2004.00142.x>.
- Santos, X., Cheylan, M., 2013. Taxonomic and functional response of a Mediterranean reptile assemblage to a repeated fire regime. *Biol. Conserv.* 168, 90–98. <https://doi.org/10.1016/j.biocon.2013.09.008>.
- Santos, T., Diaz, J.A., Perez-Tris, J., Carbonell, R., Telleria, J.L., 2008. Habitat quality predicts the distribution of a lizard in fragmented woodlands better than habitat fragmentation. *Anim. Conserv.* 11, 46–56. <https://doi.org/10.1111/j.1469-1795.2007.00146.x>.
- Santos, J.L., Sitters, H., Keith, D.A., Geary, W.L., Tingley, R., Kelly, L.T., 2022. A demographic framework for understanding fire-driven reptile declines in the ‘land of the lizards’. *Glob. Ecol. Biogeogr.* 31, 2105–2119. <https://doi.org/10.1111/geb.13520>.
- Schloerke, B., Cook, D., Larmarange, J., Briatte, F., Marbach, M., Thoen, E., Elberg, A., Crowley, J., GGally: Extension to ‘ggplot2’. R package version 2.1.2. <https://CRAN.R-project.org/package=GGally>.
- Senior, A.F., Böhm, M., Johnstone, C.P., McGee, M.D., Meiri, S., Chapple, D.G., Tingley, R., 2021. Correlates of extinction risk in Australian squamate reptiles. *J. Biogeogr.* 48, 2144–2152. <https://doi.org/10.1111/jbi.14140>.
- Shine, R., Elphick, M.J., 2001. The effect of short-term weather fluctuations on temperatures inside lizard nests, and on the phenotypic traits of hatchling lizards. *Biol. J. Linn. Soc.* 72, 555–565. <https://doi.org/10.1111/j.1095-8312.2001.tb01338.x>.
- Shine, R., Barrott, E.G., Elphick, M.J., 2002. Some like it hot: effects of forest clearing on nest temperatures of montane reptiles. *Ecology* 83, 2808–2815. [https://doi.org/10.1890/0012-9658\(2002\)083\[2808:SLIHEO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2808:SLIHEO]2.0.CO;2).
- Shine, R., Brown, G.P., Elphick, M.J., 2016. Effects of intense wildfires on the nesting ecology of oviparous montane lizards. *Austral. Ecol.* 41, 756–767. <https://doi.org/10.1111/aec.12362>.
- Sitters, H., Di Stefano, J., 2020. Integrating functional connectivity and fire management for better conservation outcomes. *Conserv. Biol.* 34, 550–560. <https://doi.org/10.1111/cobi.13446>.
- Smith, A.L., Bull, C.M., Driscoll, D.A., 2013. Successional specialization in a reptile community cautions against widespread planned burning and complete fire suppression. *J. Appl. Ecol.* 50, 1178–1186. <https://doi.org/10.1111/1365-2664.12119>.
- Smith, A.L., Bull, C.M., Gardner, M.G., Driscoll, D.A., 2014. Life history influences how fire affects genetic diversity in two lizard species. *Mol. Ecol.* 23, 2428–2441. <https://doi.org/10.1111/mec.12757>.
- Spence-Bailey, L.M., Nimmo, D.G., Kelly, L.T., Bennett, A.F., Clarke, M.F., 2010. Maximising trapping efficiency in reptile surveys: the role of seasonality, weather conditions and moon phase on capture success. *Wildl. Res.* 37, 104–115. <https://doi.org/10.1071/wr09157>.
- Swan, M., Christie, F., Sitters, H., York, A., Di Stefano, J., 2015. Predicting faunal fire responses in heterogeneous landscapes: the role of habitat structure. *Ecol. Appl.* 25, 2293–2305. <https://doi.org/10.1890/14-1533.1>.
- Telemeco, R.S., Elphick, M.J., Shine, R., 2009. Nesting lizards (*Bassiana duperreyi*) compensate partly, but not completely, for climate change. *Ecology* 90, 17–22. <https://doi.org/10.1890/08-1452.1>.
- Thompson, G.G., Thompson, S.A., 2007. Usefulness of funnel traps in catching small reptiles and mammals, with comments on the effectiveness of the alternatives. *Wildl. Res.* 34, 491–497. <https://doi.org/10.1071/WR06081>.
- Thompson, G.G., Thompson, S.A., 2009. Comparative temperature in funnel and pit traps. *Aust. J. Zool.* 57, 311–316. <https://doi.org/10.1071/ZO09052>.
- Tingley, R., Macdonald, S.L., Mitchell, N.J., Woinarski, J.C.Z., Meiri, S., Bowles, P., Chapple, D.G., 2019. Geographic and taxonomic patterns of extinction risk in Australian squamates. *Biol. Conserv.* 238, 108203 <https://doi.org/10.1016/j.biocon.2019.108203>.
- Triska, M.D., Craig, M.D., Stokes, V.L., Pech, R.P., Hobbs, R.J., 2017. Conserving reptiles within a multiple-use landscape: determining habitat affiliations of reptile communities in the northern jarrah forest of south-western Australia. *Aust. J. Zool.* 65, 21–32. <https://doi.org/10.1071/ZO16074>.
- Tuff, K.T., Tuff, T., Davies, K.F., 2016. A framework for integrating thermal biology into fragmentation research. *Ecol. Lett.* 19, 361–374. <https://doi.org/10.1111/ele.12579>.
- Uetz, P., 2023. The Reptile Database. <http://www.reptile-database.org> (accessed 17 August 2023).
- URS Forestry, n.d. Australia's Green Triangle: A growing region with significant opportunities for forest sector investment. https://www.agriculture.gov.au/sites/default/files/sitecollectiondocuments/forestry/green_triangle_investment_ver8.pdf (accessed 21 November 2023).
- Van Dyke, J.U., Thompson, M.B., Burrige, C.P., Castelli, M.A., Clulow, S., Dissanayake, D.S.B., Whittington, C.M., 2021. Australian lizards are outstanding models for reproductive biology research. *Aust. J. Zool.* 68, 168–199. <https://doi.org/10.1071/ZO21017>.
- Webb, J.K., Shine, R., Pringle, R.M., 2005. Canopy removal restores habitat quality for an endangered snake in a fire suppressed landscape. *Copeia* 2005, 894–900. <https://www.jstor.org/stable/4098662>.
- Wilson, M.C., Chen, X.Y., Corlett, R.T., Didham, R.K., Ding, P., Holt, R.D., Yu, M.J., 2016. Habitat fragmentation and biodiversity conservation: key findings and future challenges. *Landsc. Ecol.* 31, 219–227. <https://doi.org/10.1007/s10980-015-0312-3>.
- Wong, D.T.Y., Gruber, B., Sarre, S.D., Osborne, W.S., 2020. Agricultural modification to vegetation drives presence and abundance of a threatened fossorial legless lizard. *Austral. Ecol.* 46, 437–448. <https://doi.org/10.1111/aec.12986>.
- Zylinski, S., Swan, M., Sitters, H., 2022. Contrasting responses of native and introduced mammal communities to fire mosaics in a modified landscape. *Ecol. Appl.* 32, e2570.