



Reptile responses to anthropogenic habitat modification: A global meta-analysis

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Abstract

Aim: The aim was to determine how reptile populations respond to anthropogenic habitat modification and determine whether species traits and environmental factors influence such responses.

Location: Global.

Time period: 1981–2018.

Major taxa studied: Squamata.

Methods: We compiled a database of 56 studies reporting how habitat modification affects reptile abundance and calculated standardized mean differences in abundance (Hedges' g). We used Bayesian meta-analytical models to test whether responses to habitat modification depended on body size, clutch size, reproductive mode, habitat specialization, range size, disturbance type, vegetation type, temperature and precipitation.

Results: Based on 815 effect sizes from 376 species, we found an overall negative effect of habitat modification on reptile abundance (mean Hedges' $g = -0.43$, 95% credible intervals = -0.61 to -0.26). Reptile abundance was, on average, one-third lower in modified compared with unmodified habitats. Small range sizes and small clutch sizes were associated with more negative responses to habitat modification, although the responses were weak and the credible intervals overlapped zero. We detected no effects of body size, habitat specialization, reproductive mode (egg-laying or live-bearing), temperature or precipitation. Some families exhibited more negative responses than others, although overall there was no phylogenetic signal in the data. Mining had the most negative impacts on reptile abundance, followed by agriculture, grazing, plantations and patch size reduction, whereas the mean effect of logging was neutral.

Main conclusions: Habitat modification is a key cause of reptile population declines, although there is variability in responses both within and between species, families and vegetation types. The effect of disturbance type appeared to be related to the intensity of habitat modification. Ongoing development of environmentally sustainable practices that ameliorate anthropogenic impacts is urgently needed to prevent declines in reptile populations.

KEYWORDS

agricultural intensification, deforestation, ecological disturbance, extinction risk, habitat modification, land-use change, lizards, reptiles, snakes, Squamata

1 | INTRODUCTION

Transformation and degradation of the world's ecosystems by humans have caused widespread biodiversity loss (Newbold et al., 2015). Current extinction rates are estimated to be 100–1,000 times higher than background rates (Ceballos et al., 2015; Pimm et al., 2014), and c. 28% of all species on the IUCN Red List are threatened with extinction (IUCN, 2019b). Expansion of production landscapes for forestry, agriculture and mining continues in many parts of the world, placing further pressure on ecosystems and communities as habitats are cleared, fragmented or otherwise modified (Curtis, Slay, Harris, Tyukavina, & Hansen, 2018; Tilman, Balzer, Hill, & Befort, 2011). Urgent action is needed to curtail extinction rates and enable species recovery. One approach towards achieving this relies on identification of the traits that make species most sensitive to habitat modification and understanding how these relationships are affected by environmental factors. Such approaches can help in predicting the sensitivity of species to environmental change, with potential to inform the conservation of poorly studied species and regions.

A large body of work, mostly on birds and mammals, provides the foundation for much of what we know about how, why and where animal species become threatened with extinction (e.g., Cardillo et al., 2008; Davidson, Hamilton, Boyer, Brown, & Ceballos, 2009; Owens & Bennett, 2000). For instance, bird species threatened by habitat loss are typically small-bodied habitat specialists, whereas those threatened by human persecution and introduced predators have larger bodies and longer generation times (Owens & Bennett, 2000). Insectivorous and large frugivorous forest bird species are most sensitive to habitat loss and fragmentation, and effects are stronger in the tropics compared with temperate regions (Bregman, Sekercioglu, & Tobias, 2014). High extinction risk in mammals is associated with large home range size, low population density, high weaning age and small geographical range size (Cardillo et al., 2008). Amphibian sensitivity to habitat modification is also highest for species with small range sizes and for species with terrestrial or lotic larval habitats (cf. lentic larval habitats) (Nowakowski, Thompson, Donnelly, & Todd, 2017). Finally, across the four terrestrial vertebrate classes, carnivores, habitat specialists and larger species had a lower probability of presence in habitat remnants compared with other species (Keinath et al., 2017).

In contrast to birds and mammals, we know comparatively little about how reptiles respond to environmental change, despite them being one of the world's most species-rich groups of vertebrates (> 10,800 species; Uetz, 2018). This is because reptiles are routinely understudied in ecology and conservation (Gardner, Barlow, & Peres, 2007; Tingley, Meiri, & Chapple, 2016), with only 4% of habitat fragmentation studies focusing on reptiles, compared with >50%

for birds and c. 18% for both mammals and plants (McGarigal & Cushman, 2002). Likewise, only c. 67% of reptile species have been assessed for the Red List, compared with 85% for amphibians and 100% for both birds and mammals (IUCN, 2019b). This large disparity is an impediment to the design, prioritization and implementation of conservation programmes.

The limited work done on reptiles has shown that species-level extinction risk increases with body size and habitat specialism (Böhm et al., 2016; Tingley, Hitchmough, & Chapple, 2013). Local-scale studies suggest that range size, habitat use and diet can influence sensitivity to habitat modification (Neilly, Nordberg, VanDerWal, & Schwarzkopf, 2018; Todd, Nowakowski, Rose, & Price, 2017). However, there have been no large-scale analyses assessing how reptile populations respond to anthropogenic habitat modification across a range of species, ecosystems and disturbance types. Such knowledge is crucial because the extinction process begins with extirpations of populations (Purvis, Cardillo, Grenyer, & Collen, 2005). Furthermore, as ectotherms, reptiles possess traits such as complex thermoregulatory strategies and lower energy use, movement and habitat space requirements, relative to birds and mammals. In contrast, birds of equivalent size and some mammals (e.g., ungulates, bats) have higher energetic demands, are generally more mobile and have larger space requirements. These fundamental differences might mean that reptiles respond to habitat modification in a different manner from other animal groups. Indeed, a meta-analysis showed that reptiles are generally more sensitive than birds, mammals and amphibians to habitat loss and fragmentation (Keinath et al., 2017).

Here, we present the largest and most comprehensive analysis to date of population responses of squamate reptiles (lizards, snakes and worm lizards) to anthropogenic habitat modification, including logging, plantations, mining, agriculture and livestock grazing. We focus on squamates because they comprise >95% of reptile species, and inclusion of non-squamates (i.e., turtles and crocodylians) is less intuitive owing to their different biology and evolutionary history. We compiled a database of 815 effect sizes to test the following predictions:

1. Species with larger body sizes will be more sensitive to habitat modification owing to their higher energetic needs and requirements for space (Böhm et al., 2016; Keinath et al., 2017; Perry, Garland, & Garland, 2002).
2. Species with smaller clutch sizes will be more sensitive to habitat modification owing to their reduced ability to compensate for increased mortality (Fahrig, 2001; Keinath et al., 2017; Quesnelle, Lindsay, & Fahrig, 2014).
3. Oviparous (egg-laying) species will be more sensitive than viviparous (live-bearing) species owing to the potential loss of

appropriate nesting conditions and limited control of incubation temperatures (Martin & Murray, 2011; Shine, Elphick, & Barrott, 2003; Tiatragul, Hall, Pavlik, & Warner, 2019).

4. Species with small range sizes will be more sensitive to habitat modification owing to their presumably narrower niche breadth (Böhm et al., 2016; Cardillo et al., 2008; Slatyer, Hirst, & Sexton, 2013).
5. Habitat specialists will be more sensitive to habitat modification owing to their adaptation to a narrower range of environmental conditions (Nowakowski et al., 2017; Slatyer et al., 2013).

We also used the database to determine whether some disturbances have stronger impacts on reptiles than others, whether there are consistent differences in the effects of habitat modification among vegetation types and whether responses of reptiles to habitat modification differ according to temperature and precipitation, which are key drivers of ectotherm abundance and distribution (Powney, Greyner, Orme, Owens, & Meiri, 2010).

2 | METHODS

We searched the Web of Science and Scopus databases in December 2017 using the search string: (reptile* OR lizard* OR snake* OR squamat* OR gecko* OR skink* OR lacertid* OR agamid* OR varanid* OR iguan* OR python* OR elapid* OR colubrid* OR viper* OR

amphisbaen*) AND ("land use" OR logging OR silvicultur* OR forestry OR agricultur* OR farm* OR crop* OR grazing OR pasture OR pastoral OR plantation OR "habitat disturbance" OR "habitat alteration" OR "habitat degradation" OR "habitat destruction" OR "habitat modification" OR "habitat loss" OR "habitat fragmentation" OR matrix OR urban* OR mining OR mined OR weed* OR "exotic plant" OR "invasive plant"). This returned 2,311 records from Web of Science and 3,621 from Scopus, with 4,162 unique records remaining after removal of duplicates (see Supporting Information Appendix S1 for the PRISMA diagram).

Paper titles, abstracts and other bibliographic information were compiled in a database. Each title and abstract of each paper were independently screened by two of six reviewers (T.S.D., S.B., K.B., T.J.B., C.F. and T.G.) and classed as either "include" or "exclude" for full text inspection based on the selection criteria detailed below. Any conflicts in the classifications were resolved by T.S.D. For the 466 records classed as "include", T.S.D. downloaded and inspected the full texts to determine their suitability.

To be included in our database, a study needed to be a peer-reviewed journal article containing data on squamate abundance at the species level. Data needed to be collected using standardized sampling methods from at least one modified habitat treatment and an unmodified reference treatment and standardized for sampling effort. Habitat modification treatments were classified as livestock grazing, agriculture, logging, plantations, mining, patch size reduction or "other" (see Table 1). We also initially included cropping and

TABLE 1 List of species' traits and environmental variables that were used in statistical models and the sources of the data

Variable	Definition	Data source
Body mass	Body mass (in grams) derived from allometric equations and snout-vent or total lengths	Feldman, Sabath, Pyron, Mayrose, and Meiri (2016)
Clutch size	Mean or mid-point of clutch size	Feldman (2015), Meiri (2018)
Reproductive mode	Oviparous (egg-laying) or viviparous (live-bearing). Species with a mixed reproductive mode were excluded from analysis owing to small sample size (11 effect sizes)	Feldman (2015), Meiri (2018)
Habitat specialization	Number of major habitat types occupied	IUCN (2019a)
Range size	Measured as the total area of distribution maps (in square kilometres)	IUCN (2019a); Roll et al. (2017)
Disturbance type	Grazing, agriculture ^a , logging, plantation ^b , mining, patch size reduction ^c or other ^d	Original studies
Vegetation type	Forest, woodland, shrubland or grassland	Original studies
Temperature	Mean temperature of the warmest quarter (BIO10) within a 5 km radius of study locations (in degrees Celsius)	http://worldclim.org/
Precipitation	Mean annual precipitation (BIO12) within a 5 km radius of study locations (in millimetres)	http://worldclim.org/

^a"Agriculture" was used when the disturbance type was a mixture of cropping and grazing or when insufficient information was provided to classify the treatment as one or the other.

^b"Plantation" was used when the comparison was between plantation forest and original vegetation. Studies that compared logged/thinned plantation forest with unlogged/unthinned plantation forest were included in "logging".

^c"Patch size reduction" was used when the comparison was between large areas of continuous vegetation and smaller patches of the same vegetation type that were isolated from the rest by land conversion. We also included in this category one study that surveyed reptiles at the edges and interior of habitat fragments.

^d"Other" was used when the disturbance type could not be classified confidently as one of the other categories, such as disturbance by rock collectors, military exercises, ski runs, off-road vehicles or weed invasion, or where combinations of disturbances existed (e.g., grazing and mining, grazed habitat fragments).

urbanization as disturbance types, but no studies for these categories remained after the screening process. “Unmodified” reference areas needed to be situated in the same vegetation and landform types as disturbed areas in order to provide a suitable representation of the original fauna. Reference areas in many studies were not completely unmodified because no such areas exist in many ecosystems. Thus, reference treatments often represent areas that were less disturbed or modified than the modified treatments. We excluded studies where data were presented only for species that exhibited a statistically significant response to disturbance, because this represents a reporting bias. We also excluded unreplicated studies (only one survey site in each treatment) and studies where it was not possible to calculate sample sizes or standard deviations.

As with any taxa, detection probabilities can be an important consideration in reptile surveys, but insufficient studies reported this information to be included in our analyses. However, we do not think that this introduces a systematic bias to the results. Of the studies that have assessed drivers of reptile detection probability, most found that survey design or weather effects were important (e.g., Treilibs, Pavey, Raghu, & Bull, 2016; Wolf, Renken, Fantz, Gao, & Millspaugh, 2016), rather than vegetation structure. Studies in woodlands, forests and shrublands all found no effect of vegetation structure on reptile detection probabilities (Craig et al., 2009; Schlesinger, 2007; Smith, Bull, & Driscoll, 2012; Uribe & Estades, 2014; Wolf et al., 2016), although one study found that detection probability varied between two forest types (Chergui, Fahd, & Santos, 2019). With regard to survey design and weather variables, we assume that published studies took appropriate steps to minimize potential biases, such as standardizing survey times and weather conditions across sites and treatments. On balance, we are confident that our results are robust to any potential bias related to detection probabilities.

2.1 | Data collation

We extracted data from the text, tables, figures and appendices of papers. Where available, we recorded mean abundance, total abundance, standard deviation, standard error and the number of survey sites for each species in each treatment. If mean abundance or standard deviation was not reported, we derived these from the total abundance, sample size and standard error, where possible. Where necessary, we contacted study authors to obtain original data or additional information. We averaged values where data were presented for multiple years or seasons. We excluded records that were not identified to the species level or could not be attributed to a currently recognized and formally described species.

We used the means, standard deviations and sample sizes to calculate standardized mean differences (Hedges' *g*) and sampling variances with the “*escalc*” function in the *metafor* package in R (Viechtbauer, 2010). Effect sizes are presented in units of the pooled standard deviation, such that a value of 0.5 represents a difference between the two groups equivalent to half of a standard deviation. Negative values indicate that a species responded negatively to

habitat modification (e.g., lower abundance in grazed compared with ungrazed areas), and the opposite for positive values. We excluded one data point (*Cophosaurus texanus* in desert grassland; Jones, 1981) that had an extreme effect size (927.5) and variance (30,724.9) compared with the remaining data (−10.3 to 9.1; 0.04–7.7). After excluding studies where it was not possible to calculate a variance estimate, 56 studies provided data suitable for meta-analysis. A list of data sources is provided in the Appendix.

Given that Hedges' *g* is an amalgam of the means and variances, a large effect size can arise either from a large treatment difference or from a very small pooled variance (Rosenberg, Rothstein, & Gurevitch, 2013). To assess the sensitivity of our results to the use of Hedges' *g*, we also calculated the logarithmic response ratio by dividing abundance in the treatment area (X_T) by that in the control area (X_C) and taking the logarithm of this number. Sampling variance was calculated as follows:

$$\text{variance} = \frac{SD_T^2}{N_T X_T^2} + \frac{SD_C^2}{N_C X_C^2},$$

where *SD* represents standard deviation and *N* sample size for treatment (T) and control (C) sites. Given that the logarithmic response ratio cannot be calculated if the mean is zero for either the treatment or the control, this analysis was based on 530 effect sizes that did not include zeroes.

We checked the species names from the original studies against the Reptile Database checklist from November 2018 (Uetz, 2018) and updated names where taxa had moved genera, species had been combined or the spelling had changed. To identify any species that had been split or raised from taxonomic synonymy since the original study, we cross-checked study locations against reptile range maps (IUCN, 2019a; Meiri et al., 2017; Roll et al., 2017) to determine whether each data point fell within the range of the reported species name. If this was not the case, we inspected the list of all intersecting species and identified the correct species name for that data point. We excluded any points where the species name and location could not be resolved confidently.

For each data point, we recorded a number of ecological and environmental traits predicted to be important determinants of population sensitivity to habitat disturbance (Table 1). The ecological traits were body mass, clutch size, reproductive mode, habitat specialization and range size (Table 1). Following previous studies (Böhm et al., 2016; Todd et al., 2017), we calculated an index of habitat specialization by counting the number of major habitat types (e.g., forest, savanna, wetlands, rocky areas) listed in the IUCN Red List profile for each species. This represents a coarse measure of habitat specialization, with lower numbers representing greater specialization. We derived range size from species distribution maps (IUCN, 2019a; Roll et al., 2017). A full set of trait data was not available for all study species. Records with missing values were excluded from the statistical models for each of those predictors (see Section 2.2). We recorded vegetation types as forest, woodland, shrubland or grassland. We calculated the

mean temperature of the warmest quarter of the year and mean annual precipitation within a 5 km radius around each study location (Table 1). We chose this radius as an approximation of local climatic variables because the spatial extent of the study sites was not reported in most studies.

2.2 | Statistical analyses

We used Bayesian mixed effects models to analyse variation in effect sizes, implemented in the *brms* package in R (Bürkner, 2018). We fitted models assuming a normal distribution and included random effects for species and study identity to account for non-independence between effect sizes from the same study or species. We determined that this random effects structure was suitable using model selection (described in the next paragraph). To account for sampling variance, we weighted effect sizes using their standard errors. We specified non-informative normal priors ($\mu = 0$, $\sigma = 10$) for the fixed effects and weakly informative half Cauchy priors ($\mu = 0$, $\sigma = 1$) for the random effects (Bürkner, 2017; Williams, Rast, & Bürkner, 2018). We fitted models to both the Hedges' *g* and logarithmic response ratio data, with the latter presented in Supporting Information Appendix S2.

To identify an appropriate random effects structure, we fitted and ranked six models containing different combinations of study identity, species and taxonomic family as random effects, in addition to a phylogenetic covariance matrix (Supporting Information Appendix S2, Table S2.1). These models also contained the six continuous fixed effects (thus representing the most complex model we fitted). We created a phylogenetic covariance matrix using the "inverseA" function of MCMCglmm (Hadfield, 2010) and the squamate phylogeny of Tonini, Beard, Ferreira, Jetz, and Pyron (2016). We trimmed this phylogeny to include only species present in our database and also excluded from the database 12 species that were not present in the phylogeny. Model ranking using leave-one-out cross-validation (Vehtari, Gabry, & Gelman, 2019; Vehtari, Gelman, & Gabry, 2017) indicated that the best-supported model was that with random effects of species and study identity (Supporting Information Appendix S2, Table S2.1).

To test the effects of categorical predictors [reproductive mode ($n = 786$ effect sizes for Hedges' *g*), disturbance type (718, excluding the "other" disturbance type) and vegetation type (815)] on reptile responses to habitat modification, we fitted a univariate model for each predictor variable that excluded the intercept. We chose this approach because intercept models for categorical predictors with more than two levels use one level as the reference, with which all other levels are compared. Removing the intercept allows us to determine whether each level is significantly different from zero, rather than from the reference level, which is of less interest. We excluded the "other" category from the disturbance type model because it is not informative to generate a mean effect size for this mixture of differing disturbances. We fitted a single model for the continuous predictor variables (body mass, clutch size, range size, habitat specialization, precipitation and temperature; 609 effect sizes), which

we first centred and scaled by subtracting the mean and dividing by the standard deviation of each variable. None of the variables were highly correlated with each other (all Pearson's $r \leq \pm .42$).

We also assessed whether there are broad taxonomic patterns in the data by fitting a model with family as the explanatory variable. To avoid making family-level inferences based on only one or two species, we restricted this analysis to families with data for three or more species ($n = 784$ effect sizes). We also tested for a phylogenetic signal by estimating the proportion of variance explained by phylogenetic variance (H^2), following the approach of Nakagawa and Santos (2012). An H^2 value of zero indicates no phylogenetic relatedness between effect sizes, and a value of one indicates that interspecific differences in effect sizes are exactly proportional to their phylogenetic relatedness. We calculated the phylogenetic signal for a null model and for a model with the disturbance-type variable, both of which contained random effects of species and study identity and the phylogenetic covariance matrix.

We did not include interactions in the models owing to the large number of possible combinations, low replication for combinations of variables, and the difficulties inherent in interpreting interactions involving multi-level categorical variables. For all models, we considered predictor variables important when the 95% credible intervals (CIs) of the posterior estimates did not overlap zero. For each model, we ran four chains of 10,000 iterations each, with a burn-in of 1,000 iterations, resulting in 36,000 samples. We assessed convergence by inspecting trace plots and ensuring that the Gelman–Rubin statistic was < 1.1 (Gelman & Rubin, 1992).

We used a funnel plot and Egger's test (Egger, Davey Smith, Schneider, & Minder, 1997) to assess potential publication bias. Visual inspection of the funnel plot suggested no systematic asymmetry in effect sizes (Supporting Information Appendix S2, Figure S2.1), although Egger's test was significant for asymmetry ($z = -2.20$, $p = .028$). The test was not statistically significant ($z = -1.70$, $p = .089$) when a negative outlier on the left-hand side of the plot was removed (Hedges' *g* = -10.30). This might suggest a tendency for more negative results to be reported, but overall there does seem to be a strong signal of publication bias.

3 | RESULTS

We analysed 815 effect sizes for 376 species (Figure 1), with 59% of effect sizes representing a negative response to habitat modification, 36% positive and 5% neutral (equal abundance in modified and unmodified sites). There were 194 cases (24%) where the study species was not recorded in the modified treatment and 92 cases (11%) where the species was not recorded in the "unmodified" treatment. The mean effect size (Hedges' *g*) was -0.43 (95% CI: -0.61 to -0.26), demonstrating an overall effect of reduced abundance in modified habitat compared with reference areas. The results were very similar for the logarithmic response ratio (mean = -0.42 , 95% CI = -0.64 to -0.20), which corresponds to an average of one-third lower abundance in modified compared with unmodified areas.

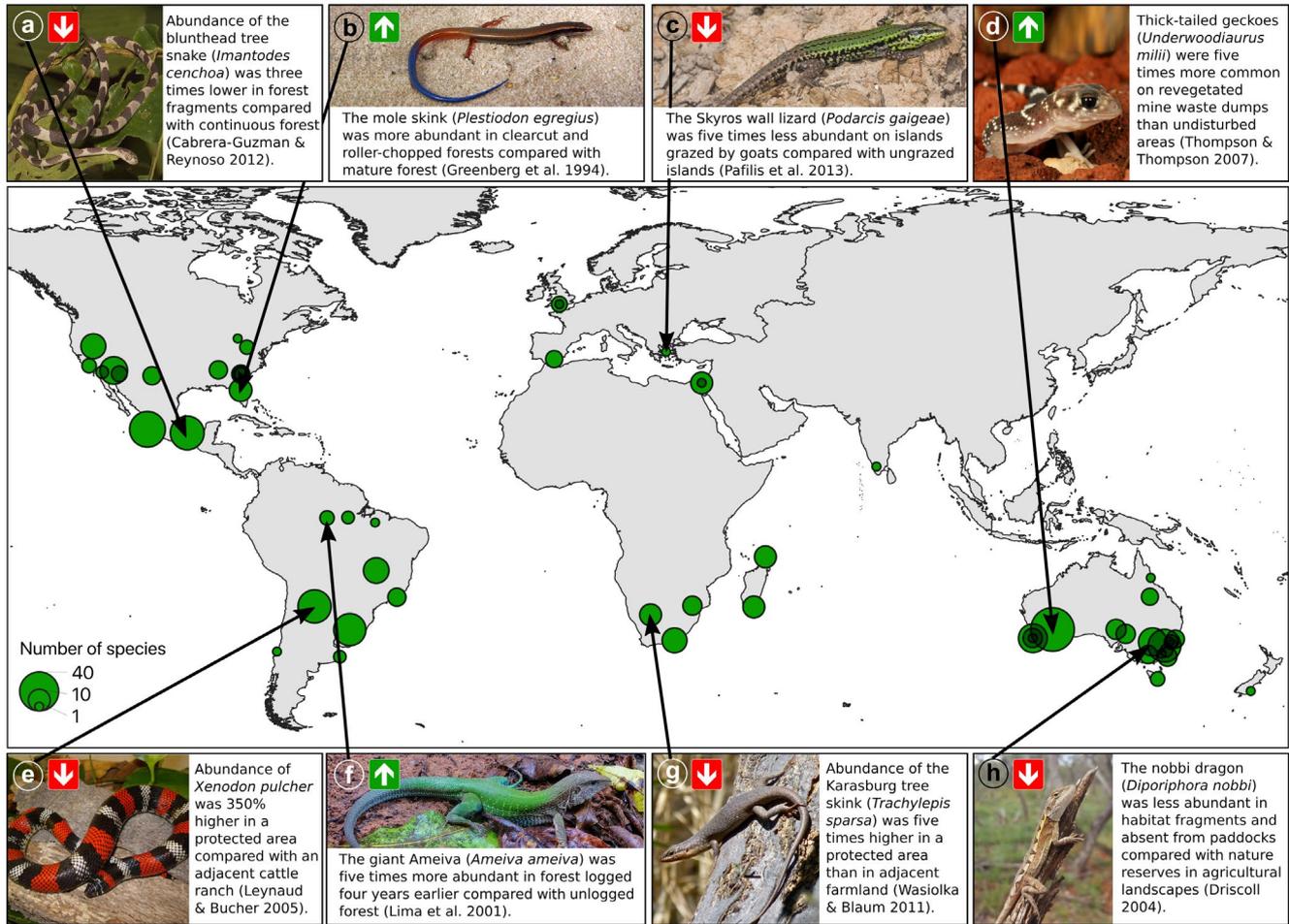


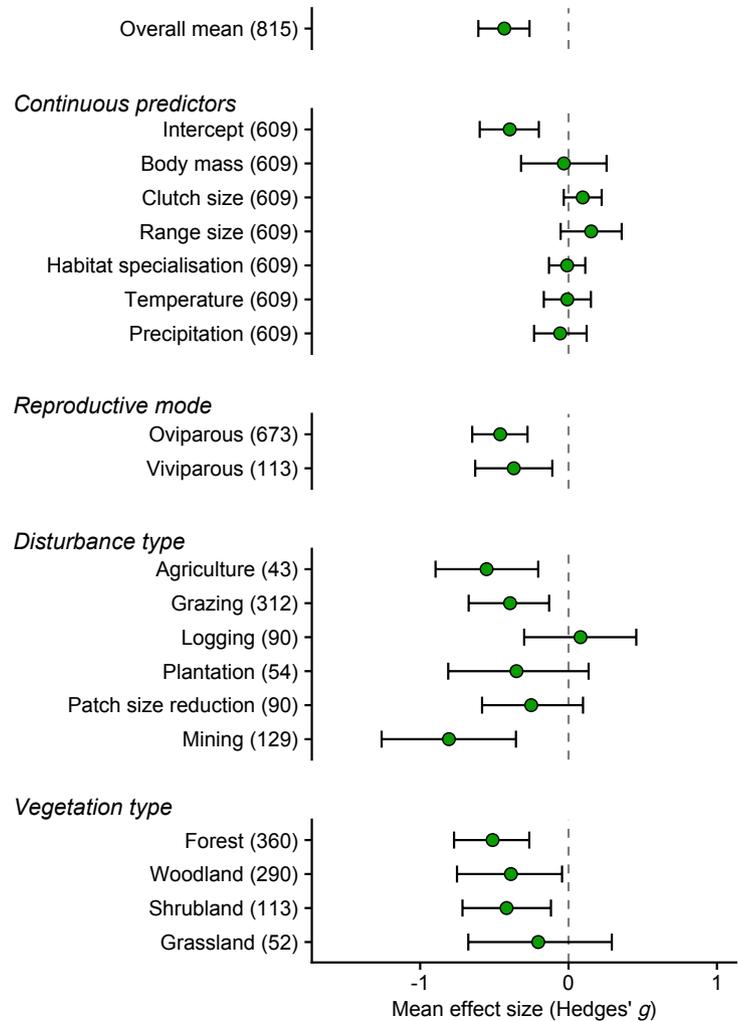
FIGURE 1 Map of study locations, with the size of each circle scaled according to the number of species from each study. Boxes provide examples of species that responded either negatively (a, c, e, g, h) or positively (b, d, f) to habitat modification. Red downward arrows represent a decrease in abundance in response to habitat modification, and the opposite for green upward arrows. Photograph credits: (a) Pavel Kirillov CC BY-SA 2.0; (b) Glenn Bartolotti CC BY-SA 4.0; (c) Benny Trapp CC BY 3.0; (d) Patrick Kavanagh CC BY 2.0; (e) Franco Souza ©; (f) Gionorossi CC BY-SA 4.0; (g) Bernard Dupont CC BY-SA 2.0; (h) Tim Doherty ©

Bayesian mixed effects models revealed no apparent effects of body mass, habitat specialization, temperature or precipitation on the responses of reptiles to habitat modification (Figure 2; Supporting Information Appendix S2, Table S2.2). There were weak positive effects of clutch size (posterior mean: 0.10, CI: -0.03 to 0.22) and range size (0.15, -0.05 to 0.36) on responses to habitat modification (Supporting Information Appendix S2, Table S2.2). Oviparous (-0.46, -0.65 to -0.28) and viviparous (-0.37, -0.63 to -0.11) species had similar negative effect sizes and CIs that overlapped each other (Figure 2). All disturbance types had negative mean effect sizes, except for logging, which was essentially neutral (Figure 2). Mining had the strongest effect, followed by agriculture, grazing, plantations and patch size reduction, all with CIs not overlapping zero, except for plantations (-0.81 to 0.14) and patch size reduction (-0.58 to 0.10; Figure 2). The CIs overlapped for all disturbance types, except for logging and mining, which were the most positive and negative effects, respectively. Forest had the most negative mean effect size and

grassland the least, although the CIs overlapped for all vegetation types (Figure 2; Supporting Information Appendix S2, Table S2.2). Model results based on the logarithmic response ratio were very similar, with the main differences being that the effects of range size, logging and grasslands were more positive and the effects of plantations, patch size reduction and mining more negative (Supporting Information Appendix S2, Table S2.2; Figure S2.2).

There was no phylogenetic signal in squamate responses to habitat modification for either the null model ($H^2 = .10$, 95% CI: 0-.29) or the disturbance type model ($H^2 = .18$, 95% CI: .01-.41). The analysis based on taxonomic families showed that all families had negative mean effect sizes, except for Phrynosomatidae, which was weakly positive (Figure 3). There were four families with negative mean effects that did not overlap zero: Scincidae, Teiidae, Lacertidae and Disapdidae (Figure 3). Three additional families (Phyllodactylidae, Diplodactylidae and Iguanidae) had negative effects that marginally overlapped zero (0.04-0.07 SD units; Figure 3), although the sample size was small for Phyllodactylidae ($n = 6$).

FIGURE 2 Mean effect sizes (Hedges' g) and 95% credible intervals for the effect of habitat modification on squamate species abundance according to life-history and environmental traits. Numbers in parentheses represent the sample size for each predictor variable. Predictors are grouped according to the specification of each statistical model



4 | DISCUSSION

Our analysis is the most comprehensive work to date on the impacts of anthropogenic habitat modification on reptiles. We found an overall negative effect of habitat modification on squamate abundance, although there was high heterogeneity across species and disturbances. On average, reptile abundance was one-third lower in modified habitat. Species' traits and environmental characteristics were poor predictors of the responses of reptiles to habitat modification. There was weak support for our predictions that range size and clutch size would be negatively correlated with sensitivity to habitat modification. We did not find any support for our predictions that large body size, oviparity and habitat specialization would increase sensitivity to habitat modification. Some families exhibited an overall negative mean response to habitat modification, whereas others were more variable, but our phylogenetic analysis revealed no signal in the data. Temperature and precipitation had no detectable effect on the responses of reptiles to habitat modification, nor did vegetation type. This suggests that disturbance characteristics might be more important than phylogeny and climate as predictors of squamate sensitivity to habitat modification; that is, reptile responses to disturbance appear equally severe across different

bioclimatic gradients and vegetation types. There were some geographical biases in the availability of data, with few studies available from Asia, Africa and Europe. However, we predict similar patterns of responses in those regions because our analysis encompassed a broad range of disturbances and ecosystems, including arid, semi-arid, temperate and tropical ecosystems.

4.1 | Ecological correlates of sensitivity to habitat modification

Consistent with other taxa, the responses of reptile populations to habitat modification were positively correlated with species range size, although the effect was weak and the credible limits overlapped zero. Range size often acts as a proxy for population size, dispersal capacity and tolerance to ecological and environmental processes (Harris & Pimm, 2008; Keith, Akçakaya, & Murray, 2018; Slatyer et al., 2013). As range size increases, these correlated attributes can help to buffer populations against environmental variation, including anthropogenic disturbances. Conversely, for reptile species that occupy small ranges, their smaller population sizes, limited dispersal and higher ecological specialization may constrain

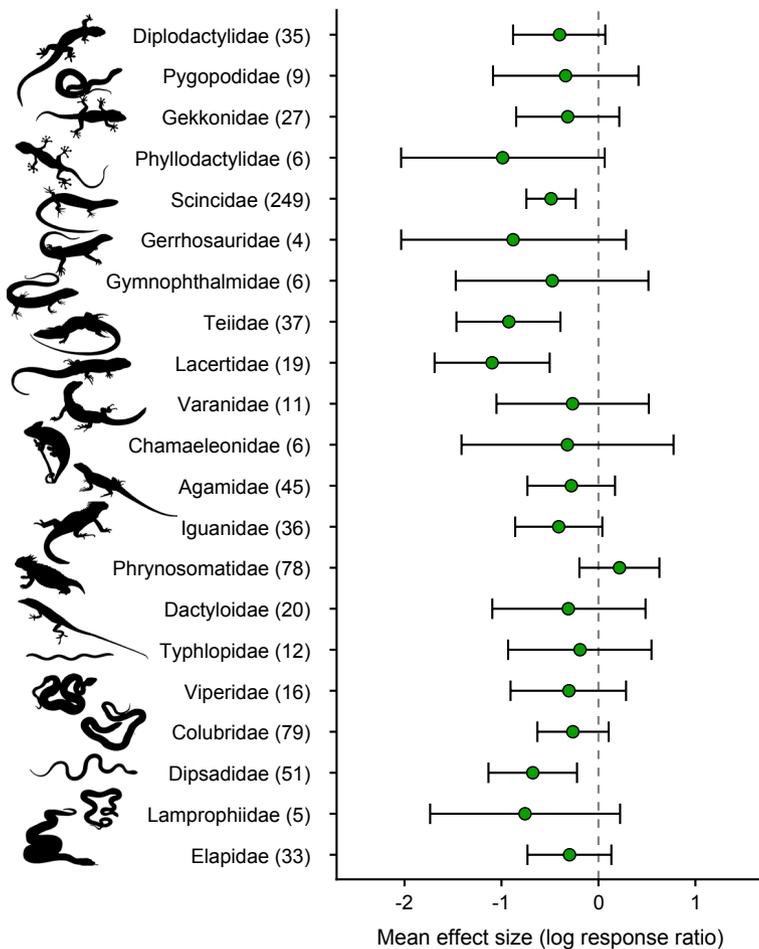


FIGURE 3 Mean effect sizes (Hedges' g) and 95% credible intervals for the effect of habitat modification on squamate species abundance for each taxonomic family. Numbers in parentheses represent the sample size for each family. Families with data for fewer than three species were excluded

local demographic and genetic processes and exacerbate negative population responses to anthropogenic disturbances. Sensitivity to disturbance may lead to a small range size, either historically or recently, as a consequence of human-caused disturbance. Thus, the current range sizes of the most sensitive species might be products of habitat modification itself. Data on both historical and current range sizes are necessary to resolve this question.

Although habitat specialists are generally considered to be more sensitive than generalists to anthropogenic disturbance (Devictor, Julliard, & Jiguet, 2008; Keinath et al., 2017), we found no support for this pattern in our data. It might be that the index of specialization that we used (number of major habitats occupied) is not an accurate proxy for specialization. Other recent studies have also failed to detect an effect of niche breadth on reptile responses to habitat modification (Frishkoff, Gabot, Sandler, Marte, & Mahler, 2019; Todd et al., 2017). This might suggest that there is not a strong relationship between niche breadth of reptile species and their sensitivity to habitat modification. However, range size is positively correlated with niche breadth in a range of taxa (Slatyer et al., 2013), including dietary niche breadth of lizards (Gainsbury & Meiri, 2017). Thus, the weak effect of range size on squamate responses to habitat modification might be representing multiple life-history traits that render species least sensitive to disturbance, including habitat generalization and large population size.

The lack of an effect of body size is surprising given that large body size is one of the most commonly cited correlates of extinction risk in a range of taxa (Purvis et al., 2005), including reptiles (Böhm et al., 2016; Meiri, 2008; Tingley et al., 2013). This result might have occurred if large reptiles, such as monitor lizards and pythons, were not sampled effectively by the survey methods used in many studies, particularly pitfall trapping. However, the size distribution of species in our database is very similar to that of all squamates (Supporting Information Appendix S2, Figure S2.4), thus suggesting that there is not a strong body size bias in our dataset. Another possibility is that the effect of large body size on species-level extinction risk might not translate well to sensitivity to habitat modification at the population level. Studies on birds and mammals found that small species were more threatened by habitat loss and modification, whereas larger species were more threatened by direct threats to survival (e.g., hunting, invasive predators; González-Suárez, Gómez, & Revilla, 2013; Owens & Bennett, 2000). Smaller species might be more sensitive to habitat loss because their reduced mobility hinders dispersal between isolated habitat fragments. Nonetheless, our results for squamates essentially show no effect of body mass on their sensitivity to habitat modification. The effect of body size on risk of decline might be evident only when a full suite of threatening processes is considered.

There was some support for our prediction that small clutch size would increase the sensitivity of a species to habitat modification

owing to reduced rates of potential population growth in disturbed landscapes. Species with larger clutches tended to respond more positively to habitat modification, although the effect was weak and the CIs overlapped zero. In human-modified landscapes, animals may need higher reproductive rates to counter higher mortality during dispersal through a hostile matrix (Rotem, Ziv, Giladi, & Bouskila, 2013) or because of increased rates of predation (Chalfoun, Thompson, & Ratnaswamy, 2002; Hansen, Sato, Michael, Lindenmayer, & Driscoll, 2019). Lizard clutch size is positively correlated with reproductive rate (Meiri, Brown, & Sibly, 2012), and simulations suggest that reproductive rate has a greater effect on the amount of habitat needed for population persistence than matrix quality or degree of habitat fragmentation (Fahrig, 2001). If landscapes are not managed to improve survival and population size of species with small clutch sizes, reptile assemblages in many disturbed landscapes are likely to be biased towards species with higher reproductive output.

We found no support for our prediction that egg-laying (oviparous) species would be more sensitive than live-bearing (viviparous) species, which we expected would occur owing to the loss of potential nesting sites following habitat modification and limited control of incubation temperatures by oviparous species. The finding that egg-laying and live-bearing reptiles are affected in a similar way by habitat modification implies either that reproductive mode has no influence or, more likely, that there are counter-balancing effects of the two modes. Scaling such effects by the size of the mother, to obtain a measure of reproductive burden, or estimating reproductive output as rates (i.e., number of eggs laid per unit time; Meiri et al., 2012) might prove more informative, but data are relatively scarce. Ultimately, other vital rates in isolation or in combination with reproductive traits including generation time, dispersal capacity and survival rates at different life stages might better approximate determinants of reptile population dynamics that would influence population responses during and after exposure to environmental disturbance.

One family, Phrynosomatidae, was an anomaly to the general pattern of negative responses to habitat modification. Across the 24 species from that family with data, 60% of responses were either neutral or positive, primarily in response to livestock grazing, but also in response to logging, patch size reduction and other disturbances. This suggests that phrynosomatids, such as the spiny lizards (*Sceloporus*), side-blotched lizards (*Uta*) and horned lizards (*Phrynosoma*), are adapted to disturbed environments or to the conditions that anthropogenic disturbances create. This might stem from the high richness of Phrynosomatids in arid regions (Wiens, Kozak, & Silva, 2013), where the sparser vegetation cover might resemble disturbed environments more so than denser vegetation in mesic systems. In contrast, the strong negative effects for Scincidae, Teiidae, Lacertidae and Disapididae suggest that most species in these families are highly likely to exhibit population declines in response to habitat modification. Given that there was variation in responses within all families, a fruitful area for future research will be focused analyses of specific families or functional groups that attempt to resolve these nuances (e.g., Todd et al., 2017).

There was no detectable effect of precipitation or temperature on the responses of reptiles to habitat modification. This is despite

previous work showing a strong relationship between maximum temperature and the effect of habitat loss/fragmentation on reptiles (Mantyka-Pringle, Martin, & Rhodes, 2012). Specifically, as temperature increased, so did the chances of being negatively affected by habitat loss/fragmentation (Mantyka-Pringle et al., 2012). Similar to our results, that study also found no relationship between precipitation and reptile responses to habitat loss/fragmentation. Further research is clearly needed to gain a better understanding of how habitat modification and climatic variables might interact to affect reptile populations, including an assessment of the relative effects of current climate compared with climate change.

4.2 | Disturbance type affects population response

There was variation in the effects of different disturbance types on squamate abundance, although all had a mean negative effect size, except for logging. The strong negative impact of mining on reptile populations reflects the fact that open-cut or "surface" mining invariably results in complete habitat destruction in the mined area. All of the mining studies assessed here were conducted in disturbed areas that had been revegetated 3–20 years earlier, which suggests that effect sizes would be even stronger if these areas had not been revegetated.

Agriculture and grazing also had negative effects on reptile abundance. No species exhibited a demonstrably positive response to the general "agriculture" category, but several species were more abundant in grazed compared with ungrazed areas (e.g., Jones, 1981). This might be attributable to altered microclimates creating improved thermoregulatory conditions for some species (Yates, Norton, & Hobbs, 2000) or to the proliferation of disturbance specialists (Devictor et al., 2008). Nonetheless, the mostly negative responses of squamates to agriculture and livestock grazing is worrying given that these industries cover c. 37% of the land area of the world (FAO, 2018). Wherever possible, it is important that farming practices that promote reptile diversity and abundance are implemented, such as retaining or restoring woody cover between cultivated areas (Nopper, Lauströer, Rödel, & Ganzhorn, 2017; Pulsford, Driscoll, Barton, & Lindenmayer, 2017).

The overall effect of logging was essentially neutral, with a mean effect size close to zero and wide CIs, because there were similar numbers of positive and negative responses. Species such as *Plestiodon egregius* and *Ameiva ameiva* were more abundant in logged compared with unlogged forests (Figure 1b,f). Higher abundance in areas subjected to logging might be attributable to greater basking opportunities after canopy removal (Huang, Porter, Tu, & Chiou, 2014; Pike, Webb, & Shine, 2011). A recent global analysis found that air temperatures are, on average, 4.1 °C warmer outside forests compared with under the forest canopies (De Frenne et al., 2019), which emphasizes the strong potential for logging to disrupt reptile community composition by altering microclimatic conditions. To this end, it is important also to emphasize that logging can have large negative impacts on reptile populations (Todd & Andrews, 2008).

Other species in our database were found in lower abundance in logged compared with unlogged areas, such as *Plestiodon inexpectatus* in Florida (Greenberg, Neary, & Harris, 1994) and *Saprosincus mustelinus* in south-eastern Australia (Webb, 1995). These contrasting positive and negative responses to logging support earlier work showing an overall neutral effect of silviculture on reptile species richness (Thompson, Nowakowski, & Donnelly, 2016) and highlight the risk of community metrics masking the negative effects of habitat modification on individual species (Devictor & Robert, 2009).

4.3 | Limitations and future research

Overall, our results suggest that most of the traits we tested do not predict squamate responses to habitat modification. This aligns with other studies finding that traits are poor predictors of broad-scale responses of other taxa to habitat loss or modification (Bartomeus, Cariveau, Harrison, & Winfree, 2018; Hatfield, Orme, Tobias, & Banks-Leite, 2018). There are multiple reasons why this might be. Firstly, general patterns might not emerge if the responses of species to disturbance vary in different parts of their range (Frishkoff et al., 2019; Nimmo, Kelly, Farnsworth, Watson, & Bennett, 2014; Orme et al., 2019). Secondly, if the responses of species vary between disturbance types and are influenced by different trait combinations, then the strength and generality of single traits or phylogenetic patterns would be reduced (Driscoll, Smith, Blight, & Sellar, 2020; Williams et al., 2010). Thirdly, other traits that we did not assess might be important, such as traits related to thermal biology. For instance, lizards in Costa Rica and Colombia with lower critical thermal maxima were more sensitive to habitat conversion than those with higher critical thermal maxima (Nowakowski et al., 2018). Further work is needed to assess how these patterns extend across a range of ecosystems and disturbances. Finally, the variability in responses we recorded across species and studies might be attributable, in part, to temporal and spatial aspects of disturbance regimes that were not assessed here, such as the magnitude, frequency and scale of disturbances. Incorporating such information is not feasible for the wide range of disturbances we studied, because there would probably be little to no replication for many combinations of disturbance types and characteristics. The overall lack of predictive ability suggests that analyses encompassing a taxonomic order as large as Squamata and varying disturbance types might be inappropriate for identifying reptile species most at risk of population decline. We suggest that individual analyses focused on specific disturbance types are more suited to the examination of disturbance characteristics and interactions between life-history traits and environmental factors (e.g., Keinath et al., 2017; Thorn et al., 2018).

5 | CONCLUSIONS

Our results show that squamates, like other taxa, are unquestionably sensitive to anthropogenic habitat modification. Some of our results,

particularly regarding body size and habitat specialization, differ from those of previous generalizations on other taxa (Keinath et al., 2017; Owens & Bennett, 2000). More generally, there are a number of case studies showing that body size, habitat specialization and niche breadth have a range of effects or no relationship with disturbance (e.g., Frishkoff et al., 2019; Henle, Davies, Kleyer, Margules, & Settele, 2004; Todd et al., 2017). Given this, and the high level of variation among reptile responses to anthropogenic disturbances, it is evident that development of a robust predictive framework based on traits will need further consideration. Nevertheless, we would expect negative population responses to habitat modification to have important implications for reptile communities, including shifts in species richness, abundance and composition (Newbold et al., 2016; Thompson et al., 2016). Clearly, to prevent those species with the most negative responses to anthropogenic disturbance potentially going extinct, the ongoing development of more environmentally sustainable practices that ameliorate anthropogenic impacts is urgently needed.

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DATA ACCESSIBILITY STATEMENT

The data used in this study are available at datadryad.org (<https://doi.org/10.5061/dryad.5x69p8d0n>).

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BIOSKETCH

Tim S. Doherty is a wildlife ecologist specializing in the fields of disturbance ecology and predator–prey ecology. His research aims to improve our understanding and management of the natural world, particularly regarding the impacts of humans on the environment. He achieves this through a combination of local field experiments and quantitative syntheses at continental and global scales.

SUPPORTING INFORMATION

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

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APPENDIX

LIST OF DATA SOURCES

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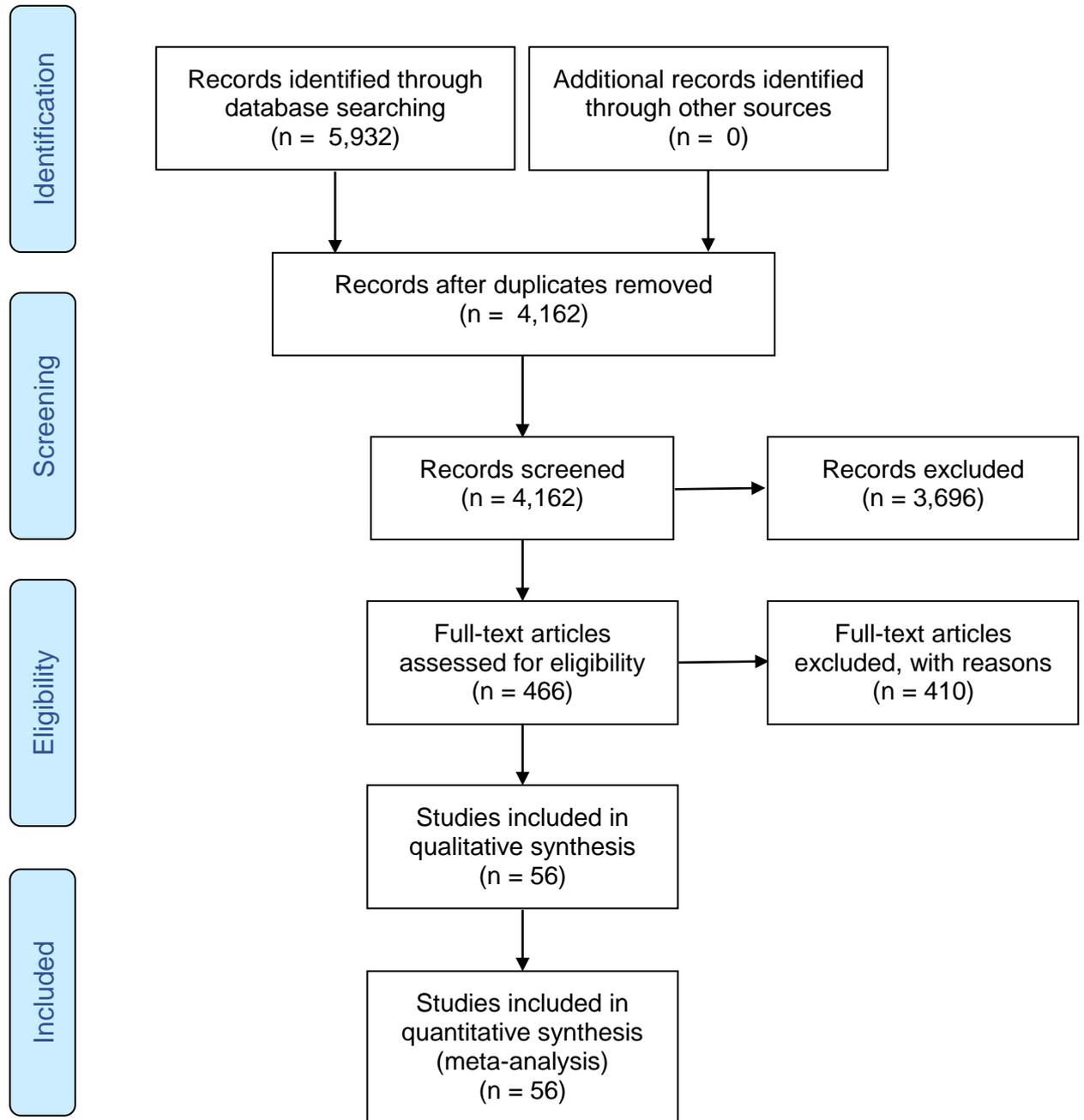
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Supporting information for *Reptile responses to anthropogenic habitat modification: a global meta-analysis*

Appendix S1: PRISMA diagram.

Appendix S2: Additional results.

Appendix S1: PRISMA diagram.



Appendix S2: Additional results.

Table S2.1 Identification of an appropriate random effects structure using leave-one-out cross-validation model selection. LOOIC, leave-one-out information criterion. We selected the random effects structure of the model with the lowest LOOIC.

Hedges' g

Random effects structure	LOOIC
Study ID + Species	1646.1
Study ID + Species + Phylogeny	1646.2
Study + Species + Family	1651.8
Study ID + Phylogeny	1697.1
Study ID	1869.9
No random effects	1942.4

Log response ratio

Random effects structure	LOOIC
Study ID + Species	1286.2
Study ID + Species + Phylogeny	1289.4
Study + Species + Family	1293.8
Study ID + Phylogeny	1326.1
Study ID	1362.3
No random effects	1415.9

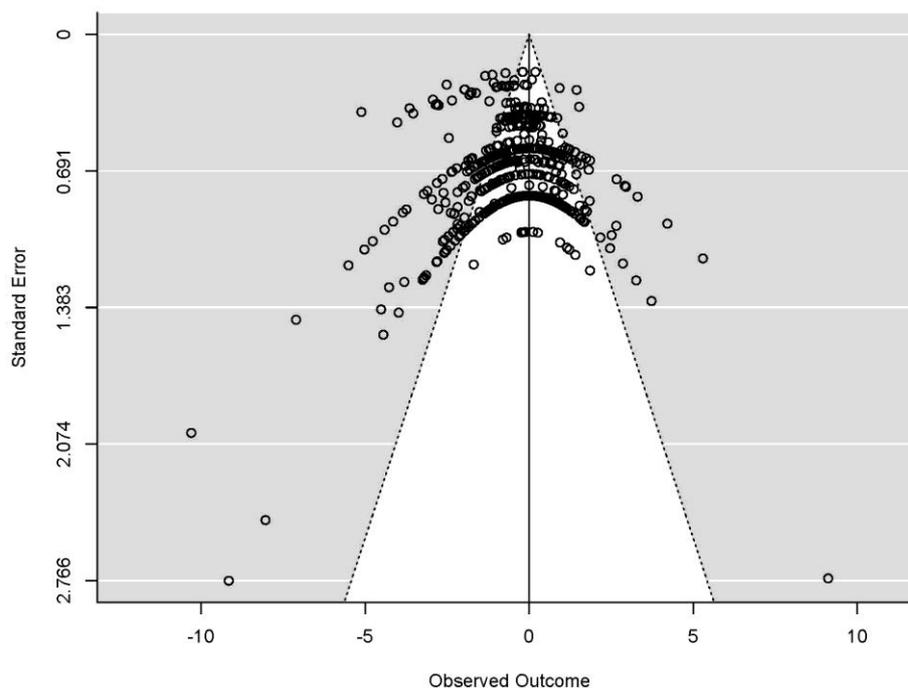


Fig. S2.1 Funnel plot of effect sizes (Hedges' g) plotted against the inverse standard error of sampling variances. The white area bordered by dashed lines represents the region of 95% pseudo confidence intervals where 95% of studies are expected to fall in the absence of bias and heterogeneity. Although difficult to see in the plot, ~85–90% of studies fall within this region.

Table S2.2. Mean effect sizes (Hedges' *g* and log response ratio) and 95% credible intervals for predictor variables. Bold values indicate where the credible intervals do not include zero.

Model	Term	Hedges' <i>g</i>			Log response ratio		
		Posterior mean	Lower 95% CI	Upper 95% CI	Posterior mean	Lower 95% CI	Upper 95% CI
Continuous model	Intercept	-0.40	-0.60	-0.20	-0.31	-0.58	-0.04
	Body mass	-0.03	-0.32	0.26	0.01	-0.23	0.25
	Clutch size	0.10	-0.03	0.22	0.10	-0.10	0.31
	Range size	0.15	-0.05	0.36	0.24	-0.05	0.53
	Habitat specialisation	-0.01	-0.13	0.11	-0.02	-0.20	0.16
	Temperature	-0.01	-0.17	0.15	0.05	-0.17	0.28
	Precipitation	-0.06	-0.23	0.12	-0.01	-0.25	0.23
	Reproductive mode	Oviparous	-0.46	-0.65	-0.28	-0.46	-0.69
	Viviparous	-0.37	-0.63	-0.11	-0.32	-0.71	0.08
Disturbance type	Agriculture	-0.55	-0.90	-0.20	-0.51	-1.19	0.19
	Grazing	-0.39	-0.67	-0.13	-0.25	-0.55	0.03
	Logging	0.08	-0.30	0.46	0.43	-0.01	0.88
	Plantation	-0.35	-0.81	0.14	-0.76	-1.48	-0.02
	Patch size reduction	-0.25	-0.58	0.10	-0.55	-0.99	-0.12
	Mining	-0.81	-1.26	-0.35	-1.24	-1.73	-0.70
Vegetation type	Forest	-0.51	-0.77	-0.26	-0.49	-0.82	-0.18
	Woodland	-0.39	-0.75	-0.04	-0.51	-0.93	-0.08
	Shrubland	-0.42	-0.71	-0.12	-0.38	-0.72	-0.02
	Grassland	-0.20	-0.68	0.29	0.12	-0.39	0.66

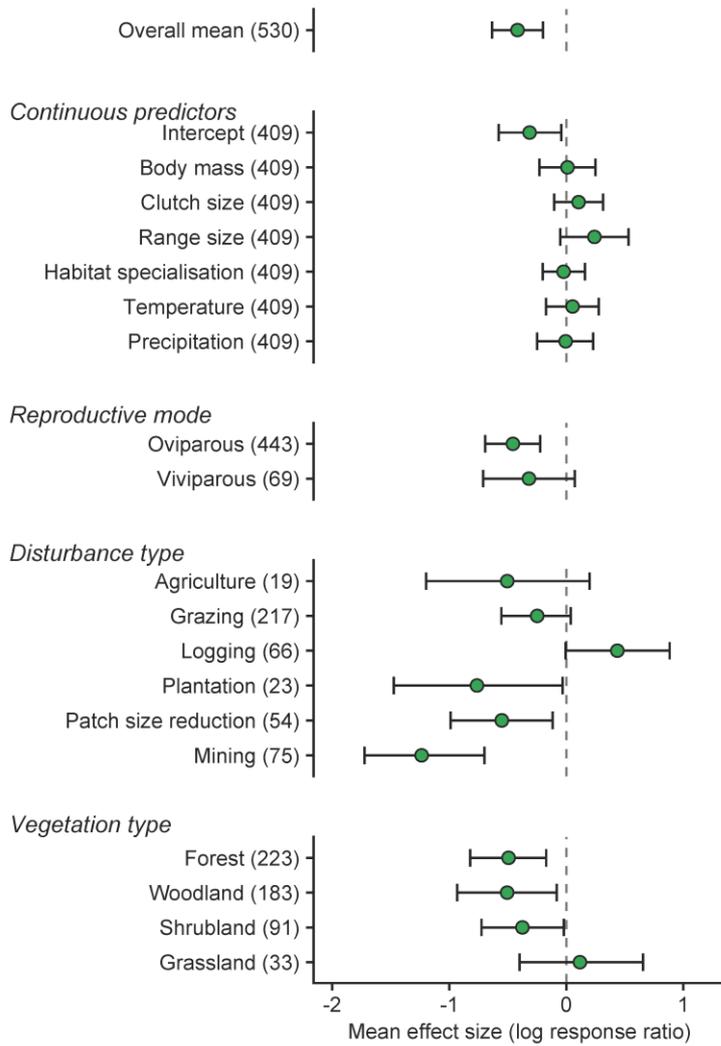


Fig. S2.2. Mean effect sizes (log response ratio) and 95% credible intervals for the effect of habitat modification on squamate species abundance according to life history and environmental traits. Numbers in parentheses represent the sample size for each predictor variable. Predictors are grouped according to the specification of each statistical model.

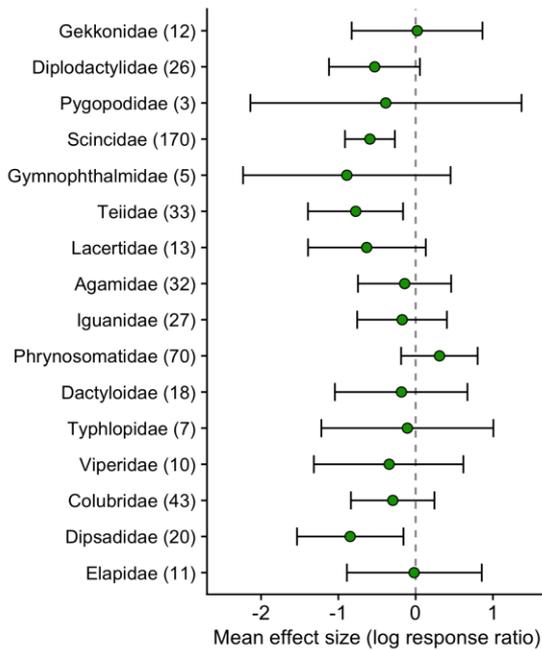


Fig. S2.3. Mean effect sizes (log response ratio) and 95% credible intervals for the effect of habitat modification on squamate species abundance for each taxonomic family. Numbers in parentheses represent the sample size for each family. Families with data for fewer than three species were excluded.

Table S2.3. Mean effect sizes (Hedges' *g* and log response ratio) and 95% credible intervals for the taxonomic family model. Bold values indicate where the credible intervals do not include zero.

Family	Hedges' <i>g</i>			Log response ratio		
	Posterior mean	Lower 95% CI	Upper 95% CI	Posterior mean	Lower 95% CI	Upper 95% CI
Agamidae	-0.28	-0.73	0.17	-0.14	-0.75	0.46
Chamaeleonidae	-0.32	-1.41	0.77	-	-	-
Colubridae	-0.26	-0.63	0.11	-0.30	-0.84	0.24
Dactyloidae	-0.31	-1.09	0.49	-0.18	-1.04	0.67
Diplodactylidae	-0.40	-0.88	0.07	-0.53	-1.12	0.06
Dipsadidae	-0.68	-1.13	-0.22	-0.85	-1.53	-0.16
Elapidae	-0.30	-0.73	0.13	-0.02	-0.89	0.86
Gekkonidae	-0.32	-0.85	0.22	0.02	-0.83	0.86
Gerrhosauridae	-0.88	-2.03	0.29	-0.89	-2.23	0.45
Gymnophthalmidae	-0.48	-1.47	0.52	-0.17	-0.76	0.40
Iguanidae	-0.41	-0.86	0.04	-0.63	-1.39	0.13
Lacertidae	-1.10	-1.69	-0.50	-	-	-
Lamprophiidae	-0.76	-1.74	0.22	-	-	-
Phrynosomatidae	0.22	-0.20	0.63	0.31	-0.19	0.80
Phyllodactylidae	-0.99	-2.04	0.06	-	-	-
Pygopodidae	-0.34	-1.09	0.41	-0.39	-2.14	1.37
Scincidae	-0.49	-0.74	-0.23	-0.59	-0.91	-0.27
Teiidae	-0.92	-1.46	-0.39	-0.77	-1.39	-0.16
Typhlopidae	-0.19	-0.93	0.55	-0.11	-1.22	1.01
Varanidae	-0.27	-1.05	0.52	-	-	-
Viperidae	-0.30	-0.91	0.28	-0.34	-1.32	0.62

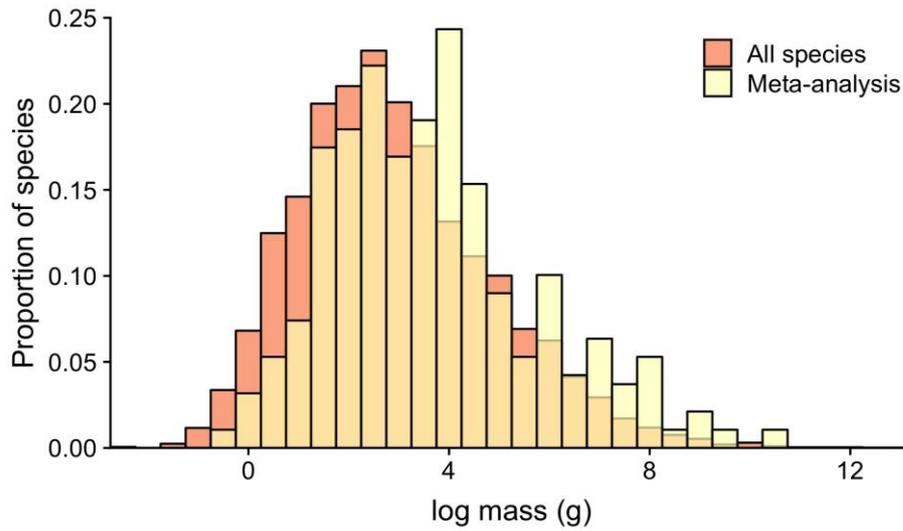


Fig. S2.4 Size-frequency distributions for all squamates and the species included in our database. Body mass data are from Feldman, A., Sabath, N., Pyron, R.A., Mayrose, I. & Meiri, S. (2016) Body sizes and diversification rates of lizards, snakes, amphisbaenians and the tuatara. *Global Ecology and Biogeography*, **25**, 187–197.