

Vegetation cover and configuration drive reptile species distributions in a fragmented landscape

S. J. Mulhall^{A,*} , H. Sitters^A and J. Di Stefano^A

For full list of author affiliations and declarations see end of paper

***Correspondence to:**

S. J. Mulhall
School of Ecosystem and Forest Sciences,
University of Melbourne, 4 Water Street,
Creswick, Vic. 3363, Australia
Email: sarah.mulhall@unimelb.edu.au

Handling Editor:

Thomas Prowse

Received: 9 April 2021

Accepted: 2 October 2022

Published: 28 October 2022

Cite this:

Mulhall SJ *et al.* (2023)
Wildlife Research, **50**(10), 792–806.
doi:[10.1071/WR21063](https://doi.org/10.1071/WR21063)

© 2023 The Author(s) (or their employer(s)). Published by CSIRO Publishing.
This is an open access article distributed under the Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License (CC BY-NC-ND).

OPEN ACCESS

ABSTRACT

Context. Habitat loss and fragmentation are key drivers of biodiversity loss worldwide, yet the influence of landscape structure on species distributions is unknown. Globally, reptiles are thought to be especially sensitive to landscape modification due to their limited capacity for dispersal and reliance on native vegetation. New knowledge of how landscape structure influences species distributions is needed to inform conservation strategies. **Aims.** Our principal aim was to examine the influence of landscape structure on the distributions of 40 terrestrial reptile species in Victoria, southeast Australia. **Methods.** We obtained species occurrence records from the Victorian Biodiversity Atlas, and used MaxEnt to model the distributions of reptile species within Victoria using biophysical and landscape structure variables. A moving window analysis was applied to a land cover map to derive five landscape structure metrics; two metrics represented landscape cover and three represented landscape configuration. **Key results.** Climate variables were generally found to be the strongest drivers of species distributions, although 80% of reptile species were also influenced by landscape structure (permutation importance $\geq 5\%$). Of the five landscape structure variables, extent of native vegetation had the greatest influence (30 of 40 species), followed by habitat shape. For *Lerista bougainvillii* and *Tiliqua rugosa*, native vegetation cover had a greater influence on their distributions than climate variables. Most species responded positively to native vegetation extent, whereas responses to other landscape structure variables were varied. **Conclusions.** Although most studies of reptile distributions only use biophysical variables in modelling, our research shows that at the scale of our study area, reptile species distributions were also influenced by landscape structure; extent of native vegetation was an important predictor for most species. Integrating landscape structure in modelling has the potential to improve our ability to predict species distributions. **Implications.** Because species distributions are likely to shift due to climate change, knowledge of the influence of landscape structure on distributions will help land managers to facilitate successful range expansions in fragmented landscapes. Our findings indicate that management focused on increasing the extent of native vegetation is likely to provide benefit to most reptile species.

Keywords: fragmentation, habitat loss, landscape structure, MaxEnt, reptiles, species distribution modelling, squamate.

Introduction

Habitat loss and fragmentation occur globally due to processes such as the expansion of agriculture and plantation forestry, and as a result, 79% of the world's forested area is currently considered fragmented (Potapov *et al.* 2017). Landscape structure, defined as the composition and configuration of landscape elements (Cushman *et al.* 2008), influences species distributions, with many species persisting entirely in structurally modified landscapes (Bennett *et al.* 2006; Fletcher *et al.* 2018). A major challenge for ecologists and land managers is understanding (1) which components of landscape structure drive species' responses, and (2) how landscape structure influences species distributions relative to other known drivers such as climate (Cushman *et al.* 2008).

Landscape modification and fragmentation can influence species in various ways, including increased risk of extinction (Crooks *et al.* 2017). Increases in the amount of habitat edge have been associated with increased rates of predation (Weldon and Haddad 2005; Hansen *et al.* 2019), and changes in land cover may influence road kills (Rincón-Aranguri *et al.* 2019). Further, changes in the spatial configuration and distance between habitat patches can alter connectivity and affect the capacity of species to move through the landscape and access key resources (Driscoll *et al.* 2013; Nimmo *et al.* 2019). In modified landscapes, species may alter their movement patterns to avoid unfavourable habitat (Hansen *et al.* 2020). This may in turn influence migration patterns and rates of recolonisation and dispersal, leading to reduced gene flow and consequently reduced genetic diversity (Neuwald and Templeton 2013; Herrmann *et al.* 2017). Genetic diversity is necessary for population persistence because it improves fitness and helps animals persist in the face of both stochastic events and shifts in environmental conditions (Hughes *et al.* 2008; Banks *et al.* 2013).

Although reptiles are one of the most diverse vertebrate groups, far less is known about their responses to landscape structure compared with birds and mammals (McGarigal and Cushman 2002; Böhm *et al.* 2013). This is concerning, because reptiles worldwide are considered particularly vulnerable to habitat loss and landscape fragmentation (Rodrigues 2005; Araújo *et al.* 2006; Cabrera-Guzmán and Reynoso 2012; Munguia-Vega *et al.* 2013). Indeed, a global meta-analysis of the impact of habitat modification on squamate reptiles found that modified habitat predominantly had a negative impact on species abundance (Doherty *et al.* 2020). Reptiles are known to respond differently to climatic variables compared with other vertebrate taxa, in part due to their thermoregulatory requirements (Powney *et al.* 2010; Buckley *et al.* 2012), and therefore may also respond differently to landscape structure. For example, in an urban environment jacky dragons (*Amphibolurus muricatus*) used open areas of lawn for basking (a thermoregulatory behaviour), but preferred to forage in nearby native vegetation that afforded them more cover (Burgin *et al.* 2011). Reptiles are primarily found in native vegetation and have a limited capacity for dispersal; therefore, loss of native vegetation cover is likely to influence their occurrence (Dubey and Shine 2010; Munguia-Vega *et al.* 2013).

Australia has the highest levels of reptile species diversity and endemism in the world, with around 1000 described species in 18 families (Webb *et al.* 2014). Since European colonisation around half of Australia's forests have been significantly modified or cleared (Bradshaw 2012). Victoria is Australia's most cleared state with around 34% of native vegetation remaining intact, primarily due to the growth of the wheat, sheep and cattle industries in the 1890s (Bradshaw 2012). The state is currently experiencing unprecedented population growth and is forecast to grow by at least 1.5% per year, reaching 8 million people by

2031 (Commissioner for Environmental Sustainability Victoria 2018a). This has led to record levels of housing development and urban land use, particularly at the fringes of the capital city of Melbourne, putting increased pressure on biodiversity (Commissioner for Environmental Sustainability Victoria 2018b). Fragmentation has already been implicated in the decline of Australian reptile species (Driscoll 2004; Brown *et al.* 2008), including the threatened striped legless lizard (*Delma impar*) (Scroggie *et al.* 2019) and the pygmy blue-tongue lizard (*Tiliqua adelaidensis*), which was considered extinct until it was rediscovered in 1992 (Armstrong *et al.* 1993).

Species distribution models are important tools for understanding relationships between environmental variables and species occurrence, and have been used widely in conservation planning and management (Araújo and Peterson 2012; Guisan *et al.* 2013; Guillera-Aroita *et al.* 2015). However, although fragmentation is commonly implicated in reptile species declines, most species distribution models are developed using only climate variables. In this study, our aim was to model the distributions of reptile species in Victoria using a combination of biophysical (i.e. climate, soils) and landscape structure variables. We quantified five landscape structure metrics, two representing habitat cover and three representing configuration. We modelled each species using the same set of predictor variables to allow us to compare the relative contribution of structural and biophysical predictors, and to identify the extent to which landscape structure influences reptile species distributions across structurally modified landscapes.

Methods

Study area

The study was conducted in Victoria, the southernmost state of mainland Australia (Fig. 1). We chose Victoria as our study system because in addition to a diverse reptile community it has a substantial gradient in both biophysical states and landscape structure; high levels of land clearing and urbanisation since European colonisation have resulted in marked landscape change. Victoria has a total land area of 227 496 km² and is Australia's most densely populated state, with a total population of 6.3 million people (2017 figure) (Australian Bureau of Statistics 2018). Just over three-quarters (77%) of the population are concentrated in the state's capital city of Melbourne (Australian Bureau of Statistics 2018). The total extent of native vegetation is estimated to have decreased by about half since European colonisation (i.e. pre 1750) (Eigenraam *et al.* 2013). Nevertheless, Victoria has a rich diversity of ecosystems including grasslands, wet and dry forest, coastal habitats, woodlands, and alpine and mallee communities (Cheal 2010). In most areas of the state the climate is temperate,

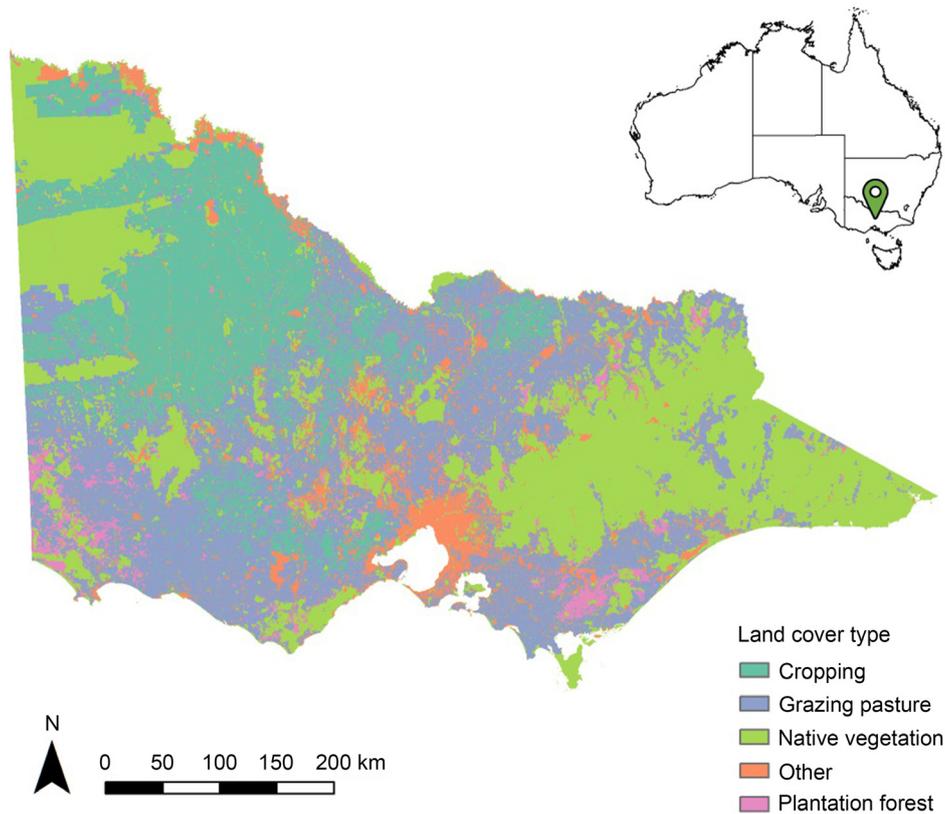


Fig. 1. Map showing the distribution of the five land cover types (cropping, grazing pasture, native vegetation, plantation forest and other) across Victoria, Australia.

with mild/warm-hot, dry summers (December to February) and cold, wet winters (Bureau of Meteorology 2016). The average minimum temperature for Victoria is 4.5°C in winter, with an average maximum of 27.4°C in summer. The annual average rainfall is 637 mm.

Species occurrence data

We obtained reptile species occurrence records from the Victorian Biodiversity Atlas, a database that collates data of species observations across Victoria (State Government of Victoria 2018). We included records between 2005 and 2017 to increase the congruence between the sample data and the date of spatial layers (i.e. 2016/2017) used to represent landscape structure. Turtles and sea snakes were excluded from our dataset, as were any records that did not identify individuals by both the genus and species names. Records were also removed if they included descriptions suggesting that an individual may have been sighted outside its range (for example, records that were described as ‘beach washed’ or ‘found in predator scat’). To improve independence and spatial accuracy, data were thinned to one occurrence point per 100-m cell, and records with an accuracy of >100 m were excluded. Finally, we excluded occurrence

points within 5 km of the state boundary where landscape structure could not be evaluated accurately (see below), resulting in a dataset of 5749 species occurrence records. Records with additional naming information were renamed to only include the genus and species (for example, ‘*Liopholis whitii* PLAIN BACK MORPH’ was renamed ‘*Liopholis whitii*’, and ‘*Eulamprus tympanum marnieae*’ and ‘*Eulamprus tympanum tympanum*’ were renamed ‘*Eulamprus tympanum*’).

Background data

To account for spatial sampling bias, we generated background locations using the target group sampling method. This involved using the species occurrence locations described above as background data, operating under the assumption that the same sampling biases will apply to taxonomically related species sampled using similar methods as those used to observe the focal species (Merow et al. 2013). Because the 5749 occurrence records that we extracted were fewer than the recommended number of background points for MaxEnt (Elith et al. 2011), an additional 5000 points were generated within the core distribution of the occurrence records. We achieved this by using the 5749 data points to calculate a 50% kernel density polygon and then selecting

the additional points at random from within this space. This resulted in a background sample of approximately 10 000 locations that was used as background in all models. Kernel density estimation was conducted using the `adehabitatHR` package (Calenge 2006) in the R statistical environment (R Core Team 2020).

Predictor variables

Predictor variables were selected within two broad categories: landscape structure and biophysical variables.

Landscape structure variables

A map of land cover types for Victoria was obtained from the DataVic website (State of Victoria (Agriculture Victoria) 2018). The original layer included 15 land cover types, which we reclassified into five classes: (1) cropping; (2) grazing pasture; (3) native vegetation; (4) plantation forests; and (5) other (e.g. horticulture and urban areas) (Fig. 1). The layer was clipped to the study area boundary and converted to a raster layer with a pixel size of 250 × 250 m using ArcGIS Desktop 10.5. A moving window analysis of the land cover layer was performed using FRAGSTATS (ver. 4.2; McGarigal *et al.* 2012) to calculate five landscape structure metrics: (1) Contagion Index; (2) Euclidean nearest neighbour (mean); (3) Native Vegetation Cover; (4) Shape Index (arithmetic mean); and (5) Shannon's Diversity Index (Table 1) (McGarigal 2015). We used a square window with a side length of 5 km, and accepted samples with a maximum 10% of border/no data for all metrics. This analysis calculates a specified metric within a 5-km window for each pixel defined by the base land cover layer, resulting in a spatial layer of the specified metric with the same pixel size (250 × 250 m). In preliminary analysis we calculated a range of metrics, but chose the five listed above because they were effective at characterising different aspects of landscape structure and were minimally correlated (Pearson's correlation: $-0.2 < r < 0.6$).

Biophysical variables

We selected climate variables known to influence reptile species distributions: annual mean temperature; annual precipitation; maximum temperature of the warmest month; and minimum temperature of coldest month. These variables have been successfully used to model distributions of Australian elapid snakes (Cabrelli *et al.* 2014) and skinks (Cabrelli and Hughes 2015). Bioclimatic data at a spatial resolution of ~1 km² was obtained from the WorldClim ver. 2 database (Fick and Hijmans 2017).

A spatial layer of soil surface texture for Victoria was obtained from Agriculture Victoria (Department of Jobs, Precincts and Resources). Soil surface texture is a classification system that estimates the relative amounts of sand, silt and clay particles, and influences some physical properties of soil (National Committee on Soil and Terrain 2009). The 19 categories in the original soil layer were reclassified into six broader soil categories (sands, sandy loam, loams, clay loams, light clays, medium clay), plus riverine (riverine areas where surface texture is not categorised) using information from Agriculture Victoria (State of Victoria (Agriculture Victoria) 2020).

Species distribution modelling

We used MaxEnt to develop species distribution models in the R statistical environment (R Core Team 2020) using the `dismo` package (Hijmans *et al.* 2020). MaxEnt uses presence-background data to model species distributions, and performs well compared to other algorithms (Elith *et al.* 2006) and on datasets with a range of sample sizes (Wisz *et al.* 2008). We used MaxEnt to develop species distribution models for 40 reptile species with ≥30 occurrence records. We chose a minimum of 30 records as the cut off for analysis, because MaxEnt performs well for samples of this size or greater (Wisz *et al.* 2008).

Our aim was to compare the relative influence of different predictor variables on species distributions (rather than to

Table 1. Description of landscape structure variables used in reptile species distribution modelling (Source: McGarigal 2015).

Variable name	Variable description	Ecological importance
Contagion Index	Extent of aggregation or clumping of patch types in the landscape	Aggregation of patches influences landscape connectivity and access to resources, including habitat, food and mates
Euclidean distance to nearest neighbour	Basic measure of patch isolation, which measures the shortest distance (m) between patches	Influences landscape connectivity and access to resources, including habitat, food and mates
Native vegetation cover	Extent of the native vegetation class (%) within 5 km square moving windows across the study area	Reptiles generally prefer native vegetation, and may be expected to respond positively to increased landscape cover
Shape Index	Measure of patch shape complexity compared to a standard shape	Relates to the relative perimeter-to-area ratio, which influences the amount of edge environment
Shannon's Diversity Index	Measure of the diversity of each patch type in the landscape	More diverse landscapes may benefit habitat generalists which are able to exploit a wider variety of habitats. Because reptiles generally prefer native vegetation, they may respond negatively to increased diversity

identify the parsimonious model), so distribution models were generated for all 40 species using the same set of predictors, features and regularisation parameters. We used hinge features only to simplify the model while enabling the representation of non-linear responses, and chose the default regularisation value as a practical option for modelling multiple species (Merow *et al.* 2013). We selected the logistic output to allow for comparison of species responses to the different predictor variables (Merow *et al.* 2013). Area under the curve (AUC) values were used to assess the predictive ability of the models. AUC measures the area under the Receiver Operating Characteristic curve, and in the context of presence-background data represent the ability of a model to discriminate between species presences and background sample points. We followed the thresholds set out in Thuiller *et al.* (2003), where AUC values greater than 0.9 represent excellent predictive ability, 0.8–0.9 represent good predictive ability, 0.7–0.8 represent fair predictive ability, 0.6–0.7 represent poor predictive ability, and less than 0.6 represents models that perform little better than random. We used five-fold cross-validation to estimate the uncertainty associated with predictive ability, presenting the mean, minimum and maximum AUC values from the five runs. Maps of the relative likelihood of occurrence predicted by MaxEnt were produced for all 40 species in R using the raster (Hijmans 2020), tidyverse (Wickham *et al.* 2019) and cowplot (Wilke 2020) packages. Graphs representing species responses to individual predictors were produced in R using tidyverse. Relative likelihood of occurrence was represented on scale from 0 to 1 to allow for comparison between predictor variables and species.

Permutation importance values were used to assess the relative influence of the environmental variables to the species distribution models. Permutation importance is calculated by randomly permuting the values of each variable between the presence and background points, and measuring the resulting decrease in AUC. The bigger the decrease, the greater importance of that variable to the model. Permutation importance is considered a strong measure of variable influence because it does not depend on the pathway used to obtain the final model (Phillips 2017). We considered predictors influential if permutation importance was $\geq 5\%$.

Results

Models were run using an average of 97 occurrence records per species (range 30–357). Models for 37 of the 40 species had an AUC score above 0.8, and 17 models had an AUC score above 0.9, indicating good to excellent predictive capacity (Table 2).

The permutation importance of landscape structure variables was $\geq 5\%$ for 80% (32 of 40) of species (Table 2, Fig. 2). Extent of native vegetation cover was the most influential of the five structure variables and resulted in the highest importance values for two skink species, *Lerista bougainvillii* and *Tiliqua rugosa* (29.4 and 22.8 respectively; Table 2). We selected 12 species with notable responses to landscape structure and display their relative likelihood of occurrence maps in Fig. 3. Despite the strong influence of landscape structure on the distributions of some species, climate variables were the strongest predictors of species distributions overall (Table 2, Fig. 2).

Shape index was the most influential measure of landscape configuration, and influenced the distributions of seven species (permutation importance $\geq 5\%$). The permutation importance was higher for *Pseudonaja textilis*, *Lampropholis guichenoti* and *Lerista punctatovittata* (range 14.07–19.49) than the other species (range 5.03–5.57) (Table 2) (Fig. 3). The direction of responses to shape index varied among species; three species responded negatively and four species responded positively (Fig. 4). Contagion index and Euclidean nearest neighbour were the least influential configuration metrics (Fig. 2). Contagion index was an important variable for *L. bougainvillii* and *Notechis scutatus* (permutation importance 11.22 and 11.72 respectively) (Table 2) (Fig. 3). Both species responded negatively to contagion index, that is, relative likelihood of occurrence decreased with increasing aggregation of the landscape (Fig. 4). Only one species, *D. impar*, responded to Euclidean nearest neighbour; however, the permutation importance of this variable was low (5.22) (Table 2) (Fig. 3), with relative likelihood of occurrence increasing with distance between landscapes of the same type (Fig. 4).

Shannon's Diversity Index was an important predictor for three skinks, *T. rugosa*, *Tiliqua scincoides* and *Eulamprus tympanum* (permutation important 11.45, 10.80 and 6.37 respectively) (Table 2) (Fig. 3). The responses among species varied; *T. rugosa* responded positively to Shannon's Diversity Index, *T. scincoides* had a hump-shaped response, and *E. tympanum* had a negative response (Fig. 4).

Climate variables were key predictors in all species distribution models. Annual precipitation was important for 37 species, and was the variable with the highest permutation importance for 17 species (ranging from 24.7 to 84.5) (Table 2). Maximum temperature of the warmest month was influential in 34 species models, and was the variable with the highest permutation importance for 15 species models (ranging between 81.55 and 24.57) (Table 2). Annual mean temperature and minimum temperature of the coldest month were both influential in 27 species' models (Table 2). Soil texture was an important predictor variable for only eight species (Table 2); the soil texture permutation importance was highest for *Liopholis whitii* (11.54), which was more likely to occur on clay soils (i.e. Clay loams, Light clay and Medium clay).

Table 2. Results from modelling the distributions of reptile species across Victoria, Australia, showing the number of records (*n*) used in each model, model performance measured as area under the curve (AUC) and permutation importance of landscape structure and biophysical predictor variables.

Species name	Common name	<i>n</i>	Mean AUC	AUC s.d.	Permutation importance									
					VEG	SHA	SHDI	CON	ENN	T	P	TM warm	TM cold	SOIL
Agamidae														
<i>Amphibolurus muricatus</i>	Jacky dragon	53	0.89	0.04	21.5	2.9	0.3	1.7	0.6	17.0	11.5	24.6^A	17.0	3.0
<i>Ctenophorus fordi</i>	Mallee dragon	71	0.92	0.01	25.4	3.2	1.0	0.5	0.5	5.4	25.4	27.2^A	9.5	2.0
<i>Ctenophorus pictus</i>	Painted dragon	38	0.92	0.02	14.7	2.9	2.3	0.3	0.5	1.3	56.2^A	17.8	2.0	2.0
<i>Diporiphora nobbi</i>	Nobbi dragon	82	0.92	0.01	23.9	1.8	2.1	2.9	0.2	0.9	15.4	47.0^A	4.2	1.6
<i>Pogona barbata</i>	Bearded dragon	36	0.87	0.05	0.9	4.2	4.3	1.2	1.8	31.9	12.2	38.9^A	0.6	4.1
<i>Pogona vitticeps</i>	Central bearded dragon	57	0.93	0.01	16.7	5.0	1.4	4.2	0.2	4.2	54.1^A	12.1	0.6	1.7
Diplodactylidae														
<i>Diplodactylus vittatus</i>	Wood gecko	88	0.88	0.02	15.1	0.3	1.0	0.6	0.7	2.5	9.2	66.9^A	2.5	1.4
<i>Lucasium damaeum</i>	Beaded gecko	115	0.91	0.01	25.7	2.6	2.9	1.0	1.5	0.9	46.0^A	16.1	0.0	3.3
<i>Strophurus intermedius</i>	Southern spiny-tailed gecko	30	0.93	0.02	19.0	5.6	0.9	0.8	3.2	1.4	55.8^A	3.0	6.2	4.1
Elapidae														
<i>Austrelaps superbus</i>	Lowland copperhead	149	0.79	0.03	7.5	1.3	2.3	3.0	2.8	28.0^A	6.2	19.0	26.9	3.0
<i>Brachyurophis australis</i>	Coral snake	35	0.93	0.02	3.9	1.5	0.1	1.0	1.0	10.0	78.1^A	3.8	0.0	0.6
<i>Drysdalia coronoides</i>	White-lipped snake	50	0.90	0.03	22.2	1.0	0.4	1.0	0.1	1.2	35.9^A	24.7	12.1	1.4
<i>Notechis scutatus</i>	Tiger snake	80	0.74	0.06	8.4	3.8	1.1	11.7	1.6	0.2	30.8^A	29.4	7.4	5.7
<i>Parasuta flagellum</i>	Little whip snake	146	0.86	0.02	29.5	2.7	2.7	1.6	1.0	22.8	31.6^A	4.2	2.9	0.9
<i>Pseudechis porphyriacus</i>	Red-bellied black snake	47	0.88	0.04	5.1	1.6	1.0	5.0	1.9	26.3	32.8^A	5.5	19.5	1.2
<i>Pseudonaja textilis</i>	Eastern brown snake	82	0.80	0.05	11.3	19.5	3.1	0.9	0.9	41.2^A	8.2	0.2	11.6	3.2
Gekkonidae														
<i>Christinus marmoratus</i>	Marbled gecko	69	0.88	0.04	16.4	1.4	2.2	2.4	2.4	25.7^A	23.4	12.1	8.0	5.9
<i>Gehyra variegata</i>	Tree dtella	30	0.95	0.02	10.8	0.4	0.0	1.0	0.9	0.4	84.6^A	1.4	0.0	0.6
Pygopodidae														
<i>Delma australis</i>	Southern legless lizard	41	0.93	0.02	17.3	3.4	1.4	0.0	2.5	0.5	2.4	70.9^A	0.4	1.1
<i>Delma impar</i>	Striped legless lizard	162	0.88	0.02	24.8	0.5	1.1	0.7	5.2	14.1	5.1	39.7^A	3.7	5.0
<i>Delma inornata</i>	Olive legless lizard	89	0.96	0.01	32.9	0.6	0.8	1.9	1.1	8.9	7.2	39.5^A	6.7	0.3
Scincidae														
<i>Acritoscincus duperreyi</i>	Eastern three-lined skink	146	0.83	0.03	1.8	5.2	0.9	1.5	0.7	41.4^A	16.3	9.4	19.5	3.5
<i>Ctenotus inornatus</i>	Murray striped skink	47	0.93	0.01	9.5	1.6	0.3	0.6	0.0	20.8	0.3	63.8^A	2.6	0.4
<i>Ctenotus regius</i>	Regal striped skink	50	0.93	0.01	11.1	2.0	1.9	0.0	0.7	47.9^A	19.5	9.3	1.8	5.9
<i>Ctenotus robustus</i>	Large striped skink	132	0.86	0.02	2.7	0.9	2.5	2.3	1.1	47.2^A	15.7	25.6	0.3	1.7
<i>Eulamprus tympanum</i>	Southern water skink	100	0.88	0.03	29.8	1.4	6.4	2.0	2.9	18.2	4.0	30.4^A	2.9	2.0
<i>Lampropholis delicata</i>	Delicate skink	58	0.92	0.02	0.5	3.0	1.7	0.2	0.1	20.9	59.7^A	10.2	1.0	2.8

(Continued on next page)

Table 2. (Continued).

Species name	Common name	n	Mean AUC	AUC s.d.	Permutation importance									
					VEG	SHA	SHDI	CON	ENN	T	P	TM warm	TM cold	SOIL
<i>Lampropholis guichenoti</i>	Pale-flecked garden sunskink	276	0.80	0.02	11.4	14.9	2.8	4.5	0.2	9.8	15.3	27.0^A	5.4	8.6
<i>Lerista bougainvillii</i>	South-eastern slider	141	0.76	0.04	29.4^A	5.1	4.5	11.2	0.0	9.4	18.3	1.9	15.7	4.5
<i>Lerista punctatovittata</i>	Spotted burrowing skink	60	0.91	0.02	4.1	14.1	0.5	0.4	1.8	11.2	42.6^A	19.2	3.7	2.5
<i>Liopholis whitii</i>	White's skink	71	0.84	0.04	0.6	1.0	4.1	2.7	1.2	20.5	29.9^A	14.8	13.6	11.5
<i>Menetia greyii</i>	Grey's skink	106	0.88	0.02	6.6	0.8	0.6	1.1	0.6	1.1	57.1^A	14.7	13.2	4.2
<i>Morethia boulengeri</i>	Boulenger's skink	165	0.92	0.02	1.0	0.7	0.7	1.1	0.6	0.4	6.7	81.5^A	5.0	2.3
<i>Pseudemoia entrecasteauxii</i>	Southern grass skink	66	0.88	0.04	1.9	0.0	1.2	0.9	0.2	1.6	10.4	76.1^A	4.9	2.7
<i>Pseudemoia pagenstecheri</i>	Tussock skink	177	0.85	0.02	14.9	0.9	3.4	1.2	0.8	13.1	14.7	34.9^A	12.2	3.9
<i>Saproscincus mustelinus</i>	Weasel skink	59	0.93	0.02	9.3	4.1	1.2	0.1	0.4	16.9	48.3^A	11.2	6.6	1.7
<i>Tiliqua nigrolutea</i>	Blotched blue-tongued lizard	79	0.86	0.05	0.6	4.3	3.0	3.0	1.1	10.5	25.2	28.4^A	16.8	7.3
<i>Tiliqua rugosa</i>	Shingleback lizard	76	0.80	0.05	22.8^A	2.4	11.4	2.6	0.9	13.1	21.9	9.0	6.7	9.0
<i>Tiliqua scincoides</i>	Common blue-tongued lizard	167	0.81	0.03	12.8	3.0	10.8	4.4	0.5	20.7	24.8^A	16.8	4.3	1.8
Varanidae														
<i>Varanus varius</i>	Lace monitor	357	0.94	0.01	13.8	0.1	0.3	0.5	0.0	25.0	44.1^A	7.0	6.9	2.3

Bold values indicate predictor variables considered important to the final model (i.e. permutation importance $\geq 5\%$).

^AThe most important predictor variable driving the distribution of each species.

VEG, native vegetation cover; CON, Contagion Index; ENN, Euclidean nearest neighbour; SHA, Shape Index; SHDI, Shannon's Diversity Index; T, annual mean temperature; P, annual precipitation; TM warm, maximum temperature of warmest month; TM cold, minimum temperature of coldest month; SOIL, soil texture.

Discussion

Understanding the responses of animals to landscape structure is an important part of managing species in modified landscapes, but few studies have used landscape structure variables to model species distributions (but see Rodrigues and Lima-Ribeiro 2018; Cable et al. 2021; Senior et al. 2021). We modelled the distributions of 40 reptile species across a fragmented landscape in Victoria, Australia to compare the relative influence of landscape structure, climate and soil. We found that although climate was generally the strongest driver of species distributions, most species also respond to landscape structure. For *L. bougainvillii* and *T. rugosa*, the extent of native vegetation had the greatest influence on their modelled distribution.

Influence of landscape structure on species distributions

Our results indicate that landscape structure plays an important role in driving the distributions of some reptile species in Victoria. The extent of native vegetation was the most influential landscape structure variable, and was

important for species within all seven reptile families included in the study. Extent of native vegetation cover was an important driver of the distributions of three-quarters of the species in this study. Most of these species had a positive response to native vegetation cover, such as *Diplodactylus vittatus*, which appears to occur more commonly in regions with warm, dry climates and high vegetation cover. Likewise, *Ctenophorus fordi* was found to have a strong positive relationship with extent of native vegetation, which may be due to their association with hummock grasses (*Triodia* sp.) (Verdon et al. 2020). In semiarid parts of Australia, many reptiles, including *C. fordi*, are associated with the extent cover of hummock grasses, which are a dominant ground cover and an important resource for thermoregulation and protection from predators (Verdon et al. 2020). Habitat availability is critical to the persistence of most species, and habitat loss and modification are a clear driver of reptile declines in eastern Australia (Driscoll 2004; Brown et al. 2008) and worldwide (Doherty et al. 2020). Most reptiles, and particularly skinks (which represent most species in this study), are ground dwelling and therefore sensitive to loss and disturbance of ground and understorey layers including leaf litter (Brown 2001).

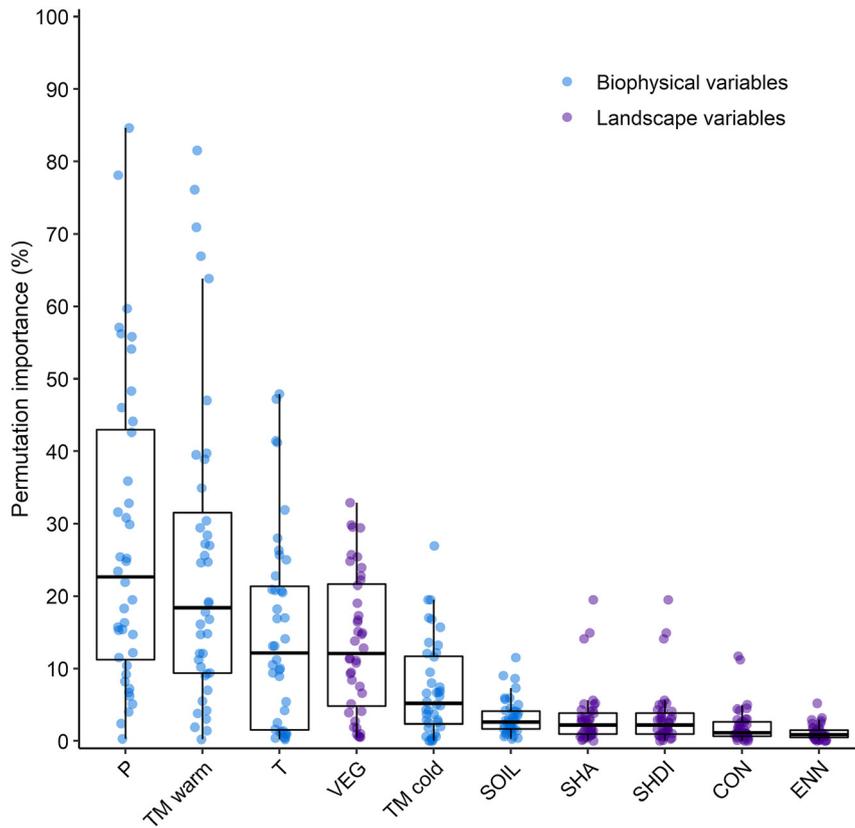


Fig. 2. Box plot showing the range of permutation importance values for variables used in MaxEnt models to predict relative likelihood of occurrence of 40 reptiles across Victoria, Australia. Midlines of the boxes represent medians, and bottom and top of the boxes represent the 25th and 75th percentiles, with whiskers extending to 1.5 times the interquartile range. Blue circles represent raw data for biophysical variables and purple circles represent raw data for landscape variables. P, annual precipitation; TM warm, maximum temperature of warmest month; T, annual mean temperature; VEG, native vegetation cover; TM cold, minimum temperature of coldest month; SOIL, soil texture; SHA, Shape Index; SHDI, Shannon's Diversity Index; CON, Contagion Index; ENN, Euclidean nearest neighbour.

Interestingly, several species had negative responses to the extent of vegetation cover. For example, *D. impar*, a small, threatened legless lizard (~300 mm long), preferred areas with less native vegetation cover, potentially reflecting this species' reliance on threatened native grassland habitat, rather than a preference for low levels of vegetation cover *per se* (Kutt 1993). Since European colonisation, grasslands have suffered extensive loss and degradation, and now remain primarily in isolated remnants (Scroggie *et al.* 2019). Disturbances such as fire and grazing may promote the persistence of *D. impar* when applied in isolation by promoting structural and floristic diversity of grasslands and increasing connectivity (Scroggie *et al.* 2019). However, when applied simultaneously, fire and grazing were associated with a high risk of local extinction, and any further loss of native vegetation cover is likely to exacerbate the decline of *D. impar* (Scroggie *et al.* 2019).

Shape index was the most influential configuration metric considered in this study, and reflects the perimeter-to-area ratio and therefore the amount of edge environment. Four species responded positively to shape index, including *P. textilis* which was more likely to occur in irregularly shaped habitat patches and where there was an intermediate level of native vegetation cover. More irregular, elongated patches have a higher perimeter-to-area and are therefore more exposed to surrounding land cover types, which may advantage species that engage in landscape complementation and

require resources in multiple land cover types (Nimmo *et al.* 2019). *Pseudonaja textilis* are a widely distributed species known to exploit agricultural areas where prey species (specifically *Mus musculus*) are abundant (Whitaker and Shine 2003). Similarly, for two species (*N. scutatus* and *L. bougainvillii*), relative likelihood of occurrence was higher when the contagion index was low (representing low clumping and high intermixing of patch types), yet had hump-shaped responses to vegetation cover extent, such that occurrence was more likely when vegetation cover was intermediate. This suggests that although vegetation cover is important, these species may be able to take advantage of resources associated with increased intermixing of different land use types.

In contrast, several species, including *L. punctatovittata*, were more likely to occur in more regular-shaped habitat. Irregular and elongated patches may also have undesirable implications for species that inhabit them, including increased exposure to introduced plants and animals (Brown *et al.* 2006) and disease (Jellinek *et al.* 2014; Uriostegui-Velarde *et al.* 2018). Negative relationships have been found between exotic plant cover and both the abundance and richness of lizard species (Jellinek *et al.* 2004). Because weed cover is expected to be higher in irregular shaped habitat, such areas may represent less suitable habitat for reptiles. Additionally, more elongated patches have a higher edge-to-area ratio; edges are subject to more to extreme climatic conditions and

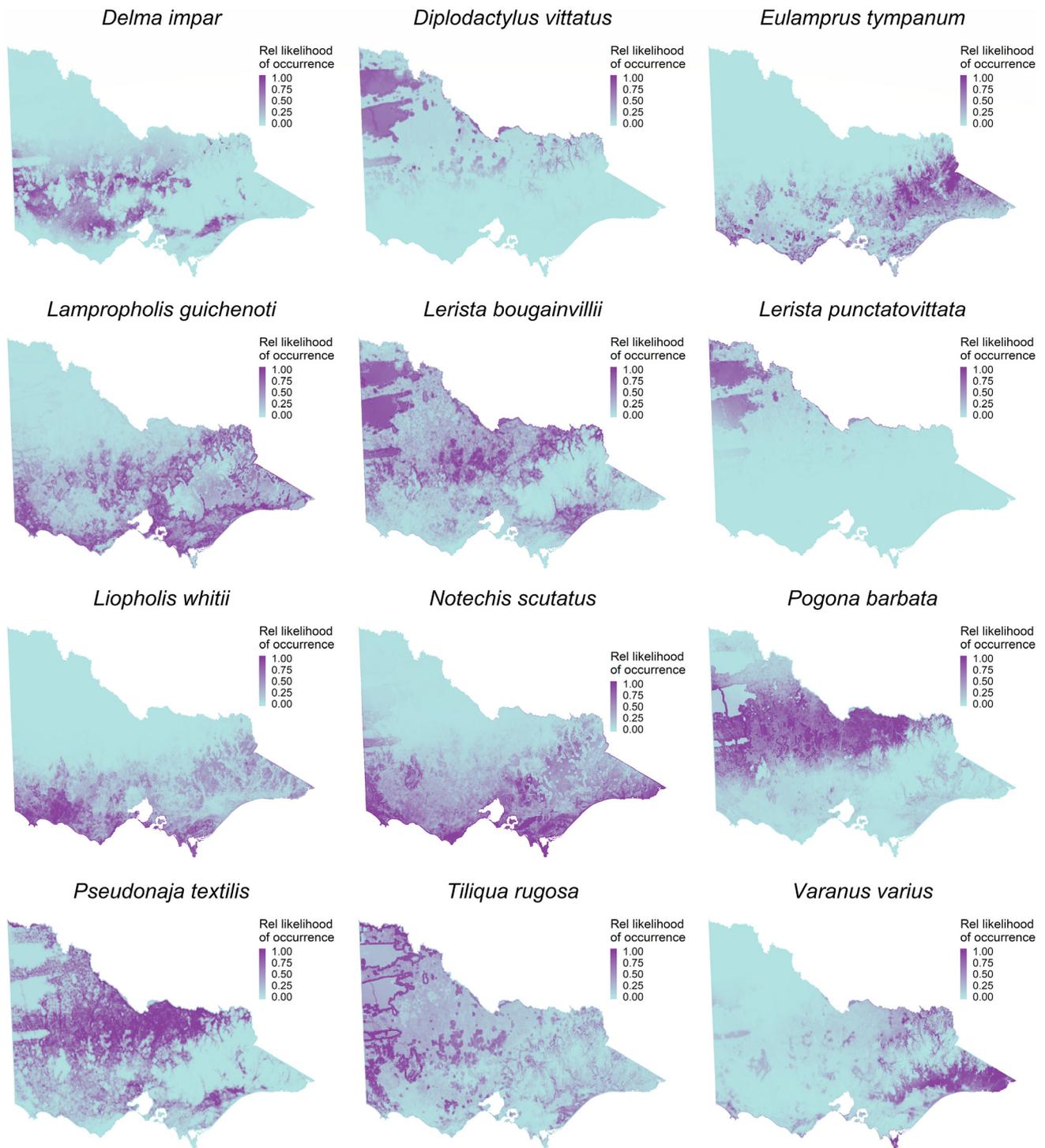


Fig. 3. MaxEnt predictions of relative likelihood of occurrence across Victoria, Australia, for 12 of the 30 reptile species with notable responses to landscape structure variables. Purple represents areas of high relative suitability; blue represents areas of low relative suitability.

more extreme variations in temperature, which may impact the ability of reptiles to thermoregulate (Jellinek et al. 2004). Shape index has also been found to negatively influence plant species richness, possibly due to the greater availability

of resources in more regular-shaped patches (Li et al. 2020), which may in turn afford more resources for animals.

Shannon's Diversity Index was important to the distributions of three reptile species, but the directions of relationships

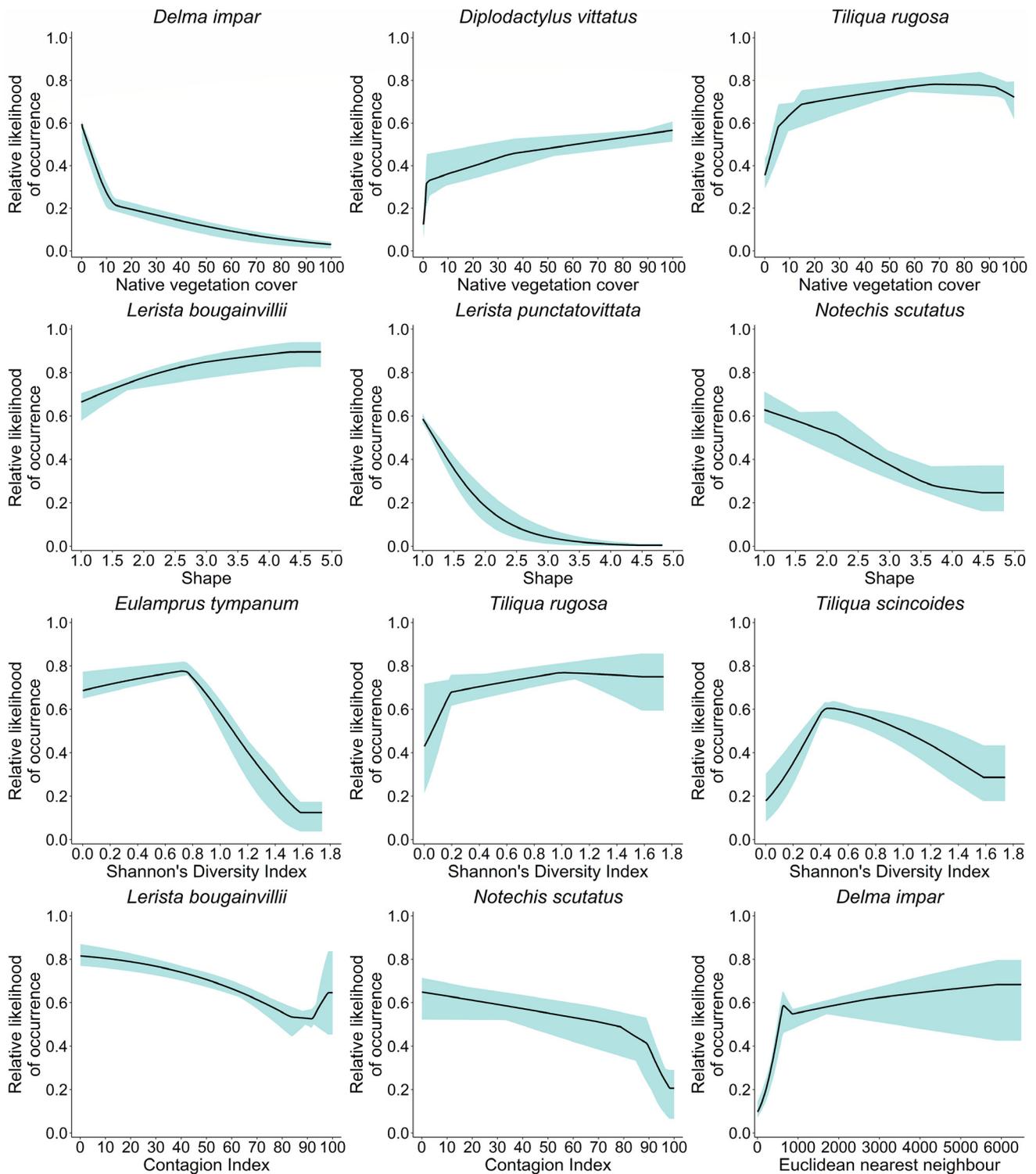


Fig. 4. Selected reptile species responses to landscape structure variables (native vegetation cover, Shape, Shannon's Diversity Index, Contagion Index, and Euclidean nearest neighbour) predicted by MaxEnt models. Relative likelihood of occurrence values are presented on a scale from 0 to 1 to allow for comparison among species and predictor variables. Black lines represent the mean response predicted by the MaxEnt model; blue bands represent minimum and maximum values predicted from five-fold cross validation.

were variable. *Eulamprus tympanum* responded negatively to increasing diversity, and positively to native vegetation

cover. This is probably at least partly due to this species' preference for shelter sites with logs (Langkilde *et al.* 2003),

which are likely to be more common in native vegetation than other land cover types. In general, the presence of other land cover types is thought to negatively impact reptile species persistence, and a global meta-analysis found most types of habitat modification (including mining, grazing, agriculture, plantations and patch size reduction) have an overall negative impact on reptile species abundance (Doherty *et al.* 2020). In south-eastern Australia, agriculture is thought to negatively affect reptiles (Driscoll 2004), and pine plantations have been shown to act as a barrier to connectivity in some species and increase connectivity for others (Mortelliti *et al.* 2015). In our study, *T. rugosa*, a habitat generalist, was more likely to occur in areas with moderate levels of diversity and native vegetation cover. This species is known to favour open habitat and commonly found on roadsides, and may utilise both natural and artificial shelter (Norval and Gardner 2020), characteristics that may provide it with the flexibility to exploit multiple land cover types.

Although our study shows that native vegetation cover and configuration influences the distributions of some species at a statewide scale, it is important to note other reptiles may respond to aspects of landscape structure at finer spatial scales. Habitat cover and configuration, as well as other aspects of landscape structure such as the edge-to-area ratio, influence microclimate and the availability of shade, which is required for thermoregulation. South-eastern Australia is also subject to low-frequency, high-intensity fires (Murphy *et al.* 2013) that create mosaics of vegetation age classes in the landscape. Where species select different age classes, fire may represent an important additional source of habitat fragmentation, which is likely to influence distributions and threaten species persistence (Sitters and Di Stefano 2020). Furthermore, it is anticipated following future changes to the climate, many species worldwide will alter their present distributions (Bezeng *et al.* 2018). However, such range expansions will not be possible if the landscape structure does not facilitate this movement. Incorporating landscape structure, as well as dynamic predictor variables such as fire (Senior *et al.* 2021; Swan *et al.* 2021), into models may improve our ability to predict future species distributions and enable more informed management strategies.

Influence of biophysical variables on species distributions

We found climate variables, especially annual precipitation and the maximum temperature of the warmest month, were the strongest drivers of species distributions for almost all reptile species. Multiple studies have shown climate is a key factor determining both the current and future distributions of reptiles (Ihlow *et al.* 2012; Cabrelli *et al.* 2014; Hosseinzadeh *et al.* 2020) and their nesting habitat (Pike 2013). Environmental temperature plays a particularly important role in regulating the metabolic rates and activity patterns of ectotherms (Buckley *et al.* 2012), and regulates

the reproductive success and sex determination in many species (Witt *et al.* 2010; Ihlow *et al.* 2012; Castelli *et al.* 2021).

Models of both reptile and amphibian species distributions have predicted that, on average, species are likely to experience increases in their climatic range due to climate change (Araújo *et al.* 2006; Hosseinzadeh *et al.* 2020). However, both groups are generally considered to be poor dispersers, and this factor, combined with extensive fragmentation, means that we should not assume that species have the ability and pathways to disperse and colonise new habitat (Araújo *et al.* 2006). Indeed, modelling of European amphibians and reptiles has shown that when models assume no dispersal, virtually all species are projected to experience range contractions (Araújo *et al.* 2006). Therefore, it is important that other non-climatic factors like dispersal (Sahlean *et al.* 2014; Rodrigues and Lima-Ribeiro 2018) and changes to landscape structure (Uriostegui-Velarde *et al.* 2018) are incorporated into models if we are to properly understand the factors driving current and future species distributions.

Soil texture was an important driver of the distributions of a fifth of the species in this study, including common species such as *T. rugosa* and *L. guichenoti*, which both showed an aversion to clay loams. Clay soils experience seasonal changes, becoming waterlogged during the wet season and cracked during the dry season (Woinarski *et al.* 1999). Although clay soils may provide an important temporary water source for frogs (Ferreira *et al.* 2018), this seasonality may be unsuitable for many reptiles (Woinarski *et al.* 1999). Notable differences have also been reported among reptile communities on sandy and clay soils that support different plant communities in arid and semiarid parts of Australia (Driscoll *et al.* 2012). Amphisbaenians, which likely share traits with other burrowing reptiles with absent or reduced limbs, prefer sandy, loose soils and avoid compact, heavy soils – presumably due to the reduced energetic costs of moving underground in sandy soils (Martín *et al.* 2013). Interestingly, however, we found no relationships between sandy textured soils and either *Lerista* species, which are semifossorial and known for their ability to ‘swim’ through sand (Morinaga and Bergmann 2020).

The importance of scale

Scale is an important factor in ecological studies because species respond to different drivers at different spatial scales (Cushman and McGarigal 2004). In the context of presence–background modelling, the area within which background locations are sampled (landscape extent) is an important consideration because it can influence model outputs (Elith *et al.* 2011; Merow *et al.* 2013). We chose the state of Victoria in south-eastern Australia as the landscape extent for all modelled species because it has a substantial

gradient in both biophysical characteristics and landscape structure – the two groups of predictor variables of primary interest. Although using a common landscape extent to model the distributions of multiple species is a common approach (Guerin and Lowe 2013; Liu *et al.* 2013; Hageer *et al.* 2017; Swan *et al.* 2021), the importance of particular predictor variables is likely to be influenced by the range size of each species. For example, in our study, the relative influence of climate compared with landscape structure may be reduced for species whose range is larger than the landscape extent. Results should be interpreted with this in mind because the geographic range size of the species we modelled is variable.

Management implications

Although native vegetation is generally considered important for reptiles, most studies that model species distributions at large spatial scales focus on species responses to climate variables. Nevertheless, landscape structure is expected to be important to reptiles because the composition and configuration of habitat influence access to resources including shelter, food and mates (Fischer and Lindenmayer 2007). Our findings show that the extent of native vegetation had an important influence on the distribution of many terrestrial reptile species in our data set, including endangered species such as *D. impar*, *E. tympanum* and *V. varius*. Therefore, management that focuses on minimising the removal of native vegetation and increasing revegetation is fundamental to maintaining species persistence. Our study also showed that the configuration of native vegetation was important for some reptiles, including common species such as *L. guichenoti* and *P. textilis*. This suggests there is potential to use landscape structure metrics such as configuration to help identify patches of native vegetation where habitat restoration and revegetation are likely to have the greatest conservation outcomes (Jellinek 2017). Strategic revegetation may be especially pertinent in regions such as Victoria, where increases in human population and urban development over the next three decades (Commissioner for Environmental Sustainability Victoria 2018a) are likely to have further negative consequences for biodiversity.

References

- Araújo MB, Peterson AT (2012) Uses and misuses of bioclimatic envelope modeling. *Ecology* **93**, 1527–1539. doi:10.1890/11-1930.1
- Araújo MB, Thuiller W, Pearson RG (2006) Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography* **33**, 1712–1728. doi:10.1111/j.1365-2699.2006.01482.x
- Armstrong G, Reid J, Hutchinson MN (1993) Discovery of a population of the rare scincid lizard *Tiliqua adelaidensis* (Peters). *Records of the South Australian Museum* **26**, 153–155.
- Australian Bureau of Statistics (2018) Population projections, Australia. Population projections (based on assumptions of fertility, mortality and migration) for Australia, states and territories and capital cities. Available at <https://www.abs.gov.au/statistics/people/population/population-projections-australia/latest-release#>. [Verified 27 November 2020]
- Banks SC, Cary GJ, Smith AL, Davies ID, Driscoll DA, Gill AM, *et al.* (2013) How does ecological disturbance influence genetic diversity? *Trends in Ecology & Evolution* **28**, 670–679. doi:10.1016/j.tree.2013.08.005
- Bennett AF, Radford JQ, Haslem A (2006) Properties of land mosaics: implications for nature conservation in agricultural environments. *Biological Conservation* **133**, 250–264. doi:10.1016/j.biocon.2006.06.008
- Bezeng BS, Tesfamichael SG, Dayananda B (2018) Predicting the effect of climate change on a range-restricted lizard in southeastern Australia. *Current Zoology* **64**, 165–171. doi:10.1093/cz/zox021
- Böhm M, Collen B, Baillie JEM, Bowles P, Chanson J, Cox N, *et al.* (2013) The conservation status of the world's reptiles. *Biological Conservation* **157**, 372–385. doi:10.1016/j.biocon.2012.07.015
- Bradshaw CJA (2012) Little left to lose: deforestation and forest degradation in Australia since European colonization. *Journal of Plant Ecology* **5**, 109–120. doi:10.1093/jpe/rtr038
- Brown GW (2001) The influence of habitat disturbance on reptiles in a box-ironbark eucalypt forest of south-eastern Australia. *Biodiversity & Conservation* **10**, 161–176. doi:10.1023/A:1008919521638
- Brown GP, Phillips BL, Webb JK, Shine R (2006) Toad on the road: use of roads as dispersal corridors by cane toads (*Bufo marinus*) at an invasion front in tropical Australia. *Biological Conservation* **133**, 88–94. doi:10.1016/j.biocon.2006.05.020
- Brown GW, Bennett AF, Potts JM (2008) Regional faunal decline – reptile occurrence in fragmented rural landscapes of south-eastern Australia. *Wildlife Research* **35**, 8–18. doi:10.1071/WR07010
- Buckley LB, Hurlbert AH, Jetz W (2012) Broad-scale ecological implications of ectothermy and endothermy in changing environments. *Global Ecology and Biogeography* **21**, 873–885. doi:10.1111/j.1466-8238.2011.00737.x
- Bureau of Meteorology (2016) Climate classification maps. Available at http://www.bom.gov.au/jsp/ncc/climate_averages/climate-classifications/index.jsp. [Verified 27 November 2020]
- Burgin S, Wotherspoon D, Hitchen DJ, Ridgeway P (2011) Habitat use by the jacky lizard *Amphibolurus muricatus* in a highly degraded urban area. *Animal Biology* **61**, 185–197. doi:10.1163/157075511X566515
- Cable AB, O'Keefe JM, Deppe JL, Hohoff TC, Taylor SJ, Davis MA (2021) Habitat suitability and connectivity modeling reveal priority areas for Indiana bat (*Myotis sodalis*) conservation in a complex habitat mosaic. *Landscape Ecology* **36**, 119–137. doi:10.1007/s10980-020-01125-2
- Cabrelli AL, Hughes L (2015) Assessing the vulnerability of Australian skinks to climate change. *Climatic Change* **130**, 223–233. doi:10.1007/s10584-015-1358-6
- Cabrelli AL, Stow AJ, Hughes L (2014) A framework for assessing the vulnerability of species to climate change: a case study of the Australian elapid snakes. *Biodiversity and Conservation* **23**, 3019–3034. doi:10.1007/s10531-014-0760-0
- Cabrera-Guzmán E, Reynoso VH (2012) Amphibian and reptile communities of rainforest fragments: minimum patch size to support high richness and abundance. *Biodiversity and Conservation* **21**, 3243–3265. doi:10.1007/s10531-012-0312-4
- Calenge C (2006) The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* **197**, 516–519. doi:10.1016/j.ecolmodel.2006.03.017
- Castelli MA, Georges A, Cherryh C, Rosauer DF, Sarre SD, Contador-Kelsall I, Holleley CE (2021) Evolving thermal thresholds explain the distribution of temperature sex reversal in an Australian dragon lizard. *Diversity and Distributions* **27**, 427–438. doi:10.1111/ddi.13203
- Cheal D (2010) Growth stages and tolerable fire intervals for Victoria's native vegetation data sets. Fire and adaptive management report no. 84. Department of Sustainability and Environment, East Melbourne, Vic., Australia.
- Commissioner for Environmental Sustainability Victoria (2018a) Victorian State of the Environment 2018 Summary Report. Commissioner for Environmental Sustainability Victoria, Melbourne, Australia. Available at <https://www.ces.vic.gov.au/reports/state-environment-2018>
- Commissioner for Environmental Sustainability Victoria (2018b) Victorian State of the Environment 2018: Scientific Assessments Part III. Commissioner for Environmental Sustainability Victoria, Melbourne, Australia. Available at <https://www.ces.vic.gov.au/reports/state-environment-2018>

- Crooks KR, Burdett CL, Theobald DM, King SRB, Di Marco M, Rondinini C, Boitani L (2017) Quantification of habitat fragmentation reveals extinction risk in terrestrial mammals. *Proceedings of the National Academy of Sciences of the United States of America* **114**, 7635–7640. doi:10.1073/pnas.1705769114
- Cushman SA, McGarigal K (2004) Hierarchical analysis of forest bird species–environment relationships in the Oregon Coast Range. *Ecological Applications* **14**, 1090–1105. doi:10.1890/03-5131
- Cushman SA, McGarigal K, Neel MC (2008) Parsimony in landscape metrics: strength, universality, and consistency. *Ecological Indicators* **8**, 691–703. doi:10.1016/j.ecolind.2007.12.002
- Doherty TS, Balouch S, Bell K, Burns TJ, Feldman A, Fist C, *et al.* (2020) Reptile responses to anthropogenic habitat modification: a global meta-analysis. *Global Ecology and Biogeography* **29**, 1265–1279. doi:10.1111/geb.13091
- Driscoll DA (2004) Extinction and outbreaks accompany fragmentation of a reptile community. *Ecological Applications* **14**, 220–240. doi:10.1890/02-5248
- Driscoll DA, Banks SC, Barton PS, Lindenmayer DB, Smith AL (2013) Conceptual domain of the matrix in fragmented landscapes. *Trends in Ecology & Evolution* **28**, 605–613. doi:10.1016/j.tree.2013.06.010
- Driscoll DA, Whitehead CA, Lazzari J (2012) Spatial dynamics of the knob-tailed gecko *Nephrurus stellatus* in a fragmented agricultural landscape. *Landscape Ecology* **27**, 829–841. doi:10.1007/s10980-012-9734-3
- Dubey S, Shine R (2010) Restricted dispersal and genetic diversity in populations of an endangered montane lizard (*Eulamprus leuraensis*, Scincidae). *Molecular Ecology* **19**, 886–897. doi:10.1111/j.1365-294X.2010.04539.x
- Eigenraam M, Chua J, Hasker J (2013) Environmental-economic accounting: Victorian experimental ecosystem accounts version 1.0. Victorian Department of Sustainability and Environment, Melbourne, Vic., Australia.
- Elith J, Graham CH, Anderson RP, Dudík M, Ferrier S, Guisan A, *et al.* (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography* **29**, 129–151. doi:10.1111/j.2006.0906-7590.04596.x
- Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ (2011) A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* **17**, 43–57. doi:10.1111/j.1472-4642.2010.00725.x
- Ferreira AS, Jehle R, Stow AJ, Lima AP (2018) Soil and forest structure predicts large-scale patterns of occurrence and local abundance of a widespread Amazonian frog. *PeerJ* **6**, e5424. doi:10.7717/peerj.5424
- Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* **37**, 4302–4315. doi:10.1002/joc.5086
- Fischer J, Lindenmayer DB (2007) Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography* **16**, 265–280. doi:10.1111/j.1466-8238.2007.00287.x
- Fletcher RJ, Banks-Leite C, Barlow J, Ewers RM, Rosindell J, Holt RD, *et al.* (2018) Is habitat fragmentation good for biodiversity? *Biological Conservation* **226**, 9–15. doi:10.1016/j.biocon.2018.07.022
- Guerin GR, Lowe AJ (2013) Multi-species distribution modelling highlights the Adelaide geosyncline, South Australia, as an important continental-scale arid-zone refugium. *Austral Ecology* **38**, 427–435. doi:10.1111/j.1442-9993.2012.02425.x
- Guillera-Arroita G, Lahoz-Monfort JJ, Elith J, Gordon A, Kujala H, Lentini PE, *et al.* (2015) Is my species distribution model fit for purpose? Matching data and models to applications. *Global Ecology and Biogeography* **24**, 276–292. doi:10.1111/geb.12268
- Guisan A, Tingley R, Baumgartner JB, Naujokaitis-Lewis I, Sutcliffe PR, Tulloch AIT, *et al.* (2013) Predicting species distributions for conservation decisions. *Ecology Letters* **16**, 1424–1435. doi:10.1111/ele.12189
- Hageer Y, Esperón-Rodríguez M, Baumgartner JB, Beaumont LJ (2017) Climate, soil or both? Which variables are better predictors of the distributions of Australian shrub species? *PeerJ* **5**, e3446. doi:10.7717/peerj.3446
- Hansen NA, Sato CF, Michael DR, Lindenmayer DB, Driscoll DA (2019) Predation risk for reptiles is highest at remnant edges in agricultural landscapes. *Journal of Applied Ecology* **56**, 31–43. doi:10.1111/1365-2664.13269
- Hansen NA, Driscoll DA, Michael DR, Lindenmayer DB (2020) Movement patterns of an arboreal gecko in fragmented agricultural landscapes reveal matrix avoidance. *Animal Conservation* **23**, 48–59. doi:10.1111/acv.12505
- Herrmann H-W, Pozarowski KM, Ochoa A, Schuett GW (2017) An interstate highway affects gene flow in a top reptilian predator (*Crotalus atrox*) of the Sonoran Desert. *Conservation Genetics* **18**, 911–924. doi:10.1007/s10592-017-0936-8
- Hijmans RJ (2020) raster: geographic data analysis and modeling. R package version 3.4-5. Available at <https://CRAN.R-project.org/package=raster>
- Hijmans RJ, Phillips S, Leathwick J, Elith J (2020) dismo: species distribution modeling. R package version 1.3-3. Available at <https://CRAN.R-project.org/package=dismo>
- Hosseinzadeh MS, Fois M, Zangi B, Kazemi SM (2020) Predicting past, current and future habitat suitability and geographic distribution of the Iranian endemic species *Microgecko latifi* (Sauria: Gekkonidae). *Journal of Arid Environments* **183**, 104283. doi:10.1016/j.jaridenv.2020.104283
- Hughes AR, Inouye BD, Johnson MTJ, Underwood N, Vellend M (2008) Ecological consequences of genetic diversity. *Ecology Letters* **11**, 609–623. doi:10.1111/j.1461-0248.2008.01179.x
- Ihlow F, Dambach J, Engler JO, Flecks M, Hartmann T, Nekum S, *et al.* (2012) On the brink of extinction? How climate change may affect global chelonian species richness and distribution. *Global Change Biology* **18**, 1520–1530. doi:10.1111/j.1365-2486.2011.02623.x
- Jellinek S (2017) Using prioritisation tools to strategically restore vegetation communities in fragmented agricultural landscapes. *Ecological Management & Restoration* **18**, 45–53. doi:10.1111/emr.12224
- Jellinek S, Driscoll DA, Kirkpatrick JB (2004) Environmental and vegetation variables have a greater influence than habitat fragmentation in structuring lizard communities in remnant urban bushland. *Austral Ecology* **29**, 294–304. doi:10.1111/j.1442-9993.2004.01366.x
- Jellinek S, Parris KM, McCarthy MA, Wintle BA, Driscoll DA (2014) Reptiles in restored agricultural landscapes: the value of linear strips, patches and habitat condition. *Animal Conservation* **17**, 544–554. doi:10.1111/acv.12121
- Kutt AS (1993) A preliminary evaluation of the use of fluorescent pigments to track the movements of the striped legless lizard *Delma impar* (Reptilia: Pygopodidae). In 'Herpetology in Australia'. (Eds D Lunney, D Ayers) pp. 179–183. (Royal Zoological Society of New South Wales)
- Langkilde T, O'Connor D, Shine R (2003) Shelter-site use by five species of montane scincid lizards in south-eastern Australia. *Australian Journal of Zoology* **51**, 175–186. doi:10.1071/ZO02073
- Li Z, Han H, You H, Cheng X, Wang T (2020) Effects of local characteristics and landscape patterns on plant richness: a multi-scale investigation of multiple dispersal traits. *Ecological Indicators* **117**, 106584. doi:10.1016/j.ecolind.2020.106584
- Liu C, White M, Newell G, Griffioen P (2013) Species distribution modelling for conservation planning in Victoria, Australia. *Ecological Modelling* **249**, 68–74. doi:10.1016/j.ecolmodel.2012.07.003
- Martín J, López P, García LV (2013) Soil characteristics determine microhabitat selection of the fossorial amphibaenian *Trogonophis wiegmanni*. *Journal of Zoology* **290**, 265–272. doi:10.1111/jzo.12033
- McGarigal K (2015) FRAGSTATS help. (Department of Environmental Conservation, University of Massachusetts: Amherst)
- McGarigal K, Cushman SA (2002) Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. *Ecological Applications* **12**, 335–345. doi:10.1890/1051-0761(2002)012[0335:CEOEAT]2.0.CO;2
- McGarigal K, Cushman SA, Ene E (2012) FRAGSTATS v4: spatial pattern analysis program for categorical and continuous maps. Available at <http://www.umass.edu/landeco/research/fragstats/fragstats.html>
- Merow C, Smith MJ, Silander JA Jr (2013) A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography* **36**, 1058–1069. doi:10.1111/j.1600-0587.2013.07872.x
- Morinaga G, Bergmann PJ (2020) Evolution of fossorial locomotion in the transition from tetrapod to snake-like in lizards. *Proceedings of the*

- Royal Society B: *Biological Sciences* **287**, 20200192. doi:10.1098/rspb.2020.0192
- Mortelliti A, Michael DR, Lindenmayer DB (2015) Contrasting effects of pine plantations on two skinks: results from a large-scale 'natural experiment' in Australia. *Animal Conservation* **18**, 433–441. doi:10.1111/acv.12190
- Munguia-Vega A, Rodriguez-Estrella R, Shaw WW, Culver M (2013) Localized extinction of an arboreal desert lizard caused by habitat fragmentation. *Biological Conservation* **157**, 11–20. doi:10.1016/j.biocon.2012.06.026
- Murphy BP, Bradstock RA, Boer MM, Carter J, Cary GJ, Cochrane MA, et al. (2013) Fire regimes of Australia: a pyrogeographic model system. *Journal of Biogeography* **40**, 1048–1058. doi:10.1111/jbi.12065
- National Committee on Soil and Terrain (2009) 'Australian Soil and Land Survey Field Handbook.' 3rd edn. (CSIRO Publishing: Melbourne, Vic., Australia)
- Neuwald JL, Templeton AR (2013) Genetic restoration in the eastern collared lizard under prescribed woodland burning. *Molecular Ecology* **22**, 3666–3679. doi:10.1111/mec.12306
- Nimmo DG, Avitabile S, Banks SC, Bliège Bird R, Callister K, Clarke MF, et al. (2019) Animal movements in fire-prone landscapes. *Biological Reviews* **94**, 981–998. doi:10.1111/brv.12486
- Norval G, Gardner MG (2020) The natural history of the sleepy lizard, *Tiliqua rugosa* (Gray, 1825) – insight from chance observations and long-term research on a common Australian skink species. *Austral Ecology* **45**, 410–417. doi:10.1111/aec.12715
- Phillips SJ (2017) A brief tutorial on MaxEnt. Available at https://biodiversityinformatics.amnh.org/open_source/maxent/. [Accessed 10 June 2022]
- Pike DA (2013) Climate influences the global distribution of sea turtle nesting. *Global Ecology and Biogeography* **22**, 555–566. doi:10.1111/geb.12025
- Potapov P, Hansen MC, Laestadius L, Turubanova S, Yaroshenko A, Thies C, et al. (2017) The last frontiers of wilderness: tracking loss of intact forest landscapes from 2000 to 2013. *Science Advances* **3**, e1600821. doi:10.1126/sciadv.1600821
- Powney GD, Grenyer R, Orme CDL, Owens IPF, Meiri S (2010) Hot, dry and different: Australian lizard richness is unlike that of mammals, amphibians and birds. *Global Ecology and Biogeography* **19**, 386–396. doi:10.1111/j.1466-8238.2009.00521.x
- R Core Team (2020) R: a language and environment for statistical computing. Available at <https://www.R-project.org/>
- Rincón-Aranguri M, Urbina-Cardona N, Galeano SP, Bock BC, Páez VP (2019) Road kill of snakes on a highway in an Orinoco ecosystem: landscape factors and species traits related to their mortality. *Tropical Conservation Science* **12**, doi:10.1177/1940082919830832
- Rodrigues JFM, Lima-Ribeiro MS (2018) Predicting where species could go: climate is more important than dispersal for explaining the distribution of a South American turtle. *Hydrobiologia* **808**, 343–352. doi:10.1007/s10750-017-3436-4
- Rodrigues MT (2005) The conservation of Brazilian reptiles: challenges for a megadiverse country. *Conservation Biology* **19**, 659–664. doi:10.1111/j.1523-1739.2005.00690.x
- Sahlean TC, Gherghel I, Papeş M, Strugariu A, Zamfirescu ŞR (2014) Refining climate change projections for organisms with low dispersal abilities: a case study of the Caspian whip snake. *PLoS ONE* **9**, e91994. doi:10.1371/journal.pone.0091994
- Scroggie MP, Peterson GNL, Rohr DH, Nicholson E, Heard GW (2019) Disturbance has benefits as well as costs for fragmented populations of a cryptic grassland reptile. *Landscape Ecology* **34**, 1949–1965. doi:10.1007/s10980-019-00865-0
- Senior KL, Giljohann KM, McCarthy MA, Rainsford FW, Kelly LT (2021) Predicting mammal responses to pyrodiversity: from microbats to macropods. *Biological Conservation* **256**, 109031. doi:10.1016/j.biocon.2021.109031
- Sitters H, Di Stefano J (2020) Integrating functional connectivity and fire management for better conservation outcomes. *Conservation Biology* **34**, 550–560. doi:10.1111/cobi.13446
- State Government of Victoria (2018) Victorian Biodiversity Atlas fauna records (unrestricted) for sites with high spatial accuracy. Available at <https://datashare.maps.vic.gov.au/> [Accessed 18 June 2018]
- State of Victoria (Agriculture Victoria) (2018) Victorian land use information system 2016–2017. Available at <https://discover.data.vic.gov.au/dataset/victorian-land-use-information-system-2016-2017>
- State of Victoria (Agriculture Victoria) (2020) Victorian resources online. Soil surface texture. Available at http://vro.agriculture.vic.gov.au/dpi/vro/vrosite.nsf/pages/soil_texture-soil-surface [Accessed 11 September 2020]
- Swan M, Le Pla M, Di Stefano J, Pascoe J, Penman TD (2021) Species distribution models for conservation planning in fire-prone landscapes. *Biodiversity and Conservation* **30**, 1119–1136. doi:10.1007/s10531-021-02136-4
- Thuiller W, Araujo MB, Lavorel S (2003) Generalized models vs. classification tree analysis: predicting spatial distributions of plant species at different scales. *Journal of Vegetation Science* **14**, 669–680. doi:10.1111/j.1654-1103.2003.tb02199.x
- Uriostegui-Velarde JM, González-Romero A, Pineda E, Reyna-Hurtado R, Rizo-Aguilar A, Guerrero JA (2018) Configuration of the volcano rabbit (*Romerolagus diazi*) landscape in the Ajusco-Chichinautzin Mountain Range. *Journal of Mammalogy* **99**, 263–272. doi:10.1093/jmammal/gyx174
- Verdon SJ, Watson SJ, Nimmo DG, Clarke MF (2020) Are all fauna associated with the same structural features of the foundation species *Triodia scariosa*? *Austral Ecology* **45**, 773–787. doi:10.1111/aec.12894
- Webb JK, Harlow PS, Pike DA (2014) Australian reptiles and their conservation. In 'Austral Ark: the State of Wildlife in Australia and New Zealand'. (Eds A Stow, N Maclean, G Holwell) pp. 354–381. (Cambridge University Press: Cambridge, UK)
- Weldon AJ, Haddad NM (2005) The effects of patch shape on indigo buntings: evidence for an ecological trap. *Ecology* **86**, 1422–1431. doi:10.1890/04-0913
- Whitaker PB, Shine R (2003) A radiotelemetric study of movements and shelter-site selection by free-ranging brownsnakes (*Pseudonaja textilis*, Elapidae). *Herpetological Monographs* **17**, 130–144. doi:10.1655/0733-1347(2003)017[0130:ARSOMA]2.0.CO;2
- Wickham H, Averick M, Bryan J, Chang W, McGowan LD, François R, et al. (2019) Welcome to the tidyverse. *The Journal of Open Source Software* **4**, 1686. doi:10.21105/joss.01686
- Wilke CO (2020) cowplot: streamlined plot theme and plot annotations for 'ggplot2'. R package version 1.1.1. Available at <https://CRAN.R-project.org/package=cowplot>
- Wisz MS, Hijmans RJ, Li J, Peterson AT, Graham CH, Guisan A, NCEAS Predicting Species Distributions Working Group (2008) Effects of sample size on the performance of species distribution models. *Diversity and Distributions* **14**, 763–773. doi:10.1111/j.1472-4642.2008.00482.x
- Witt MJ, Hawkes LA, Godfrey MH, Godley BJ, Broderick AC (2010) Predicting the impacts of climate change on a globally distributed species: the case of the loggerhead turtle. *Journal of Experimental Biology* **213**, 901–911. doi:10.1242/jeb.038133
- Woinarski JCZ, Fisher A, Milne D (1999) Distribution patterns of vertebrates in relation to an extensive rainfall gradient and variation in soil texture in the tropical savannas of the Northern Territory, Australia. *Journal of Tropical Ecology* **15**, 381–398. doi:10.1017/S0266467499000905

Data availability. The data that support this study are available in FigShare at <https://doi.org/10.26188/61dbdefb9427d>.

Conflicts of interest. The authors declare no conflicts of interest.

Declaration of funding. This research was supported by the Holsworth Wildlife Research Endowment and the Parks Victoria Applied Park Management Research Scholarship.

Acknowledgements. We thank Trent Penman for contributions to the original study design and for analytical advice; Sarah McColl-Gausden and Kate Parkins for additional analytical advice and support; Geoff Brown for advice on taxonomic changes; and Courtney Whitford for comments that improved this manuscript.

Author affiliation

^ASchool of Ecosystem and Forest Sciences, University of Melbourne, 4 Water Street, Creswick, Vic. 3363, Australia.