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Policy analysis

Geographic and taxonomic patterns of extinction risk in Australian squamates

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ABSTRACT

Australia is a global hotspot of reptile diversity, hosting ~10% of the world's squamate (snake and lizard) species. Yet the conservation status of the Australian squamate fauna has not been assessed for > 25 years; a period during which the described fauna has risen by ~40%. Here we provide the first comprehensive conservation assessment of Australian terrestrial squamates using IUCN Red List Categories and Criteria. Most (86.4%; n = 819/948) Australian squamates were categorised as Least Concern, 4.5% were Data Deficient, and 7.1% (range 6.8%–11.3%, depending on the treatment of Data Deficient species) were threatened (3.0% Vulnerable, 2.7% Endangered, 1.1% Critically Endangered). This level of threat is low relative to the global average (~18%). One species (*Emoia nativitatis*) was assessed as Extinct, and two species (*Lepidodactylus listeri* and *Cryptoblepharus egeriae*) are considered Extinct in the Wild: all three were endemic to Christmas Island. Most (75.1%) threat assessments were based on geographic range attributes, due to limited data on population trends or relevant proxies. Agriculture, fire, and invasive species were the threats that affected the most species, and there was substantial geographic variation in the number of species affected by each threat. Threatened species richness peaked on islands, in the Southern Alps, and across northern Australia. Data deficiency was greatest in northern Australia and in coastal Queensland. Approximately one-in-five threatened species were not represented in a single protected area. Our analyses shed light on the species, regions, and threats in most urgent need of conservation intervention.

1. Introduction

For over 50 years, the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN, 2018) has been an important tool for establishing global conservation priorities. However, even among terrestrial vertebrates—the world's most intensively studied group of species—25.6% of currently recognized taxa have not been evaluated against the IUCN Red List Categories and Criteria (IUCN, 2018). Within terrestrial vertebrates, estimates of extinction risk are primarily based on studies of birds, mammals, and amphibians; indeed, only ~64% of the world's ~11,000 reptile species have published extinction risk assessments (IUCN, 2018). This is despite evidence of ongoing reptile declines globally (Huey et al., 2009; Sinervo et al., 2010; Tingley et al., 2016). A recent analysis of global time series data, for example, estimated an average decline in reptile populations of 54–55% (Saha et al., 2018). Of those reptile species that have been assessed for the IUCN Red List (7023 species), 18% are assessed as threatened (meeting criteria for Vulnerable, Endangered, or Critically Endangered), and 15% considered Data Deficient (IUCN, 2018).

Here we provide the first comprehensive assessment of the extinction risk of Australian terrestrial squamates (snakes and lizards) using IUCN criteria; the first such assessment of this group in > 25 years (Cogger et al., 1993). Australia is a hotspot of squamate diversity (~1020 species; 807 lizard species, 213 snake species), hosting ~10% of the world's squamate species (Uetz et al., 2019); yet, prior to our assessment, Australia was the biogeographic realm with the lowest percentage (15%) of squamate species assessed by the IUCN (Meiri and Chapple, 2016), and most of these species were assessed using an older version of the IUCN Red List criteria. This 'assessment' gap mirrors a chronic knowledge gap, with the biggest conservation challenge for the Australian squamate fauna being a lack of information on population sizes and trends (Woinarski, 2018). The richness of the known Australian squamate fauna has increased by approximately 38% (from 738 to 1020 species, as of 2018) over the past 25 years, with an average growth rate of ~11 new species described per year (Cogger et al., 1993; Uetz et al., 2019), and we are still evaluating the number of species that actually occur in Australia. In addition, we have limited understanding of the threats facing each species (Webb et al., 2015; Woinarski et al., 2018), and the extent to which threatened squamates are conserved by Australia's network of protected areas (Lunney et al., 2017; Watson et al., 2011). Collectively, these issues have hampered efforts to assess the conservation status of the Australian squamate fauna and hence to prioritise and enact appropriate conservation management.

Our comprehensive assessment of Australian terrestrial squamates represents a major step toward addressing this knowledge gap, as we use the resulting data to: (i) elucidate key threats to Australian squamates; (ii) evaluate whether there are geographic and taxonomic biases in those threats, as well as in threatened and Data Deficient species richness; (iii) assess the extent to which the distributions of squamate species overlap with the Australian protected area network; and (iv) compare key threats, extinction risk, and data deficiency between Australian squamates and other Australian terrestrial vertebrate groups. We anticipate that our study will draw attention to species of conservation concern and spur targeted research and management on Australia's threatened, Near Threatened, and Data Deficient squamate species, thereby greatly improving our knowledge of, and conservation efforts for, this diverse group.

2. Methods

2.1. IUCN Red List categories and criteria

The IUCN Red List of Threatened Species is based on five criteria that relate to different indicators of extinction risk: rate of population decline (Criterion A); restricted geographic range and decline/fragmentation (Criterion B); small population size and decline (Criterion C); very small or restricted populations (Criterion D); and probability of extinction from quantitative analysis (Criterion E) (IUCN, 2012). Red List assessments for each species typically involve collating available published data on these indicators, which are subsequently evaluated by experts in regional or taxonomic workshops. This evaluation serves three functions: to obtain further, often unpublished, information relevant to these indicators; to compare the resulting data against quantitative thresholds to determine whether a species warrants listing in any of the three 'threatened' categories (Vulnerable, Endangered, or Critically Endangered); and to identify further research priorities and conservation measures. Species accounts and maps are then reviewed post-workshop (by IUCN staff in collaboration with experts) to ensure consistency in the application of the categories and criteria, with the agreed final global conservation status published on the IUCN Red List (www.iucnredlist.org).

2.2. Australian squamate workshops

Two five-day IUCN workshops were held in Australia to assess the extinction risk of Australian terrestrial squamates against IUCN criteria; in Perth (February 2017) and in Melbourne (June 2017). Marine and freshwater turtles, crocodiles, and sea-snakes were not evaluated, as these are assessed separately by taxa-focused IUCN Species Survival Commission Specialist Groups. Here we further restrict our analyses to terrestrial and freshwater squamates; i.e. we excluded species that were listed as occupying marine habitats, freshwater and marine habitats, or terrestrial and marine habitats (as listed in the 'systems' field recorded by the IUCN). We also excluded the three introduced squamates now present on the Australian mainland and/or adjacent islands (Asian house gecko *Hemidactylus frenatus,* the morning gecko *Lepidodactylus lugubris*, the common sun skink *Eutropis multifasciata*, and the flowerpot blind snake *Indotyphlops braminus*), as well as introduced squamates whose Australian range is restricted to Christmas Island and the Cocos (Keeling) islands (*Lycodon capucinus*, *Lygosoma bowringi*, *Gehyra mutilata*). Our final species list included 948 species, of which almost all (98.7%) are endemic to Australia and its island territories (see Table S1 for a list of species).

Each workshop involved coordinators, spatial analysts, IUCN facilitators, and approximately 25 experts who had knowledge of the species being assessed. Prior to the workshops, IUCN staff collated basic data (e.g., geographic range, population abundance, habitat and ecology, threats, conservation measures, and relevant bibliographic information for sources) on each species from existing literature and entered it into the IUCN's Species Information Service (SIS) database. The pre-entered information was reviewed by workshop participants during the workshops and modified as needed. Following agreement on the supporting information by participants, the IUCN Red List Categories and Criteria (IUCN, 2012) were applied to each species, and this was recorded in SIS. All assessments were reviewed and accepted by the IUCN, and published on the Red List website (www.iucnredlist.org) during 2018.

2.3. Species distribution data

Occurrence data for all native Australian terrestrial squamate species were collated from various sources, including museums, State and Federal Government Departments, citizen science programs, and academic researchers. These data were transformed to a common geographic coordinate system (WGS84). All records with missing geographic coordinates were removed. Records were reclassified so that they adhered to a common taxonomy following the Australian Society of Herpetologists official species list (available from http://www.australiansocietyofherpetologists.org/position-statements).

Experts subsequently reviewed all distribution maps at the two workshops. For each species, experts were presented with a printed geographic range map consisting of the collated occurrence records, a minimum convex polygon encompassing those records (the minimum extent of occurrence of each species), and an expert-derived range map from the Australian Reptile Online Database (AROD; http://www.arod.com.au/arod), overlaid on a Google Maps base map. Experts then deleted or added records on the maps where appropriate. One dedicated spatial analyst in each working group then amended the AROD range polygon in real-time with the experts using custom software. The result of this process was a refined geographic range polygon for each species, converted to a shapefile and clipped to the Australian coastline. These spatial data are available from https://www.iucnredlist.org/.

2.4. Estimating overall extinction risk

Species classified as Data Deficient introduce uncertainty into calculations of the percentage of threatened species (i.e. those classified as Vulnerable, Endangered, or Critically Endangered). We therefore estimated the percentage of threatened species using three different approaches to the treatment of Data Deficient species, following Böhm et al. (2013).

First, we assumed that the true extinction risk of Data Deficient species would fall into the three threatened categories in the same proportions as observed in currently assessed species: (CR + EN + VU)/(N-DD), where N is the total number of Australian squamate species, and CR, EN, VU, and DD are the numbers of Critically Endangered, Endangered, Vulnerable, and Data Deficient species, respectively. Second, we produced an optimistic (lower bound) estimate of the percentage of threatened species by assuming that no Data Deficient species were threatened: (CR + EN + VU)/N. Finally, we produced a pessimistic estimate by assuming that all Data Deficient species were threatened: (CR + EN + VU + DD)/N. We also report the number of Extinct and Extinct in the Wild species, but do not include these species in estimates of the numbers of threatened species, nor in our spatial analyses.

Population trajectories for each species were categorised as stable, increasing, decreasing, or unknown, based on published reports and expert assessments of population trends.

2.5. Geographic and taxonomic patterns of extinction risk

Species geographic range maps were overlaid on a 25 km × 25 km grid to estimate spatial patterns of species richness. This was done for (i) all squamate species; (ii) threatened species (using both optimistic and pessimistic estimates of the number of threatened species, as described in 2.4); and (iii) Data Deficient species. We mapped the absolute numbers and the proportions of threatened and Data Deficient species in each grid cell. We also calculated an alternative approach to visualise geographic patterns of threat, in which we converted the IUCN Red List categories into a continuous score, whereby LC = 0, NT = 1, VU = 2, EN = 3, and CR = 4. We present sums and means of those scores for each 25-km grid cell. For example, if six species were present in a grid cell, of which four were LC, 1 was VU and 1 was EN, the sum for that cell would be 5 ((4*0) + (1*2) + (1*3)), whereas the weighted mean would be 0.83 (5/6). The latter approach accounted for overall species richness in a cell. We repeated all the above analyses at 1 km resolution for Christmas Island, Lord Howe Island (group), and Norfolk Island (group). This finer spatial resolution was used to better visualise geographic patterns, given the relatively small spatial extent of the islands. We also evaluated whether threatened species were randomly distributed among snakes and lizards, and among families using Fisher's Exact Tests, with *p*-values computed via Monte Carlo simulation.

2.6. Threatening processes

Major threats were assigned for every species by experts at the workshops. We used this threat information to map the number and proportion of species threatened by agriculture (IUCN threat type 2), fire and fire suppression (IUCN threat type 7.1), and invasive and other problematic species and diseases (IUCN threat type 8.1, 8.2 and 8.4; no species were classified under the other threat 8 subcategories). We did this for all species irrespective of IUCN status, and for only threatened species (omitting Data Deficient species).

2.7. Protected area coverage

We examined the extent to which squamate species were likely to be present in the Australian protected area network, using all 10, 778 available protected areas (IUCN protected area categories I-VI) contained in the 2016 version of the Collaborative Australian Protected Area Database (https://www.environment.gov.au/land/nrs/science/capad/2016). We estimated the proportion of each species' estimated range that overlapped the protected area network, as well as the number of species (total and threatened), that: (i) did not overlap with any protected area; and (ii) had ≤10% of their geographic range within the protected area network. To provide upper and lower bounds on these calculations for threatened and non-threatened species, we either assumed that Data Deficient species were non-threatened (optimistic) or threatened (pessimistic), as above. We used a Wilcoxon Rank Sum Test to examine whether there was a difference between the median proportion of a species' geographic range within protected areas between threatened and non-threatened species. All analyses were conducted in R v3.5.2 (R Core Team, 2018).

3. Results

3.1. Overall extinction risk

Based on the results of the assessment workshops, 819 (86.4%) Australian squamate species were assessed as Least Concern (Table 1). Nineteen species (2.0%) were classified as Near Threatened. In the threatened categories, 28 (3.0%) species were Vulnerable, 26 (2.7%) were Endangered, and 10 (1.1%) were Critically Endangered. One species (*Emoia nativitatis*) was considered to have recently become extinct, and two species (*Lepidodactylus listeri* and *Cryptoblepharus egeriae*) were assessed as Extinct in the Wild. Additionally, 43 (4.5%) species were classified as Data Deficient (see Table S2 for a list of Data Deficient species). Assuming all Data Deficient species will be assigned to threatened categories in the same proportions as non-Data Deficient species, the total percentage of threatened (Vulnerable, Endangered or Critically Endangered) Australian squamates is 7.1%. Optimistic and pessimistic estimates are 6.8% and 11.3%, respectively. Population trends were assessed as stable for 59.2% ($n = 561$) of species, decreasing for 6.3% ($n = 60$), and unknown for 34.2% ($n = 324$).

Most species (68.7%; $n = 57$) that were classified in a more imperilled status than Least Concern (i.e. Near Threatened–Critically Endangered) were classified as such based largely on having a restricted geographic range (typically < 20,000 km^2) with an ongoing threat that reduces this distribution, or the quality of habitat within it (IUCN Criterion B). Including in this category those species also listed under criterion D2 (restricted area of occupancy or few locations, with a highly plausible near-future threat) increases the total percentage of species classified on the basis of their geographic range to 75.1% ($n = 72$). Indeed, geographical range sizes of threatened species were considerably smaller than those of non-threatened species (Fig. 1). Three species (3.6%) were listed under both D criteria (few mature individuals in addition to the D2 criteria noted above). A further 6.0% of species (n = 5) were classified solely due to severe (> 30%) reductions in population size over the last ten years or three generations (Criterion A). Only one threatened species (*Liopholis kintorei*) was classified as threatened based entirely on its small population size and population decline (Criterion C). The remaining two species were classified as threatened using a combination of B and C (*Simalia oenpelliensis*), and C and D (*Bellatorias obiri*) criteria.

3.2. Geographic and taxonomic patterns of extinction risk

Squamate species richness was highest in the Wet Tropics of north-eastern Australia, in the Kimberley and Pilbara regions of Western Australia, and in central Australia (Fig. 2). Geographic patterns of threat were largely congruent when summarised using different metrics. Total threatened species richness was highest in the Alps of south-eastern Australia, and in northern Australia, with a particularly high number of threatened species in the vicinity of Kakadu National Park and across the Kimberley region (Fig. 3A&C). South-western Australia also hosted high total threatened species richness. Similar geographic patterns were evident when controlling for total species richness, except that controlling for species richness emphasised threats facing squamates on Australia's island territories (Fig. 3B&D). Christmas Island, the Norfolk Island group, and the Lord Howe Island group each hosted two species (total $n = 4$ species), all of which were threatened (see insets of Fig. 3). Christmas Island was also the only known location for the one species assessed as extinct (*Emoia nativitatis*), and the two species that were considered Extinct in the Wild (*Lepidodactylus listeri* and *Cryptoblepharus egeriae*). The sum and mean of IUCN scores showed similar relative geographic patterns to total species richness (Fig. 3A&C cf. Fig. 3E) and proportional species richness (Fig. 3B&D cf. Fig. 3F), respectively.

Assuming that no Data Deficient species were threatened, we found no evidence of overall bias at the level of taxonomic family ($P = 0.61$; Table 2) or suborder ($P = 0.13$). Similarly, when assuming that all Data Deficient species were threatened, we found no evidence of overall bias at the level of taxonomic family ($P = 0.44$; Table 2) or suborder ($P = 0.89$). We found qualitatively similar results when excluding families with fewer than five species (Acrochordidae, Colubridae, Homalopsidae, Natricidae).

Although there was no evidence of taxonomic bias overall, some families possessed high proportions of threatened species, with carphodactylid geckos being the most threatened, followed by pygopodid geckos and skinks (Table 2). It is interesting to note that Carphodactylidae and Pygopodidae are the only two regionally endemic families. Assuming all Data Deficient species are threatened led to a large increase in the percentage of threatened blind snakes (Typhlopidae).

Data deficiency was highest near the Kimberley region, with secondary hotspots in coastal Queensland and across the Northern Territory (Fig. 4A). The Kimberley region remained a hotspot of data deficiency when controlling for total species richness (Fig. 4B).

3.3. Threatening processes

Invasive and other problematic species and diseases were the most prevalent threats to Australian squamates (14.6% of species; $n = 138$), followed closely by agriculture (12.4%; $n = 118$). Natural system modifications affected 9.3% of species; fire and fire suppression (threat type 7.1) affected 90% ($n = 79$) of species within this broader category. Other notable threats included biological resource use (4.4%; $n = 42$), including hunting ($n = 33$) and logging ($n = 9$), energy production and mining (4.1%; $n = 39$), and climate change and severe weather events (3.8%; $n = 36$).

Effects of agriculture were most pronounced in eastern and south-western portions of the country (Fig. 5A&B), whereas effects of fire and fire suppression were more geographically heterogenous and widespread (Fig. 5C&D). Numerous species across northern Australia, Queensland, and the Alps were impacted by invasive species (Fig. 5E); accounting for species richness highlighted additional hotspots in western Victoria and Tasmania (Fig. 5F). All species that were endemic to Christmas Island, or to the Norfolk and Lord Howe Island Groups,

Table 1
Number of terrestrial Australian squamates in each IUCN conservation status category.

Category	Percentage of species	N
Extinct	0.1	1
Extinct in the wild	0.2	2
Critically endangered	1.1	10
Endangered	2.7	26
Vulnerable	3.0	28
Near threatened	2.0	19
Least concern	86.4	819
Data deficient	4.5	43

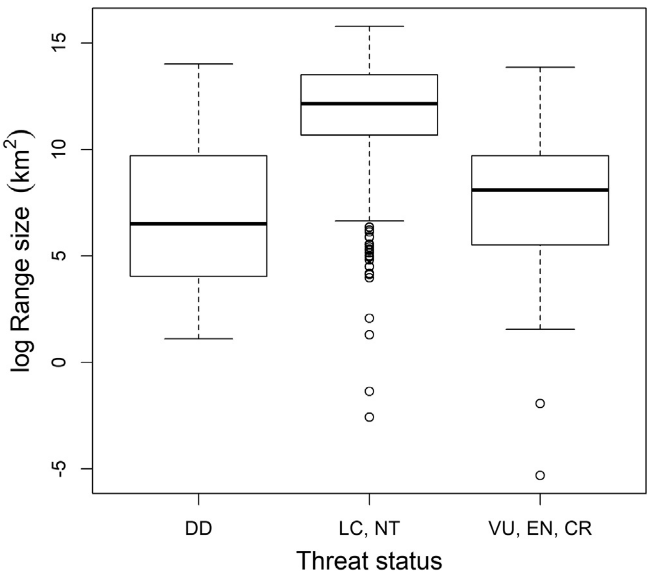

Fig. 1. Geographical range size (ln-transformed) of Data Deficient (DD), non-threatened (LC, NT) and threatened (VU, EN, CR) species. Note that only Australian portions of a species' range are included.

were threatened by invasive species.

Geographic variation in threatening processes was similar when considering only threatened species. However, compared to squamates overall, fewer threatened squamates were impacted by agriculture and fire in south-western Australia, and by fire and invasive species in Queensland (Fig. S1).

3.4. Protected area coverage

Across all 945 assessed species (excluding three species classified as Extinct/Extinct in the Wild), distributions of 3.7% (n = 35) were completely outside Australia's protected area network. Representation was not equally distributed among threatened and non-threatened species, however. Between 17.2% (optimistic; n = 11) and 21.5% (pessimistic; n = 23) of threatened species were not represented in a single protected area, compared to 2.7% (n = 24)–1.4% (n = 12) of non-threatened species. Roughly one quarter (24.1%; n = 228) of species had < 10% of their distribution in the protected area network (31.3%–39.3% of threatened species; 23.6%–22.2% of non-threatened species).

Conclusions regarding differences in the extent to which threatened and non-threatened species were protected by the network were sensitive to the treatment of Data Deficient species. When Data Deficient species were assumed to be non-threatened, threatened species' distributions overlapped to a greater extent with protected areas than did the distributions of non-threatened species (median overlap for threatened species = 32.2%; non-threatened species = 17.8%: W = 23,848, p = 0.04); however, the opposite was true when assuming that Data Deficient species were threatened (threatened species = 15.2%; non-threatened species = 18.0%; W = 44,483, p = 0.9). Nonetheless, there was substantial variation within each group in both cases, particularly for threatened species. Over one-quarter (27.9%) of Data Deficient species did not occur in a protected area, and the distributions of 51.2% of Data Deficient species had < 10% overlap with the protected area network. Threatened and Data Deficient species that do not overlap a single protected area are provided in Table S3.

4. Discussion

Our analysis of the conservation status of Australian terrestrial squamates documents how their plight has deteriorated over the past 25 years, with the proportion of species assessed as threatened nearly doubling from 1993 (Cogger et al., 1993) to 2017 (this study). As the number of recognized squamate species has grown substantially during this period (by nearly 40%), this equates to a doubling of the number of threatened species from 32 to 64. Alarmingly, the last decade has seen the first documented extinction of an Australian squamate (the Christmas Island forest skink, *Emoia nativitatis*: last recorded in the wild in 2010), and two other Christmas Island species becoming extinct in the wild (blue-tailed skink, *Cryptoblepharus egeriae*: last wild record in 2010; Lister's gecko, *Lepidodactylus listeri*: last wild record in 2012; Andrew et al., 2018). In addition, no squamate species that was considered threatened in 1993 has improved its conservation status to an extent that it is no longer considered threatened.

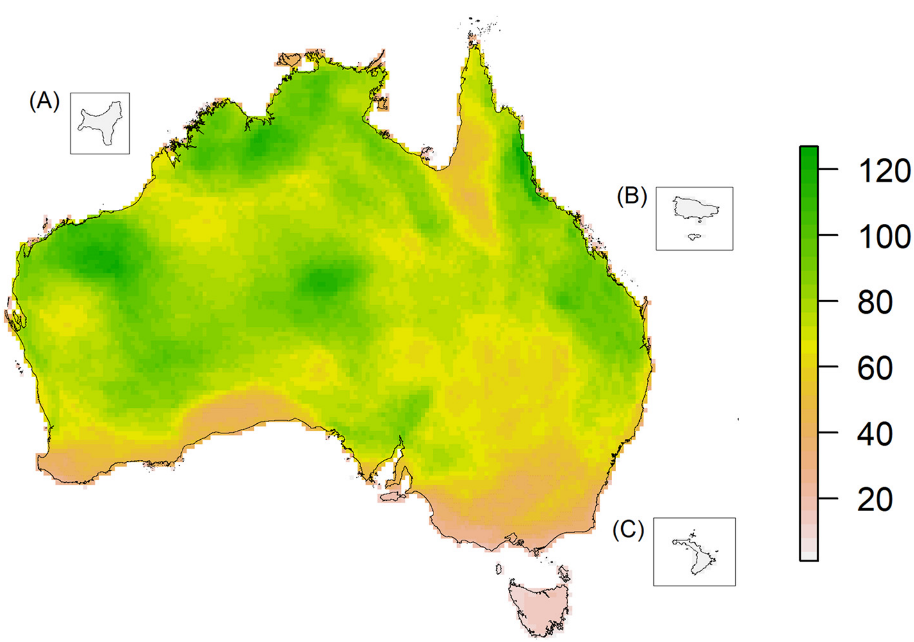

Fig. 2. Species richness of Australian squamates. Insets (not to same scale) show Christmas Island (A), Norfolk Island group (B), and Lord Howe Island group (C).

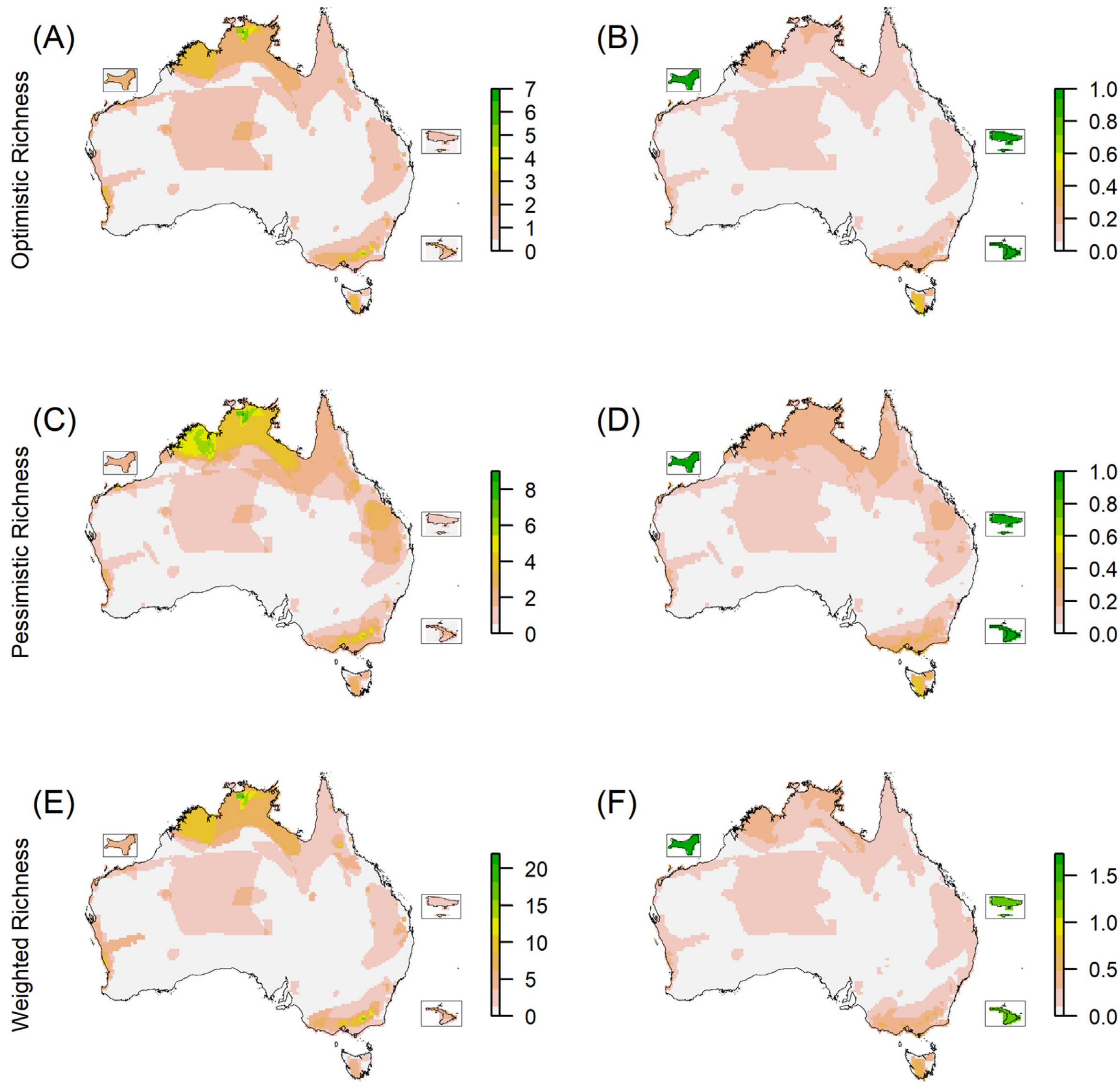

Fig. 3. Species richness of threatened Australian squamates under different assumptions. Panels (A) and (C) make optimistic and pessimistic assumptions, respectively, about the threat status of Data Deficient species (see Methods for details). Panels (B) and (D) represent the same data presented in (A) and (C), expressed as a proportion of absolute species richness (square-root transformed). Panels (E) and (F) represent weighted conservation status sums and weighted conservation status means, respectively, calculated by assigning continuous values to IUCN conservation status categories: 0 = LC, 1 = NT, 2 = VU, 3 = EN, 4 = CR. Islands shown in inset maps are the same as those in Fig. 1.

Table 2
Number of terrestrial Australian squamates within each taxonomic family and IUCN conservation status category. Optimistic estimates of the percentage of threatened species assume that DD species are not threatened; pessimistic estimates assume that all DD species are threatened.

Family	LC	NT	VU	EN	CR	EW	EX	DD	Total	Percentage threatened (optimistic)	Percentage threatened (pessimistic)
Acrochordidae	1	0	0	0	0	0	0	0	1	0	0
Agamidae	76	1	2	3	0	0	0	6	88	6	13
Carphodactylidae	22	3	2	2	1	0	0	0	30	17	17
Colubridae	4	0	0	0	0	0	0	0	4	0	0
Diplodactylidae	85	2	3	1	0	0	0	2	93	4	6
Elapidae	95	2	3	1	0	0	0	5	106	4	8
Gekkonidae	43	0	1	1	0	1	0	1	47	6	9
Homalopsidae	1	0	0	0	0	0	0	0	1	0	0
Natricidae	1	0	0	0	0	0	0	0	1	0	0
Pygopodidae	36	1	1	3	0	0	0	3	44	9	16
Pythonidae	13	0	1	0	0	0	0	0	14	7	7
Scincidae	379	10	15	13	7	1	1	17	443	8	12
Typhlopidae	35	0	0	1	1	0	0	8	45	4	22
Varanidae	28	0	0	1	1	0	0	1	31	6	10

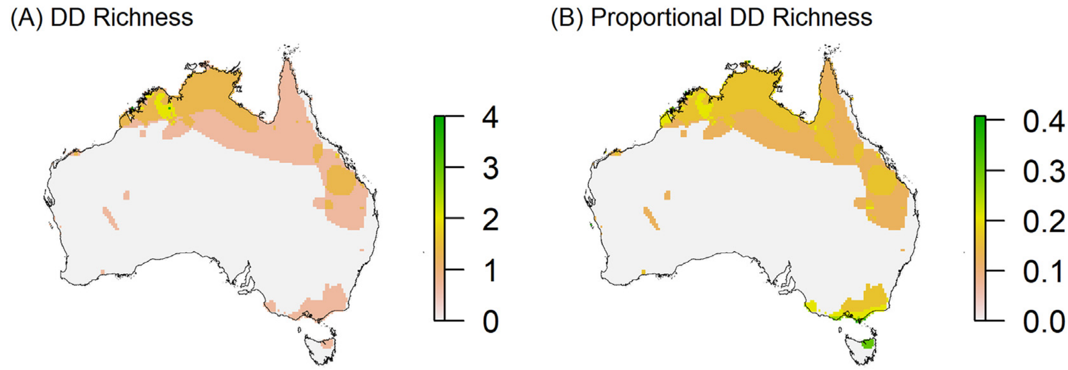

Fig. 4. Species richness of Data Deficient squamates (A), and of Data Deficient squamates expressed as a proportion of absolute species richness (B). Note that values in panel (B) are square-root-transformed to improve clarity.

4.1. Australian squamates have a lower proportion of threatened species than the global average

Our 2017 assessments revealed that 7.1% of Australian terrestrial squamates are threatened with extinction. This percentage is substantially lower than the global average for reptiles (18% as of April 2019; IUCN 2019), and for Australian terrestrial mammals (9% extinct, 18.5% threatened) and frogs (1.7% extinct, 12.1% threatened),

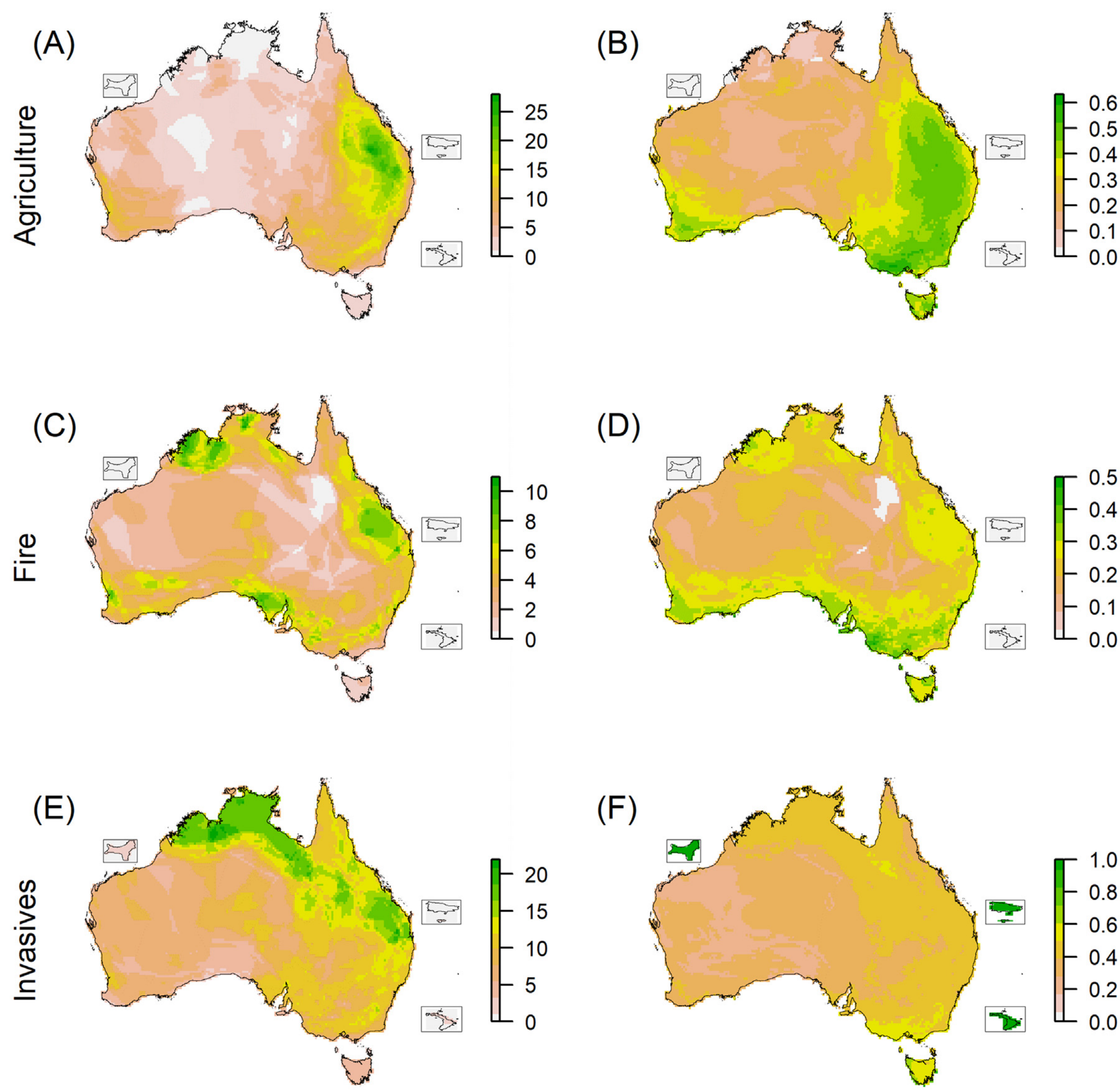

Fig. 5. The number of Australian squamate species affected by different threat types. Panels on the left show the numbers of species affected by agriculture (A), fire (C), and invasive and other problematic species and diseases (E). Panels (B), (D), and (F) represent the same data presented in (A), (C), and (E), expressed as a proportion of absolute species richness (square-root-transformed).

although it is higher than for Australian terrestrial birds (1.2% extinct, 5.3% threatened). However, the proportion of threatened species is similar to that reported for South African reptiles (5.4%; Tolley et al., 2019). To some extent, the relatively low percentage of threatened Australian terrestrial squamates may simply reflect our limited knowledge and understanding of the population sizes and trends of this group, and the threats to which they are exposed (Doherty et al., 2015; Webb et al., 2015; Woinarski et al., 2018), rather than a lower degree of imperilment.

One quarter of all Australian terrestrial squamates have an extent of occurrence smaller than 20,000 km^2 (i.e. the Red List threshold for being eligible for being considered Vulnerable; IUCN, 2012), and therefore improved knowledge of the threats impacting specific species has the potential to push many species from Least Concern, Data Deficient, or Near Threatened into a threatened category under Criterion B. This is a realistic possibility: although only 6.3% of species were reported as declining, the population trend for a third of all Australian squamate species is currently unknown. In addition, many of the known population trends were estimated from expert opinion, which may overlook real declines. The fact that Data Deficient species have geographical range sizes comparable to those of threatened species (Fig. 1) suggests that many Data Deficient species, in particular, may be at high risk of extinction.

Clear geographic biases were evident in the distributions of threatened squamates. Geographic hotspots of threat have been reported for reptiles at both local (New Zealand: Tingley et al., 2013; Africa: Tolley et al., 2016) and global scales (Böhm et al., 2013; Maritz et al., 2016). The locations of threat hotspots for Australian squamates coincide with the increased prevalence of key threatening processes, such as land clearing (south-western Western Australia, south-eastern Australia, Queensland) and invasive predators and competitors (northern Australia, alpine region, offshore islands) (Fig. 5). Offshore islands are also hotspots for threatened terrestrial birds (notably Christmas, Norfolk, and Lord Howe), as is south-eastern Australia (Garnett et al., 2011; Geyle et al., 2018). Hotspots of threatened squamate richness differ from amphibian and mammal threat hotspots, however. Threatened amphibians are predominantly clustered along the coast of northern New South Wales and southern Queensland, and in the Wet Tropics (IUCN, 2018). In contrast, mammal losses have been associated mainly with introduced predators that have extensive ranges across the Australian mainland, and thus mammal extinction risk is more spatially homogenous compared to other vertebrate groups (Burbidge et al., 2009; Woinarski et al., 2014, 2015).

Worldwide, the majority (73 of 82; 89%) of recorded Quaternary reptile extinctions have been of island endemics (Slavenko et al., 2016). This pattern is clearly evident in Australian squamates. In addition to the three Extinct or Extinct in the Wild species on Christmas Island, all endemic squamate species on that island ($n = 2$), and other offshore islands (Norfolk Island group, Lord Howe Island group; two species present on both island groups), are listed as threatened (Fig. 4). The Christmas Island reptile fauna suffered the most spectacular of these losses, largely due to catastrophic declines since the 1980s. The introduced wolf snake (*Lycodon capucinus*) is thought to have been a major driver of these declines, with non-native yellow crazy ants (*Anoplolepis gracilipes*), cats (*Felis catus*), rats (*Rattus rattus*), and centipedes (*Scolopendra subspinipes*) also being suspected as major threats. While the literature is mostly a record of loss, we recognise that intensive management (through capture of individuals from the rapidly dwindling wild populations, and establishment of a successful captive breeding program) has been instrumental in averting the extinction of an endemic skink and an endemic gecko (Andrew et al., 2018). Continuing intensive conservation efforts, especially biosecurity, will be required to ensure the persistence of native squamate species on all Australian offshore islands.

Interestingly, we detected no evidence of overall taxonomic bias in conservation status among Australian terrestrial squamates, although some families are clearly over-represented among threatened species (e.g., Carphodactylidae). This is in contrast to most other studies of reptile extinction risk, which have demonstrated that a species' susceptibility to extinction is non-random (Böhm et al., 2016b; Reed and Shine, 2002; Tingley et al., 2013), and that elevated extinction risk is clustered within particular taxonomic groups (Böhm et al., 2013; Tonini et al., 2016; Tolley et al., 2016). This may reflect a true uniformity of threat for Australian squamates; alternatively, it could simply be an artefact of incomplete knowledge of taxonomy and population trends (Woinarski, 2018), or due to the fact that familial divisions in reptiles are relatively coarse. As clear taxonomic biases exist in regard to where suspected species complexes occur (as outlined in the taxonomic notes in the Red List assessments), and newly described species possess traits that are more likely to result in their being listed as threatened species (Meiri, 2016), increased knowledge of the biodiversity of Australian squamates may result in the future detection of taxonomic biases in threat.

4.2. High rates of data deficiency relative to other Australian terrestrial vertebrates

Forty-three Australian squamate species (4.5%) were classified as Data Deficient (Table S1). This level of Data Deficiency is relatively low compared to the global average for reptiles (15%; IUCN 2019); however, the number of Data Deficient Australian squamates that lack information on population status and trends (86%) is comparable to the same figure for squamates globally (97% including Australian species; IUCN, 2018). Thus, despite the relatively low percentage of Data Deficient species found here, conservation of the Australian squamate fauna is clearly impeded by a lack of critical information on population sizes and trends. This not only impedes assessment of species under Criterion A, but also implies a lack of long-term knowledge of biology, ecology and threatening processes, which further limits the potential to assess species against Criteria B-E. Indeed, according to IUCN assessments, squamates have the highest proportion of Data Deficient species of any Australian terrestrial vertebrate group (mammals: 1.3%, birds: 0%, frogs: 0%).

Levels of Data Deficiency in squamates were particularly high in tropical northern Australia (Kimberley region, Northern Territory, northern Queensland). This lack of knowledge on the squamates of northern Australia is likely due to its relative remoteness and inaccessibility, its diverse reptile fauna, and substantial ongoing taxonomic reappraisal for many groups from this region (Rosauer et al., 2016). Targeted research should continue across northern Australia to fill this substantial knowledge gap.

4.3. Invasive species and habitat loss are key threats to Australian squamates

The major threats to Australian squamates are invasive species (predators and competitors, such as cats (*Felis catus*) and rats (*Rattus rattus*); and toxic cane toads (*Rhinella marina*), habitat loss or modification (agriculture, urbanisation, altered fire regimes, mining activities), biological resource use, and climate change. These threats are consistent with those that have been identified for reptiles at both local (e.g. South Africa: habitat loss and modification; Tolley et al., 2019) and global scales (e.g. habitat loss, harvesting, climate change; Böhm et al., 2013, 2016a; Sinervo et al., 2010). Indeed, these threats are generally the same as those identified for Australian reptiles 25 years ago (Cogger et al., 1993), although there has been an increase in the number of species recorded as impacted by invasive species (cane toads, weeds, predators) and climate change. With regard to invasive species, the extent of the threat posed by introduced predators, particularly feral cats (*Felis catus*), has undoubtedly been underestimated until recently (Doherty et al., 2015). For instance, Woinarski et al. (2018) estimated that ~649 million Australia reptiles are killed each year (or 1.8 million per day) by cats, most of which are feral. However, habitat loss continues to be a key threatening process in Australia, as the country has one of the highest rates of land clearing in the world (~395,000 ha per year in Queensland; Webb et al., 2015), with most clearing occurring and continuing in Queensland (Bradshaw, 2012). The threats facing Australian reptiles largely mirror those facing other Australian vertebrate groups (Garnett et al., 2011; Woinarski et al., 2014, 2015).

4.4. Threatened and Data Deficient squamates are poorly represented by the protected area network

We found that the distributions of many threatened and Data Deficient squamate species showed low spatial congruence with Australia's protected areas. This finding may reflect the fact that threatened and Data Deficient species have, on average, more restricted distributions than non-threatened species (Fig. 1); however, it is consistent with that reported for South African reptiles (Tolley et al., 2019). The low representation of Data Deficient species in protected areas explains why the distributions of threatened species overlapped with protected areas to a lesser extent when we assumed that Data Deficient species were threatened, compared to when we assumed that they were non-threatened. It is important to note, however, that IUCN range maps are generalised range maps and thus often depict the suspected range of a species, and not actual localities where the species occurs (which are unknown for nearly all Australian squamates). Thus, the extent to which species' ranges overlap with protected areas (or other landscape features) should be interpreted with caution. It is anticipated that the quality of IUCN range maps will be improved in the near future through the ongoing development of Extent of Suitable Habitat maps, which will provide more refined representations of species distributions. An additional caveat of our findings is that population persistence is not necessarily guaranteed just because a species occurs in one or more protected areas (Kearney et al., 2018). Nonetheless, our analysis represents an initial first-step toward understanding existing conservation measures for Australian terrestrial squamates. Future studies could usefully examine the optimal placement of additional protected areas using the distribution data collated here, in a similar fashion to a recent analysis for threatened Australian mammals (Ringma et al., 2019).

5. Conclusions

The 25-year period since the last national assessment of Australian squamates (Cogger et al., 1993) has seen a marked deterioration of their conservation status, highlighted by three species being assessed as Extinct or Extinct in the Wild, a doubling in the number of recognized threatened species, and an expansion of the number of threats impacting native species. Although intensive taxonomic study over the past few decades has increased the size of the described Australian terrestrial squamate fauna by ~38%, substantial research effort needs to continue to uncover the true diversity. The rapidly expanding list of known species, combined with the remoteness/inaccessibility of many areas, has resulted in poor knowledge of distributions, biology, ecology, threats, and population trends. Thus, targeted studies are urgently needed on the threatened, Near Threatened, and Data Deficient species recognized here.

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Declaration of Competing Interest

The authors have no conflict of interest to declare.

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