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RESEARCH ARTICLE

Correlates of extinction risk in Australian squamate reptiles

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Abstract

Aim: Identification of particular traits that predispose species to elevated extinction risk is an important component of proactive conservation. We capitalise on a recent strategic extinction risk assessment of all Australian squamate reptiles to identify intrinsic life history traits and extrinsic threats that correlate with extinction risk. We further assess whether extinction risk correlates differ between species impacted by different threatening processes (habitat loss vs. invasive species).

Location: Australia.

Taxon: Squamate reptiles.

Methods: We used the IUCN Red List data for Australian squamates, and publicly available datasets for 14 intrinsic and extrinsic traits. We used phylogenetically controlled Bayesian inference to test hypotheses regarding relationships between extinction risk and species traits, environment, and threat measures.

Results: We found that intrinsic characteristics (habitat specialisation, small range size and large body size), as well as extrinsic factors (high human footprint, accessibility from human population centres, cold temperatures and high rainfall), predispose a species to extinction. Similar predictors were important in threat-specific analyses, although relationships were generally more uncertain.

Conclusions: Our results largely accord with those of global and regional studies of extinction risk in reptiles and of terrestrial vertebrates more broadly. Our findings illustrate that there is no single pathway to extinction among Australian squamates.

KEYWORDS
Australia, body size, extinction risk, geographic range, habitat specialisation, human footprint, IUCN Red List, lizard, snake, squamate

1 | INTRODUCTION

Species extinction rates are now three orders of magnitude higher than levels recorded for pre-human history (Murray et al., 2014). A central goal of conservation biology is to identify ecological traits that correlate with species extinction risk (Bland, 2017). This area of conservation biology has seen a flurry of growth in the last decade, with global studies conducted on almost all terrestrial vertebrates, including mammals (Cardillo et al., 2008; Davidson et al., 2009; Murray et al., 2014), amphibians (Sodhi et al., 2008), birds (Lee & Jetz, 2011), and reptiles (Böhm et al., 2016; Tingley et al., 2013, 2016), as well as on freshwater fishes (Liu et al., 2016; Olden et al., 2007). Such broad comparative analyses can help identify factors (such as small range size, habitat specialisation, diet, large body size, and slow reproductive rate) that predispose species to extinction, and contribute to our understanding of why some species are more

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at risk than others (Ripple et al., 2019). Such studies are, at the very least, a call to arms, highlighting the plight facing our most vulnerable species (Cardillo & Meijaard, 2012).

Species extinction risk depends on extrinsic threats, such as habitat loss, as well as a species' ability to cope with these threats, determined by intrinsic life history and ecology (Tingley et al., 2013). Thus, incorporating information on threatening processes along with life history and ecological data can improve the predictive power of extinction risk models (Bland, 2017; Gonzalez-Suarez et al., 2013; Murray et al., 2014). For example, Owens and Bennett (2000) found that bird species threatened by overexploitation had large body sizes and long generation times, whereas species threatened by habitat loss had small body sizes and tended to be habitat specialists. In addition, variation in extinction risk drivers across different regions requires analyses that are focused on narrower spatial extents (Cardillo & Meijaard, 2012; Fisher & Owens, 2004; Fritz et al., 2009; Murray et al., 2014). For example, in contrast to findings in other regions, Fisher et al. (2003) found that the traits most commonly identified as causing decline, such as body size, small range size, diet, and habitat specialisation, were unimportant for Australia marsupials. Instead, range overlap with introduced mammals was most important. Additionally, although conservation priorities are often identified at the global scale (e.g., Grenyer et al., 2006; Pollock et al., 2017; Roll et al., 2017), conservation strategies are generally implemented across regional or national scales. This necessitates an understanding of region-specific threat drivers.

Australia is a region with an appalling history of species extinctions, especially since European colonisation (Allek et al., 2018). Mammals have been particularly hard hit: 34 species have gone extinct since the 1850s (Geyle et al., 2018; Woinarski et al., 2019). Nine species of Australian bird have become extinct since colonisation (Woinarski et al., 2019), with the additional loss of many regionally restricted subspecies (Geyle et al., 2018). Along with its unique and relatively impoverished endotherm fauna, Australia is also home to over 1000 reptile species, representing one of the most species-rich reptile assemblages globally, 96% of which are endemic (Chapple et al., 2019; Roll et al., 2017; Tingley et al., 2019). The majority of these are squamates (lizards and snakes) two are crocodiles and 24 are freshwater turtle species. Our understanding of Australian reptile extinction risk lags behind that of other vertebrate taxa, exemplified by the loss of the Christmas Island forest skink (*Emoia nativitatis*) that became extinct in the wild in 2010 (Geyle et al., 2018). This was Australia's first reptile extinction to be recorded since European colonisation, and the species was not listed as threatened under the national Environmental Protection and Biodiversity Conservation Act, 1999 (EPBC Act, 1999) or given an International Union for Conservation of Nature (IUCN) Red List status until after its wild population was lost (Geyle et al., 2018). In addition, recent research suggests that six Australian squamate species could be at high risk (>50%) of extinction by 2040, and that up to 11 species could be lost within this timeframe without management intervention (Geyle et al., 2021). Nonetheless, Australian squamates are poorly represented in formal environmental legislation (EPBC Act, 1999) compared to other vertebrate groups, limiting our understanding of the number of reptile species threatened with extinction (Walsh et al., 2013). Until recently, only ~14% of the Australian squamate fauna had been assessed using IUCN Red List criteria, the lowest proportion of any region on earth (Meiri & Chapple, 2016).

Our limited understanding of extinction risk among Australian squamates has constrained the scope of macroecological studies on threats and drivers. We are only beginning to understand the threats facing Australia's reptile fauna. Woinarski et al. (2018), for example, recently highlighted hitherto unquantified threats by feral cat predation. Correlates of extinction risk have been published only for Australian snakes (Elapids; Reed & Shine, 2002). Life history traits relating to mating systems and hunting techniques were identified as the main correlates of endangerment (Cogger et al., 1993; Reed & Shine, 2002). Global analyses of extinction risk correlates have included a subset of Australian reptiles and considered them together with species found in Asia, in focused regional analyses (Böhm et al., 2016).

The Australian reptile ‘assessment gap’ has recently been rectified, however, with all species receiving a conservation status as part of the IUCN's Global Reptile Assessment in 2017 (Chapple et al., 2019; Tingley et al., 2019). In light of this recent work, the main objectives of this study are twofold: (i) identify national correlates of extinction risk for Australian squamates; (ii) determine whether traits that predispose species to extinction differ between species that are threatened with habitat loss versus those threatened by invasive species.

We use a comprehensive dataset including both intrinsic ecological and life history traits, as well as extrinsic environmental variables and human influence measures to identify key factors associated with extinction risk (Table 1). We compare results to global and Australasian analyses (Böhm et al., 2016), and hypothesise that accessibility to human population centres is less important in the Australian context than elsewhere, given the occurrence of a diverse reptile fauna in areas where human populations are low (Powney et al., 2010), and a landscape of threats not restricted to urban areas (Tingley et al., 2019; Woinarski et al., 2018).

2 | MATERIALS AND METHODS

2.1 | Species data

This study was based on the conservation statuses of 948 Australian squamate reptile species, as defined by the IUCN Red List of Threatened Species (Chapple et al., 2019; Tingley et al., 2019). We excluded from all analyses three introduced squamates that are present on the Australian mainland and/or adjacent islands (*Hemidactylus frenatus*, *Lepidodactylus lugubris*, *Eutropis multifasciata* and *Indotyphlops braminus*) and species that have been introduced to Christmas Island and the Cocos (Keeling) islands (*Lycodon capucinus*, *Lygosoma bowringi* and *Gehyra mutilata*).

For predictor variables, we compiled a dataset of 14 intrinsic species traits and extrinsic factors (Table 1) in order to test hypotheses regarding relationships between extinction risk and species

TABLE 1 Hypotheses on the relationship between potential correlates and species traits.

Explanatory variable	Variable in analysis	Prediction	Justification	References
Intrinsic variables				
Geographic range	Range size (km^2)	–	Small range sizes correspond to smaller populations and are more vulnerable to threats acting across the entire range. Also an IUCN Red List criterion	Tingley et al. (2013) and Böhm et al. (2016)
Habitat specialisation	Residuals of regression of range size on number of biomes occupied	–	Habitat specialist are at higher risk of extinction	Tingley et al. (2013) and Böhm et al. (2016)
Island endemism	Categorical: island (including Tasmania) or mainland dwelling	+	Species with endemic island distributions have small range sizes, and have lost defence mechanisms to deal with predators (insular naivete)	Böhm et al. (2016) and Slavenko et al. (2016)
Body size	Maximum snout-vent length (lizards) or total length (snakes) in mm	+	Large-bodied species are more likely to have small population densities, slow life histories and large home ranges	Tingley et al. (2013) and Böhm et al. (2016)
Leg reduction	Categorical: fully legged (if they have four pentadactyl limbs) versus leg-reduced	+	Leg-reduced lizards are more likely to be fossorial and cryptic to predators	Meiri (2018)
Taxonomic group	Snake versus lizard	–	Australian snakes are less likely to be threatened than lizards	Tingley et al. (2019)
Reproductive mode	Categorical: viviparous or not	+	Viviparous species tend to reproduce more slowly than oviparous species	Durnham et al. (1988) and Böhm et al. (2016)
Activity phase	Categorical: diurnal, cathemeral[a] (active both day and night), nocturnal.	NA	Nocturnal and cathemeral species have activity patterns that coincide with introduced mammalian predators	Meiri et al. (2013)
Microhabitat	Categorical: surface dwelling[a], aquatic, or fossorial	NA	Surface dwelling species are more likely to vulnerable to predation by introduced predators	Meiri (2018)
Ground dwelling	Categorical: arboreal or not arboreal	–	Arboreal species are less extinction prone than ground dwelling species in Australian mammals and we expect the same may be true for reptiles	Johnson and Isaac (2009)
Extrinsic variables				
Temperature	Annual average temperature (°C)	–	Reptiles are ectotherms with slower life histories in cooler regions.	Scharf et al. (2015); Böhm et al. (2016)
Precipitation	Annual average precipitation (mm)	+	Areas experiencing high levels of precipitation have higher productivity and thus potentially higher human disturbance	Tingley et al. (2013); Böhm et al. (2016)
Biome	Categorical: desert[a], mediterranean, temperate grassland, tropical grassland, temperate forest, tropical forest	NA	Tropical and temperate grasslands host higher richness of threatened squamates	Tingley et al. (2019)
Accessibility	Distance from nearest city of >50,000	–	Australian reptile diversity is concentrated where human population is lowest	Powney et al. (2010)
Human impact	Human footprint	+	Australian reptile diversity is concentrated where human population is lowest and associated footprint is smaller	Powney et al. (2010)

Note: Prediction column indicates direction of predicted relationship between variable and threat status (+, trait state or higher levels of a continuous variable associated with higher extinction risk; –, trait state or higher levels of a continuous variable associated with lower extinction risk). NA, directional predictions are not available for these categorical variables.

[a] Indicates reference category in regression models.

traits, environment, and threat measures, as per Böhm et al. (2016). Hypotheses are listed in Table 1. Intrinsic traits were compiled as per Feldman et al. (2016) and Meiri (2018), and included body size, activity phase, reproductive mode, microhabitat (surface active, fossorial, or aquatic; semi-fossorial and semi-aquatic species were considered fossorial and aquatic, respectively), and an additional binomial variable identifying arboreal versus non-arboreal species. We also examined effects of leg reduction (in lizards). Data were collected via literature searches, museum specimens, and via input from species experts (see Feldman et al., 2016; Meiri, 2018).

Geographic range maps produced as part of the IUCN Red list assessment process (Tingley et al., 2019) were used to calculate species range sizes (km^2). Range size is an explicit criterion used to assign IUCN Red List categories, and thus we included range size as a predictor to account for its effects. IUCN range maps were also used to generate further predictor variables using ArcGIS 10.4 (Esri, 2016). These included whether the species was an island endemic, habitat specificity (approximated using the residuals of a regression of range size on number of biomes occupied because of the tight relationship between the two variables), and biome of origin (biome data obtained from https://www.worldwildlife.org/biomecategories/terrestrialecoregions). We also extracted extrinsic factors from these range maps, including mean annual precipitation (mm), annual temperature (°C; WorldClim v2; http://www.worldclim.org/), and measures of human influence, all calculated as the mean value across each species' range. Measures of human influence included species accessibility (measured as travel time to a city with >50,000 people; Weiss et al., 2018, https://malariaatlas.org/research-project/accessibility-to-cities/) and human footprint (comprising eight variables: built-up environments, population density, electric power infrastructure, crop lands, pasture lands, roads, railways and navigable waterways; Venter et al., 2018; https://doi.org/10.7927/H46T0JQ4).

Each species' IUCN Red List category (https://www.iucnredlist.org/) provided the binary response variable of extinction risk. Species classed by the Red List as 'Least Concern' or 'Near Threatened' (NT) were considered 'not at risk', whereas 'Vulnerable' (VU), 'Endangered' (EN) and 'Critically Endangered' (CR) species were considered 'at risk'. We also included species listed as extinct/extinct in the wild (*n* = 3) as 'at risk' (although we lacked sufficient trait data for the extinct species to include it in the final analysis). Though not technically threatened, these species provide the most data to correlate with extinction risk. Using a binary threat status variable rather than an ordinal response removes the effects of skewed distributions typical of the ordinal scales used in the IUCN Red List (Dinnage et al., 2020). Indeed, the distribution of conservation statuses is extremely highly skewed among assessed Australian squamates (LC = 606; NT = 9; VU = 19; EN = 14; CR = 5; EW = 2). Species not present in the global squamate phylogeny (*n* = 65; Tonini et al., 2016), classed as Data Deficient (*n* = 30), and with inadequate trait data (*n* = 198) were also excluded, resulting in a final sample size of 655 species.

In a second set of analyses, we included the main threats faced by each of the 'at risk' species, recorded as part of the 2017 Red List assessment. These were divided into main threat types as per Böhm et al. (2016); however, only habitat loss/modification (*n* = 158) and invasive species impacts (*n* = 94) were analysed, as other threat types had inadequate samples sizes. Species were often threatened by more than one process. For threat-specific analyses, species threatened by the two threat types were considered in both analyses. In all cases, the response variable was binomial; threat type (i.e., habitat loss or invasive species) or no threat type.

2.2 | Statistical analysis

Statistical analyses were carried out in R v4.0.2 (R Development Core Team, 2020). The main aim of the analysis was to identify which, if any, of the species traits correlate with species threat status. We chose to do this in a Bayesian framework, partially because Bayesian analyses are robust to multiple comparisons (Dienes, 2011; Gelman et al., 2012, 2013). Phylogenetic mixed effects models with a Bernoulii error distribution were built using the 'MCMCglmm' function in the MCMCglmm package (Hadfield, 2010). Fixed effects included all extrinsic and intrinsic variables. All continuous fixed effects were centred and scaled prior to analysis. A phylogenetic random effect was included, where the covariance between species was modelled according to a non-dated phylogeny incorporating Australian squamates (Tonini et al., 2016). We used an inverse Wishart prior for the covariance between species (*V* = 1, nu = 0.02) and normal priors with a mean of 0 and a variance of 9 for the fixed effects. Models were run for 400,000 iterations, with the first 100,000 iterations discarded as 'burn-in'. We retained every 20th sample, resulting in 15,000 samples of the posterior distribution of each parameter. Convergence was evaluated visually via trace plots and effective sample sizes.

3 | RESULTS

3.1 | Australia-wide correlates of risk

We first asked whether we could detect associations between species traits, extrinsic factors, and threat status at the national level. These analyses revealed that threat status was influenced by a range of intrinsic characteristics (habitat specialisation, i.e., residual number of biomes occupied, geographic range size and body size) as well as extrinsic factors (human footprint, accessibility from human population centres, temperature and precipitation; Figure 1 and Table S1a). Habitat specialists, species with small geographic ranges and large-bodied species were at higher risk of extinction. Species that occur in colder regions, occur in regions with more rainfall, are subjected to a large human footprint and are in close proximity to major cities were also at higher risk. There was weaker evidence (credible intervals overlapped 0) that lizards, island endemics, aquatic species, viviparous species and species that have the majority of their range in temperate grasslands were at greater risk of extinction. However, very few species in the final dataset were aquatic (*n* = 17), island endemics (*n* = 14) or occurred in temperate grasslands (*n* = 13), and thus associations

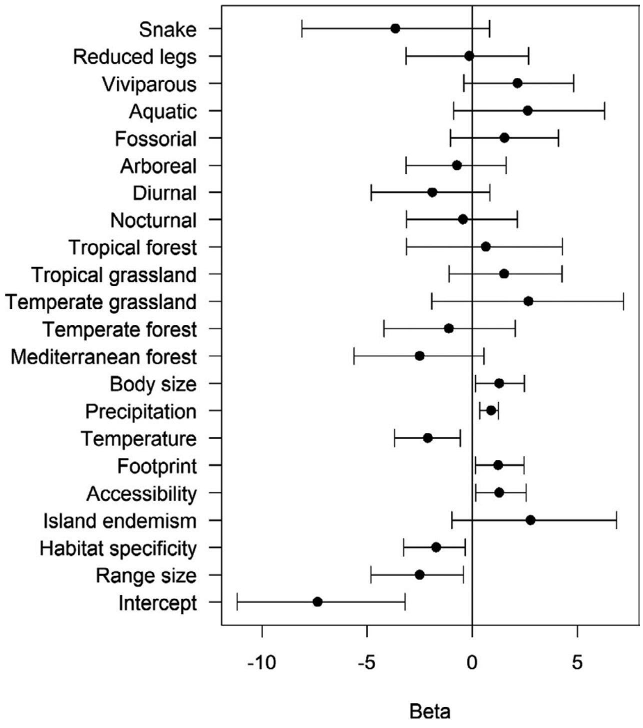

FIGURE 1 Coefficient plot showing mean and 95% credible intervals of regression coefficients, relating species traits and extrinsic factors to extinction risk in all Australian squamates

between these variables and extinction risk should be treated with caution.

3.2 | Threat-specific correlates of risk

We asked whether species threatened by specific processes would differ in correlates of extinction risk. We found that species that were threatened by habitat loss had smaller geographic ranges and occupy regions that are colder, wetter and subjected to higher human footprints compared to species not listed as being affected by this threat (Figure 2; Table S1b). Australian squamates threatened by invasive species were more likely to occupy wetter regions (Figure 3; Table S1c).

4 | DISCUSSION

Capitalising on the recent IUCN assessment of all Australian squamate species, we conducted the first investigation of associations between extinction risk and life history, ecological, environmental and human influence attributes for this diverse, yet poorly known group. Our analyses revealed multiple intrinsic and extrinsic factors influenced extinction risk. Overall, our findings accord with those of earlier studies of extinction risk in reptiles and of terrestrial vertebrates more generally.

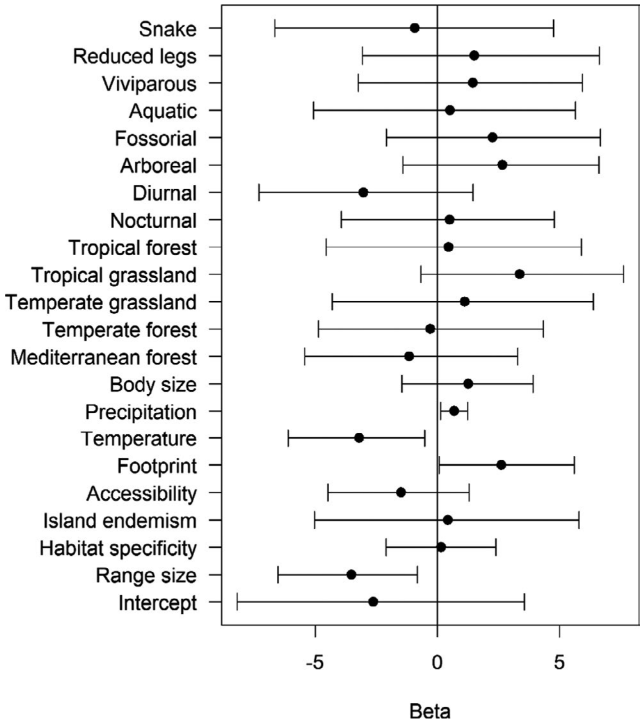

FIGURE 2 Coefficient plot showing mean and 95% credible intervals of regression coefficients, relating species traits and extrinsic factors to extinction risk in Australian squamates threatened by habitat loss

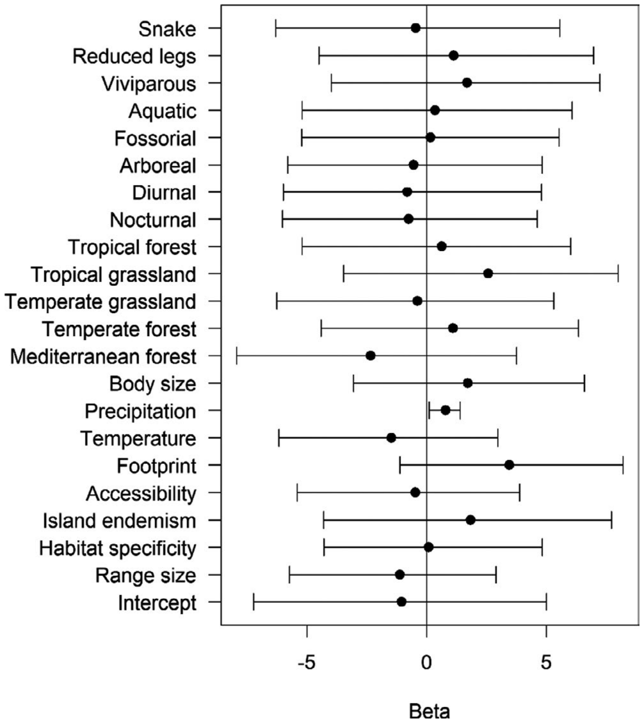

FIGURE 3 Coefficient plot showing mean and 95% credible intervals of regression coefficients, relating species traits and extrinsic factors to extinction risk in Australian squamates threatened by invasive species impacts

4.1 | Intrinsic traits

In line with the results of previous studies of reptile extinction risk, we found that large-bodied species were more vulnerable to extinction than smaller bodied species (Böhm et al., 2016; Reed & Shine, 2002; Slavenko et al., 2016; Tingley et al., 2013, 2016). Interestingly, effects of body size were apparent in our overall analyses, as well as when we considered species that are at risk from different threatening processes (habitat loss vs. invasive species). Larger body sizes are often associated with slower life histories and low population densities, or a reduced ability to avoid invasive predators, all of which are likely to increase susceptibility to extinction (Böhm et al., 2016; Tingley et al., 2013). In Australia, large species, such as Merten's Water Monitor (*Varanus mertensi*)—listed as Endangered, are more likely to decline due to lethal ingestion of toxic invasive cane toads (Feit & Letnic, 2015), a key threatening process for Australian squamates (Tingley et al., 2017).

Unsurprisingly, Australian squamate species with small geographic ranges had a higher likelihood of being threatened, and a higher likelihood of being impacted by habitat loss. Small range size is thought to enhance extinction risk because small-ranged species tend to have smaller populations and an increased susceptibility to detrimental stochastic events and genetic isolation (Böhm et al., 2016; Fisher et al., 2003; Tingley et al., 2013). Range size is also used in determining a species' IUCN status, so a strong relationship is expected a priori. Indeed, range size has been found to correlate with extinction risk in a number of taxa, including New Zealand reptiles (Tingley et al., 2013), and a global subset of 1500 reptiles (Böhm et al., 2016). The fact that range size was a strong predictor in those species threatened by habitat loss (but not invasive species) is likely because species assessed as threatened under IUCN Red List criterion B (restricted distribution), which includes the majority of Australian squamates, must also meet further criteria, including a decline of areal extent and/or quality of habitat.

Australian squamates occupying a small number of biomes were more likely to be threatened than species that occupied multiple biomes, even after accounting for geographic range size; however, this correlation was not apparent in threat-specific analyses. Previous studies of overall threat status have found similar patterns (Gonzalez-Suarez et al., 2013), including global (Böhm et al., 2016; Ducatez et al., 2014) and regional (Tingley et al., 2013) studies of reptiles. Plausibly, habitat specialisation increases extinction susceptibility because specialised species are more sensitive to environmental change than are generalists (Fisher et al., 2003).

Although the aforementioned results are in line with the results of previous studies, we did detect associations between life history, ecology and extinction risk that have not been revealed by previous work. For example, we found that viviparous species were more likely to be at risk of extinction, although the coefficient estimate for this variable included 0. Sinervo et al. (2010) predicted that viviparous lizards would have a higher extinction risk (twice that of oviparous species) due to their limited geographic ranges (i.e., many viviparous species occur only at high elevation) and impacts of climate change (also see Pincheira-Donoso et al., 2013). Similarly, there is a high percentage of viviparous species in the high elevation regions of south-eastern Australia (e.g., Feldman et al., 2015). However, previous studies of reptile extinction risk based on expert assessments (Böhm et al., 2016; Tingley et al., 2013, 2016) have not detected an association between viviparity and the likelihood of being at risk. We suspect the less frequent reproduction of viviparous squamates, relative to that of oviparous ones, could explain this result.

Our results revealed that island endemism was correlated with overall threat status, although effects were uncertain, and island endemics were relatively rare in our final dataset (*n* = 14 species). Several of Australia's threatened squamates occur only on offshore islands, notably Lord Howe Island and Norfolk Island to the east, and Christmas Island to the north west. Until recently, five endemic squamate species were known from Christmas Island, but three of these are now extinct or extinct in the wild, and the remaining two (the Christmas Island Blind Snake *Ramphotyphlops exocoeti* and the Christmas Island Forest Gecko *Cyrtodactylus sadleiri*) are Endangered, plausibly due to the arrival of invasive vertebrates and invertebrates (Chapple et al., 2019; Tingley et al., 2019). The two remaining endemic reptile species on Lord Howe island and Norfolk Island are also listed as threatened, largely due to invasive rodents (Chapple et al., 2019; Tingley et al., 2019). Globally, a large proportion of threatened species occur on islands, and 75% of all known bird, mammal, amphibian and reptile extinctions have occurred on islands (Holmes et al., 2019; Tershy et al., 2015). In Australia specifically, island endemics are disproportionately represented among extinct mammals (Woinarski et al., 2019), and all extinct and extinct in the wild reptiles were insular.

Finally, taxonomic suborder was also important: snakes were less threatened overall. Indeed, 7.1% of Australian lizards in our final dataset were threatened, compared to 2.8% of snakes. It is unclear whether this is because snakes are less threatened generally, or because less is known about their distributions and population trends.

4.2 | Extrinsic factors

Our results revealed that variables describing human impact, particularly the human footprint, were positively correlated with extinction risk. The human footprint variable used in this study included land use, encompassing some of the degradation caused by introduced stock animals, but was not inclusive of impacts by other feral animals, such as cats and cane toads. A human footprint variable more specific to Australia may have strengthened the relationship between human impact and extinction risk. We also found that accessibility of species to human settlements was correlated with extinction risk, although this effect was not apparent in threat-specific analyses. Global modelling of extinction risk in reptiles similarly found a strong association between accessibility and threat status (Böhm et al., 2016). Regions with high human footprint and that are close to human settlements are more likely to be affected by threats such as habitat loss, overexploitation and invasive species (although some invasive species, such as feral cats, are abundant in remote areas). Collectively, these findings illustrate the importance of considering anthropogenic threats in predictive models of extinction risk. Alternatively, anthropogenic measures such as the human footprint and human accessibility could be explicitly incorporated into the IUCN Red List assessment process (Böhm et al., 2016).

We also found that environmental factors were correlated with extinction risk. Species that occupy wetter and colder regions were at greater risk, as predicted from geographic patterns revealed by previous analyses (Tingley et al., 2019). These environmental correlations likely represent geographic variation in threatening processes, rather than proximal correlates of extinction risk.

5 | CONCLUSIONS

We have conducted the first analysis on correlates of extinction risk targeting the highly diverse Australian squamate fauna. We found evidence that life history traits, ecological characteristics, environmental factors and human impact jointly influence the likelihood that a species is at risk. These findings illustrate that there is no single pathway to extinction among Australian squamates and could be used to proactively identify species at risk.

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DATA AVAILABILITY STATEMENT

The data from this study are available from FigShare: https://doi.org/10.26180/14344991.v1.

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BIOSKETCH

The research team has interests in the conservation and evolutionary ecology of squamates, and led the 2017 IUCN assessment of Australian squamates. This study stems from these workshops, and formed a component of Anna Senior's doctoral research.

Author contributions: AFS, RT, SM and DGC conceived the research project; AFS, MB and SM collated the data; AFS, MB, CPJ, MDM, RT and SM conducted the analyses; AFS and DGC led the writing, with input from all authors.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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