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RESEARCH PAPER

# Correlates of extinction risk in squamate reptiles: the relative importance of biology, geography, threat and range size

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## ABSTRACT

**Aim** Evaluating the relative roles of biological traits and environmental factors that predispose species to an elevated risk of extinction is of fundamental importance to macroecology. Identifying species that possess extinction-promoting traits allows targeted conservation action before precipitous declines occur. Such analyses have been carried out for several vertebrate groups, with the notable exception of reptiles. We identify traits correlating with high extinction risk in squamate reptiles, assess whether these differ with geography, taxonomy and threats, and make recommendations for future Red List assessments.

**Location** Global.

**Methods** We collected data on biological traits and environmental factors for a representative sample of 1139 species of squamate reptiles. We used phylogenetically controlled regression models to identify general correlates of extinction risk, threat-specific correlates of risk and realm-specific correlates of risk. We also assessed the relative importance of range size versus other factors through multiplicative bivariate models, partial regressions and variance partitioning.

**Results** Range size was the most important predictor of extinction risk, reflecting the high frequency of reptiles assessed under range-based IUCN criteria. Habitat specialists occupying accessible ranges were at a greater risk of extinction: although these factors never contributed more than 10% to the variance in extinction risk, they showed significant interactions with range size. The predictive power of our global models ranged from 23% to 29%. The general overall pattern remained the same among geographical, taxonomic and threat-specific data subsets.

**Main conclusions** Proactive conservation requires shortcuts to identify species at high risk of extinction. Regardless of location, squamate reptiles that are range-restricted habitat specialists living in areas highly accessible to humans are likely to become extinct first. Prioritizing species that exhibit such traits could forestall extinction. Integration of data sources on human pressures, such as accessibility of species ranges, may aid robust and time-efficient assessments of species extinction risk.

**Keywords**
**Decline, extinction risk, lizard, phylogeny, prediction, reptile, snake.**



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## INTRODUCTION

To combat decline in biodiversity and prioritize conservation action, there is an urgent need to identify species at risk of extinction. Identifying key correlates of risk and evaluating how they vary across time, species and space is a central goal of conservation research. Such research has focused on all vertebrate groups (e.g. Olden *et al.*, 2007; Sodhi *et al.*, 2008; Davidson *et al.*, 2009; Lee & Jetz, 2011) with the exception of reptiles.

What makes one species more prone to extinction than another is likely to vary depending on biological traits and environmental factors. Habitat specialization, large body size and small geographical range frequently correlate with increased extinction risk (Owens & Bennett, 2000; Cardillo *et al.*, 2006). Higher annual precipitation, higher minimum elevation and increased human population density can predict the susceptibility of species to extinction (Cardillo *et al.*, 2004; Davies *et al.*, 2006; Luck, 2007; Tingley *et al.*, 2013). Such analyses can help identify high-risk species and regions, thus establishing conservation priorities (Murray *et al.*, 2014).

Certain traits may render species vulnerable to some threat processes but not others (Murray *et al.*, 2014). Ignoring the identity and severity of threats acting on a species may lead to models in correlative studies of extinction risk having a relatively low explanatory power (Isaac & Cowlishaw, 2004; Murray *et al.*, 2014). Bird species with high extinction risk caused by overexploitation and invasive species had long generation times and large body sizes, whilst extinction risk in species threatened by habitat loss was associated with habitat specialization and small body sizes (Owens & Bennett, 2000).

Correlates of extinction risk may also vary across space. For example, the importance of traits can vary among geographical scales: human population density is a significant predictor of risk at a global scale, but is less consistent within geographical realms (Davies *et al.*, 2006). It has been suggested that both regional and global analyses are required to contribute to a better understanding of patterns of extinction risk and their drivers (Davies *et al.*, 2006; Fritz *et al.*, 2009).

Reptiles have been neglected in global conservation prioritization due to the relative paucity of data on their extinction risk. Some smaller-scale, regional studies have identified correlates of heightened extinction risk in squamate reptiles (lizards, snakes and amphisbaenids), such as small geographical range (Tingley *et al.*, 2013), ambush foraging and lack of male–male combat (Reed & Shine, 2002), and large body size, habitat specialization and high annual precipitation (Tingley *et al.*, 2013). However, a global analysis of correlates of extinction risk has so far not been possible due to a lack of consolidated data on reptile extinction risk, distribution and life history. Recently, a global assessment of extinction risk in a representative sample of 1500 reptile species established that one-fifth of reptiles are threatened with extinction, with the proportion under threat highest in freshwater environments, tropical regions and on oceanic islands (Böhm *et al.*, 2013).

Given the lack of population data for squamates, their extinction risk is primarily based on restricted geographical range; for example, 82% of squamates were assessed under IUCN Red List criterion B (restricted geographical range) and 13% under criterion D2 (very restricted population) (Böhm *et al.*, 2013). This introduces circularity into correlative studies, since geographical range size is likely to have the strongest effect on extinction risk. Previous studies have dealt with this issue by producing an analysis of species not classified under the two range-based criteria (e.g. Purvis *et al.*, 2000; Cardillo *et al.*, 2004). However, given the lack of population and trend data for squamates, and thus the lack of assessments of extinction risk under criteria of population decline, assessments of extinction risk correlates greatly rely on establishing the significance of contributing factors in relation to range size.

Here, we build on this sampled assessment of reptile extinction risk to conduct the first global phylogenetic comparative study of squamate extinction risk. We first identify biological traits and environmental factors that correlate with elevated extinction risk. We hypothesize that, in addition to a negative effect of range size: (1) biological traits such as large body size and increased habitat specialization are positively correlated with high extinction risk; and (2) environmental factors relating to increased human influence are positively correlated with extinction risk (Table 1). We conduct further analyses on the effects of threat type, taxonomy and geography on extinction risk, and investigate the explanatory power of extinction risk correlates relative to range size. We find that range-restricted habitat specialists in areas highly accessible to humans have a higher extinction risk, with practical implications for the Red List assessment process and reptile conservation.

## METHODS

### Data

We obtained extinction risk data from a representative sample of 1500 randomly selected reptile species (Böhm *et al.*, 2013). We included all 1139 non-data-deficient squamate species in our analyses (i.e. excluding species that are too data poor to allow an estimate of extinction risk, an approach followed by previous authors; e.g. Purvis *et al.*, 2000; Cardillo *et al.*, 2004). Since Data Deficient (DD) species are likely to have traits which make their detection difficult (e.g. small body/range size, habitat specialism; Bland, 2014; Vilela *et al.*, 2014), the exclusion of DD species may bias our parameters towards the opposite end of the spectrum, i.e. larger-bodied habitat generalists in more expansive ranges. However, because of existing data gaps it is beyond the scope of this paper to address issues of data deficiency.

IUCN Red List category (IUCN, 2001) provided our response variable of extinction risk, a five-point scale from lowest (Least Concern = 1) to highest extinction risk (Critically Endangered = 5) (e.g. Cardillo *et al.*, 2004). No species were classified as Extinct or Extinct in the Wild.

Geographical range size ($km^2$) was calculated from freely available distribution maps produced as part of the IUCN Red List assessment process (Böhm *et al.*, 2013). The following biological traits were chosen as additional predictor variables based

**Table 1** Hypotheses on the relationship between intrinsic and extrinsic factors, and extinction risk. Intrinsic factors are likely to interact with specific threats.

| Factor | Variables in analysis | Prediction | Justification | Interaction with threats | References |
|---|---|---|---|---|---|
| Intrinsic factors: | | | | | |
| Geographical range size | Range size ($km^2$) | – | Small ranges contain smaller populations/are more easily affected by a single threat process across the entire range | Habitat loss | Purvis *et al.* (2000), Cardillo *et al.* (2008) |
| Island endemism | Categorical: island- or mainland-dwelling | + | Island endemics have smaller ranges and populations | Invasive species | Purvis *et al.* (2000) |
| Habitat specialism | Number of habitats occupied | – | Habitat specialists are at higher risk of extinction | Habitat loss | Owens & Bennett (2000), Gonzalez-Suarez *et al.* (2013) |
| Body size | Maximum snout–vent length | + | Large-bodied species have small population densities, slow life histories and large home ranges | Overexploitation, invasive species | Owens & Bennett (2000), Cardillo *et al.* (2008), Gonzalez-Suarez *et al.* (2013), Tingley *et al.* (2013) |
| Reproductive rate | Number of offspring per year | – | Species with slow reproductive rates are less able to compensate for high mortality rates | Overexploitation, invasive species | Gonzalez-Suarez *et al.* (2013) |
| Reproductive mode (viviparity) | Categorical: viviparous versus oviparous | + | Viviparous species tend to be larger than oviparous species | Overexploitation, invasive species | Durnham *et al.* (1988) |
| Diet (trophic level) | Categorical: Omnivore, herbivore, carnivore | + | Higher trophic levels (carnivores) more vulnerable to disturbance | | Crooks & Soule (1999) |
| Extrinsic factors: | | | | | |
| Precipitation | Annual average precipitation | + | Areas experiencing high levels of precipitation have higher productivity & potentially higher human disturbance | | Tingley *et al.* (2013) |
| Temperature | Annual average temperature | – | Reptiles are solar ectotherms, with slower life histories (hence reproduction) in areas of lower temperatures | | Scharf *et al.* (2015) |
| Elevation | Minimum elevation (in m) | + | High minimum elevations suggest smaller, more restricted ranges | | Davies *et al.* (2006) |
| Productivity | Net primary productivity | + | Higher productivity suggests potentially higher human disturbance and impact | | Luck (2007) |
| Human impact | 1. Human appropriation of net primary productivity<br>2. Human population density<br>3. Human footprint<br>4. Accessibility (distance from road) | + | Higher human disturbance and impact, higher levels of resource use and increased pressure on productive habitats, opening up of habitats to exploitation of natural resources | | Cardillo *et al.* (2008) |

on hypotheses derived from the literature (Table 1): degree of habitat specialization (calculated as the number of habitat types a species occupies), body size/mass [maximum snout–vent length (SVL; in mm)], number of offspring per year, reproductive mode (viviparous, oviparous) and diet (omnivore, herbivore, carnivore). Data were collected via literature searches, museum specimens and input from species experts (Appendix S1, Table S1). IUCN Red List assessments record the habitats occupied by each species using a classification scheme of 103 habitat types, which we combined into 15 broader habitat categories (Appendix S1, Table S2). From this, we calculated number of habitats occupied by each species.

We tested the following environmental predictor variables, based on hypotheses derived from the literature (Table 1): annual precipitation (mm), annual temperature (°C), minimum elevation (Hijmans *et al.*, 2005) and net primary productivity (NPP; g $m^{-2}$ $year^{-1}$; Imhoff *et al.*, 2004). We also tested the following aggregate measures of the level of human influence within a species range: human appropriation of NPP (HANPP, measured as % of NPP; Imhoff *et al.*, 2004), mean human population density (HPD, measured as people $km^{-2}$; CIESIN, 2005a), accessibility (measured as travel time to a city with more than 50,000 people; Nelson, 2008) and mean human footprint (human influence index, normalized per region and biome; CIESIN, 2005b). All extrinsic predictor variables were extracted as the mean value across each species' range using ArcGIS 9.3. We also divided the threat types recorded as part of the Red List assessments into five categories (Salafsky *et al.*, 2008): habitat loss or disturbance, overexploitation, introductions of invasive species, climate change and pollution (Appendix S1, Table S2). We included threat type, biogeographical realm and taxonomy (lizards, snakes) as additional variables in our analyses.

## Reptile phylogeny

We primarily relied on the dated phylogeny from Pyron *et al.* (2013), which contained 666 of the species in our dataset (hereafter referred to as 'dated phylogeny'). From this, we built a composite non-dated phylogeny (hereafter referred to as 'non-dated phylogeny') including all 1139 species in our dataset, using Phylowidget (Jordan & Piel, 2008). We set all branch lengths in our non-dated phylogeny to unity.

Most of the relationships between genera and families within our non-dated phylogeny were derived from the molecular phylogeny by Pyron *et al.* (2013) and revised using a more recent phylogeny on the origin of viviparity (Pyron & Burbrink, 2014). Literature searches on phylogenetic relationships were carried out for species not included in Pyron *et al.* (2013). Polytomies were assumed where relationships could not be resolved. Studies based on morphological evidence were only used if phylogenies based on molecular methods were unavailable. The final tree had 1005 nodes and included a species of *Sphenodon* as an outgroup. The higher-level relationships were: (1) Dibamidae and Gekkonidae near the base of the tree, (2) Scincoidea (Scincidae, Cordylidae, Gerrhosauridae, Xantusiidae) as a sister group to all other squamates (except Dibamidae and Gekkonidae), and (3) Lacertoidea (Lacertidae, Amphisbaenidae, Teiidae, Gymnophthalmidae) as a sister group to Toxifera (Anguimorpha, Iguanidae, Serpents). Lower-level relationships are detailed in Appendix S2.

## Statistical analysis

Statistical analyses were carried out in R v.3.1.2 (R Core Team, 2014). Variables were log-transformed to achieve normality. Phylogenetic relationships between species may violate assumptions about independence of character traits, so that trait-based models of extinction risk need to control for shared ancestry (Freckleton *et al.*, 2002). We followed Revell (2010) and simultaneously estimated phylogenetic signal (Pagel's $\lambda$, using maximum likelihood) and regression parameters, an approach that has been shown to outperform equivalent non-phylogenetic approaches. We implemented this using phylogenetic generalized linear models (pGLS) in the R package 'caper' (Orme *et al.*, 2012).

To overcome circularity in our data introduced by range size, we ran a number of analyses, summarized in Fig. 1(a). We first ran a univariate pGLS of all predictors on extinction risk, confirming that range size was the most significant predictor of risk (dated phylogeny, $t = -16.2$, d.f. = 664, $r^2 = 0.28$, $P < 0.001$; non-dated phylogeny, $t = -25.0$, d.f. = 1136, $r^2 = 0.35$, $P < 0.001$). Next, we conducted bivariate additive pGLS of each explanatory variable in turn on extinction risk, including range size as the second variable to control for its effect. Finally, we carried out stepwise multiple regressions, in which variables that caused the most significant increase in the explanatory power of the model were added one at a time to produce minimum adequate models (MAMs). To test whether spatial effects remained within our model, possibly contributing to variation within the data, we checked our model residuals for spatial autocorrelation using Moran's *I* in the package 'spdep' (Bivand *et al.*, 2015) by defining the spatial location of each residual as the range mid-point of the corresponding species.

To disentangle the influence of range size on extinction risk in MAMs, we carried out three additional analyses (Fig. 1b). First, we reconstructed MAMs of extinction risk excluding range size, to compare model performance and determine the most significant predictors in the absence of our range size metric. Second, we performed partial regressions of extinction risk using two sets of explanatory variables: range size and all other significant explanatory variables remaining in the MAMs. The resulting variance partitioning (Legendre & Legendre, 1998) for each MAM shows the shared variance between range size and other explanatory variables, as well as independent contributions to extinction risk of range size and other explanatory variables. Variance partitioning was run in the R package 'vegan' (Oksanen *et al.*, 2015). Third, for each variable remaining in the MAM, we tested for interactions with range size using multiplicative bivariate pGLS to check whether the relationship between each significant variable changed with range size (i.e. whether once a species is range restricted, additional factors increase in

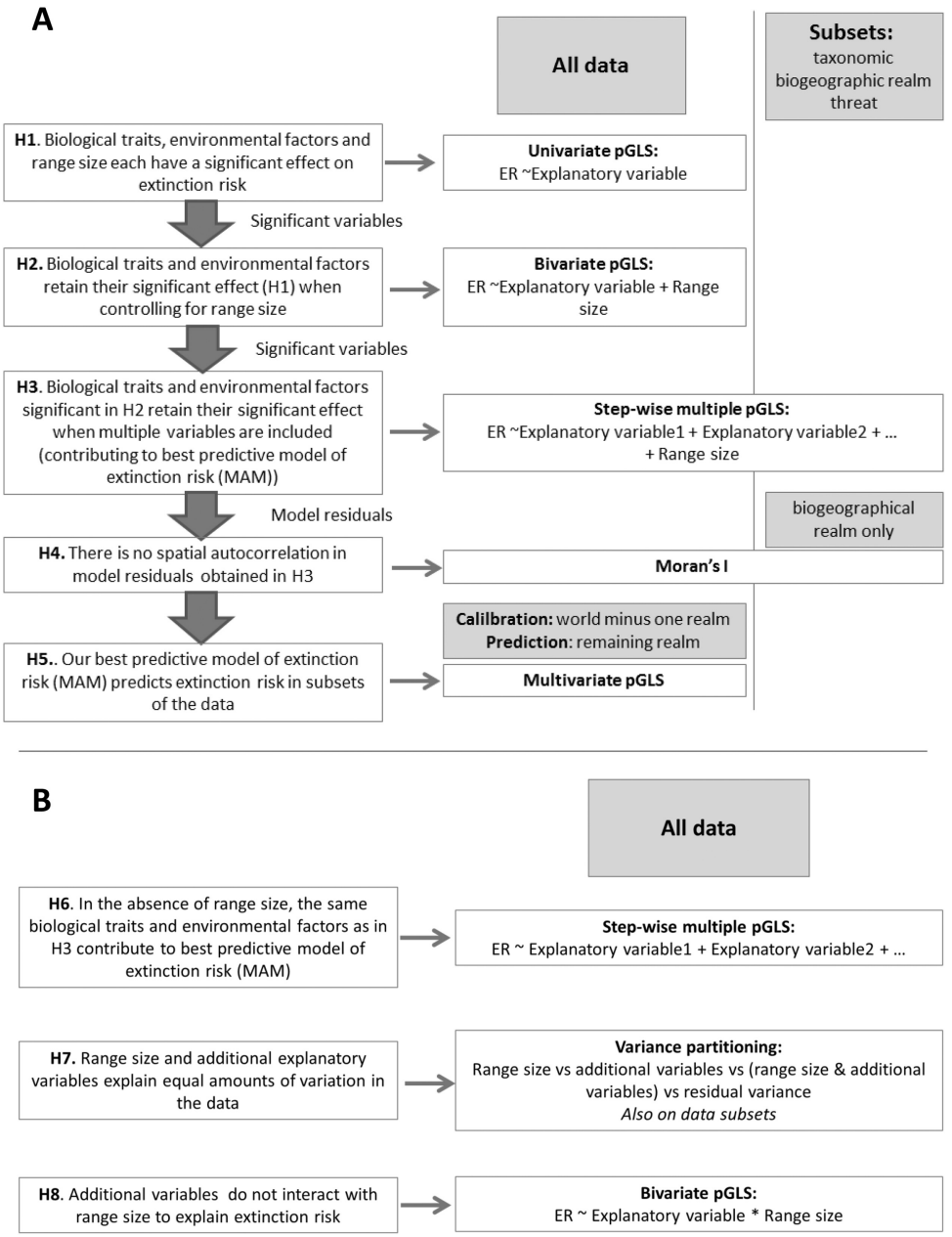


Figure 1 Explanation of analyses carried out to (a) build predictive models of extinction risk in reptiles and (b) evaluate the importance of range size versus other explanatory variables (biological traits and environmental factors). We followed this schematic to carry out our analyses using both the non-dated and dated phylogenies. ER, extinction risk; MAM, minimum adequate model; pGLS, phylogenetic generalized linear model.

importance to decide whether a range-restricted species is threatened or not).

Finally, to investigate the predictive ability of our global MAM, we re-ran our analysis on a calibration dataset consisting of the world minus one biogeographical realm (e.g. creating a calibration dataset containing all but Afrotropical species, a second calibration dataset containing all but Australasian species, etc.). Using these calibration datasets, we then used the global MAM (minus the realm) to predict the outcome for the remaining biogeographical realm. We diagnosed predictive performance of the MAM versus observed values using four metrics: mean squared error of prediction $\{\mathrm{MSEp} = \Sigma[(O-P)^2/N]\}$, bias (mean of the difference between observed and predicted extinction risk squared), percentage bias ($\%\mathrm{bias} = 100 \times \mathrm{bias}/\mathrm{MSEp}$) and percentage error of prediction $[\%\mathrm{error} = 100 \times \sqrt{\mathrm{MSEp}}/\mathrm{mean}_{\mathrm{EX}}$, where $\mathrm{mean}_{\mathrm{EX}}$ is the average extinction risk in the predicted dataset].

We conducted further pGLS on subsets of data, based on biogeographical realm, taxonomy and threats, to assess the robustness of trends detected in the complete dataset (Fig. 1a).

**Table 2** Minimally adequate model explaining extinction risk in squamates using the non-dated phylogeny

| | Coefficient | SE | $t$ | $P$ | $P$ corr | Model $r^2$ | λ |
|---|---|---|---|---|---|---|---|
| Intercept | 1.618 | 0.109 | 14.9 | <0.001 | | 0.391 | 0.000 |
| Range size | −0.098 | 0.005 | −19.5 | <0.001 | <0.001 | | |
| Accessibility | −0.060 | 0.016 | −3.8 | <0.001 | <0.001 | | |
| No. of habitats | −0.110 | 0.025 | −4.4 | <0.001 | <0.001 | | |
| Maximum SVL | 0.028 | 0.013 | 2.2 | 0.026 | 0.105 | | |

SVL, snout–vent length; λ, Pagel's lambda.
Uncorrected ($P$) and Bonferroni adjusted ($P$ corr) $P$-values are shown.

For biogeographical realms, we created six subsets containing species solely present in one of six realms (following Olson *et al.*, 2001): Afrotropical, Australasian, Indomalayan, Nearctic, Neotropical and Palaearctic. We excluded the Oceanian realm from the analysis as only seven species in our sample were from that region. We analysed two taxonomic groups separately: lizards (702 species) and snakes (423 species). We split the data into three threat categories: species affected by habitat loss alone (405 species), species affected by habitat loss and overexploitation (56 species) and species affected by habitat loss and invasive species (49 species). Threats of invasive species and overexploitation were considered in conjunction with habitat loss because too few species were affected by invasive species or overexploitation alone to allow for meaningful statistical analysis. We conducted bivariate pGLS accounting for range size and MAMs separately for each data subset, as well as variance partitioning as described above.

All analyses were run using both the dated and non-dated phylogenies to assess whether the results obtained from the two phylogenies were sufficiently similar. Where multiple hypotheses were tested simultaneously, i.e. in MAMs, we corrected for possible inflation of Type I errors using Bonferroni corrections of $P$-values.

### Species trait mapping

To investigate the spatial distribution of risk-promoting traits, we used an assemblage-based approach (Olalla-Tarraga *et al.*, 2006) to produce global distribution maps for variables that are significantly correlated with extinction risk. For each trait, we overlaid a hexagonal grid onto the stacked species distributions and calculated for each grid cell the average trait value for species present in the cell. The grid used was defined on an icosahedron, projected to the sphere using the inverse icosahedral Snyder equal area (ISEA) projection to account for the Earth's spherical nature. Each grid cell was approximately 23,000 km$^2$. We conducted the analysis using Hawth's Tools for ArcGIS 9.3 (Beyer, 2004).

## RESULTS

Because results are broadly similar between analyses, here we only report results using the non-dated phylogeny (to maximize sample size), primarily focusing on MAMs as these models best account for shared content among variables. All other results are reported in Appendix S3.

### Global correlates of squamate extinction risk

The MAM accounted for 39% of the total variance (Table 2), suggesting that species were at a greater risk of extinction if they were habitat specialists ($t = -4.4$, d.f. = 951, $P < 0.001$), had large maximum SVLs ($t = 2.2$, d.f. = 951, $P < 0.05$) and occupied more accessible range areas ($t = -3.8$, d.f. = 951, $P < 0.001$). Maximum SVL was no longer significant after Bonferroni correction, and model residuals remained significantly spatially autocorrelated (Moran's $I = 7.2$, $P < 0.001$).

#### *Effect of range size*

When excluding range size from MAM construction, accessibility and number of habitats remained the most significant effects in addition to body size, with NPP also contributing (Table S13). The model only explained 14.6% of variation in the data compared with 39% explained by the full MAM.

Range size was the largest contributing factor to extinction risk in reptiles (Fig. 2). Range size (c in Fig. 2) contributed between 24% and 47% of variation in extinction risk to our models. Additional variables within MAMs (a in Fig. 2) never contributed more than 10% independently to extinction risk, and had the greatest contribution of nearly 10% in the Nearctic model (accessibility is the sole explanatory variable). The combined contribution (b in Fig. 2) of range size and other explanatory variables varied between models, and was particularly large for the Australasian MAM. Unexplained variance was largest in nearly all models, with the exception of the Australasian realm model, where range size (c), combined variables (b) and unexplained variation (d) made nearly equal contributions.

Range size interacted significantly with all other factors, the most significant interactions being with accessibility, number of habitats and number of threats (Table 3). Accessibility lost its negative effect slowly as range size increased (i.e. closer proximity to population centres causes higher extinction risk at smaller range sizes). Similarly, habitat specialism was negatively related to extinction risk when range size was very small (species occupying fewer habitats have a higher extinction risk), though again this effect diminished as range area increased. Again, a

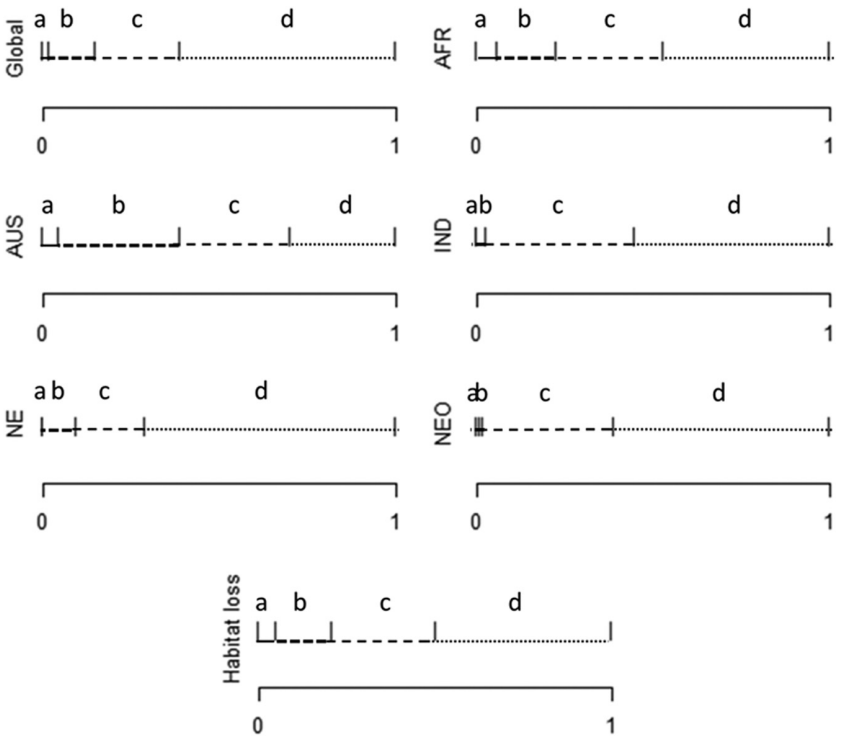


Figure 2 Variance partitioning for all minimum adequate models (MAMs) of extinction risk (global, and by geographical, and threat-type subsets), showing the different contributions of variables retained as significant within the respective MAM, as well as their shared contribution, to extinction risk: (a) combined independent contribution of all variables retained in the MAM excluding range size (solid line); (b) shared contribution of all MAM variables including range size (thick dashed line); (c) independent contribution of range size only (thin dashed line); (d) unexplained (residual) variance in the model (dotted line). The variables for each figure were selected based on the outcomes of the MAMs using the non-dated phylogeny only (see Tables 2 & 4). Biogeographical subsets: AFR, Afrotropical; AUS, Australasian; IND, Indomalayan; NE, Nearctic; NEO, Neotropical.

Table 3 Bivariate phylogenetic generalized linear model of extinction risk, including interactions of predictors with geographical range size. Here we show results for the three most significant variables: accessibility, number of habitat types and number of threats (for all results see Appendix S3, Table S13). Non-dated phylogeny only.

| | Coefficient | SE | $t$ | $P$ | Model $r^2$ | λ |
|---|---|---|---|---|---|---|
| Accessibility | | | | | | |
| Intercept | 3.430 | 0.290 | 11.8 | <0.001 | 0.396 | 0.059 |
| Range size | −0.269 | 0.026 | −10.2 | <0.001 | | |
| Accessibility | −0.344 | 0.048 | −7.2 | <0.001 | | |
| Range size × accessibility | 0.028 | 0.004 | 6.4 | <0.001 | | |
| No. of habitats | | | | | | |
| Intercept | 1.730 | 0.062 | 27.9 | <0.001 | 0.412 | 0.000 |
| Range size | −0.130 | 0.006 | −22.5 | <0.001 | | |
| No. of habitats | −0.835 | 0.085 | −9.9 | <0.001 | | |
| Range size × no. of habitats | 0.065 | 0.007 | 9.1 | <0.001 | | |
| No. of threats | | | | | | |
| Intercept | 0.496 | 0.067 | 7.4 | <0.001 | 0.501 | 0.013 |
| Range size | −0.039 | 0.005 | −7.4 | <0.001 | | |
| No. of threats | 1.288 | 0.086 | 15.0 | <0.001 | | |
| Range size × no. of threats | −0.086 | 0.008 | −11.4 | <0.001 | | |

λ, Pagel's lambda.

diminishing effect on extinction risk was found for number of threats with increasing range size.

*Predictive ability of global models*

The mean square error of prediction for our MAM ranged from 0.11 to 0.18, bias from < 0.001 to 0.003 and percentage bias from 0.01 to 1.55 (Table S9). Percentage error of prediction was broadly similar across realms, ranging between 23% and 29% (Fig. 3). Prediction error was highest for the Indomalayan realm and lowest for the Australasian realm.

## Taxonomic, geographical and threat variation in correlates of extinction risk

*Geographical realm*

Habitat specialism was significantly correlated with a high extinction risk in the Afrotropics and Neotropics, while accessibility was an important factor in the Afrotropics, Australasia and the Nearctic (Table 4). The explanatory power of MAMs varied greatly between biogeographical realms, from 70% of variation explained in the Australasian realm to 29% in both

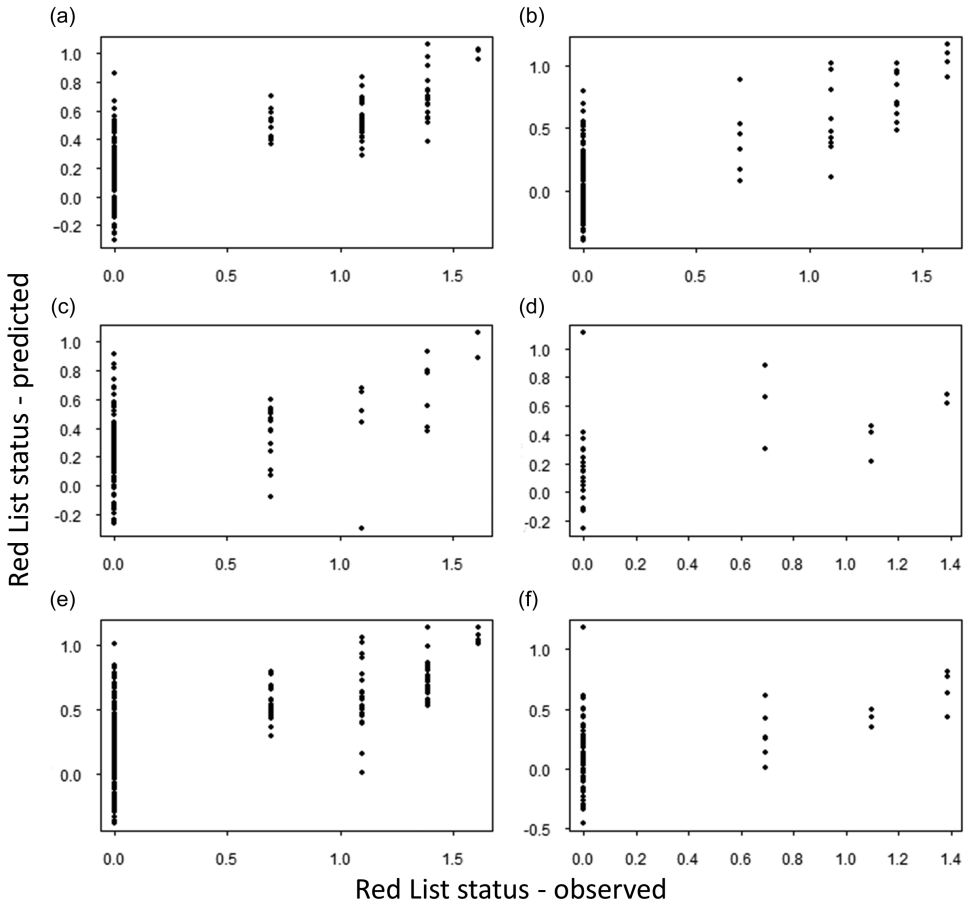


Figure 3 Observed versus predicted log Red List status derived from holdout models (the global model containing all species minus those from the stated biogeographical realm) predicting Red List status for the remaining (held out) biogeographical realm: (a) Afrotopical (%error of prediction = 23.7); (b) Australasian (%error = 23.6); (c) Indomalayan (%error = 29.0); (d) Nearctic (%error = 27.6); (e) Neotropical (%error = 25.7); (f) Palaearctic (%error = 27.1). Full diagnostics for each model are given in Table S9.

Nearctic and Palaearctic realms. Threat type was significant in the Indomalayan and Australasian MAMs, with overharvesting increasing extinction risk in both realms, and invasive species increasing extinction risk in the Australasian realm. In the Afrotropical realm, snakes had a higher extinction risk than lizards. The Palaearctic MAM only contained range size as a predictor. Geographical subsetting of the data helped to remove spatial autocorrelation in some of the subsets (Australasia, Moran's $I = -0.6$, $P = 0.72$; Indomalayan, Moran's $I = 1.3$, $P = 0.10$; Nearctic, Moran's $I = 0.01$, $P = 0.50$; Palaearctic, Moran's $I = 0.7$, $P = 0.23$) but not all of them (Afrotropical, Moran's $I = 4.0$, $P < 0.001$; Neotropical, Moran's $I = 6.0$, $P < 0.001$).

Habitat specialism and accessibility were overall the most significant predictors of extinction risk across analyses. Habitat specialism within our sample appears to be primarily confined to South America, as well as arid regions of Asia and the Middle East and Southeast Asian islands (Fig. 4a). Species with easily accessible range areas were distributed more evenly across the globe, specifically in North America (where accessibility was a significant factor), though vast areas of the Amazon Basin and deserts remain poorly accessible to humans (Fig. 4b).

### *Taxonomic subsets*

The MAM for lizards accounted for 41% of the total variance. Lizards were at a greater risk of extinction if they were habitat specialists ($t = -5.4$, d.f. = 653, $P < 0.001$), had accessible range areas ($t = -4.1$, d.f. = 653, $P < 0.001$) and large maximum SVLs ($t = 2.4$, d.f. = 653, $P < 0.05$) (Table 4). There were no significant explanatory variables bar range size for snakes.

### *Threat type*

The number of habitat types ($t = -4.5$, d.f. = 360, $P < 0.001$), maximum SVL ($t = 3.3$, d.f. = 360, $P < 0.001$) and accessibility ($t = -3.5$, d.f. = 360, $P < 0.001$) were significant factors in the MAM for species affected by habitat loss, which accounted for 51% of the total variance (Table 4). None of the traits

**Table 4** Minimally adequate models explaining extinction risk in squamates using subsets of the data based on (a) biogeographical realm, (b) taxonomy, (c) threat type. Note that predictors of extinction risk vary among biogeographical realms, and between lizards and snakes. Non-dated phylogeny only.

(a) Biogeographical realm

| | Coefficient | SE | *t* | *P* | Model $r^2$ | λ |
|---|---|---|---|---|---|---|
| Afrotropical | | | | | | |
| Intercept | 2.699 | 0.273 | 9.9 | <0.001 | 0.533 | 0.040 |
| Range size | −0.125 | 0.011 | −11.5 | <0.001 | | |
| Accessibility | −0.386 | 0.103 | −3.7 | <0.001 | | |
| No. of habitats | −0.130 | 0.055 | −2.4 | 0.020 | | |
| Taxonomy: snake | 0.145 | 0.064 | 2.3 | 0.025 | | |
| Australasian | | | | | | |
| Intercept | 2.572 | 0.328 | 7.8 | <0.001 | 0.703 | 0.000 |
| Range size | −0.117 | 0.014 | −8.3 | <0.001 | | |
| Accessibility | −0.288 | 0.132 | −2.2 | 0.032 | | |
| Threat type: overharvest | 0.083 | 0.155 | 0.5 | 0.596 | | |
| Threat type: invasives | 0.231 | 0.099 | 2.3 | 0.023 | | |
| Indomalayan | | | | | | |
| Intercept | 1.894 | 0.193 | 9.8 | <0.001 | 0.432 | 0.000 |
| Range size | −0.140 | 0.017 | −8.5 | <0.001 | | |
| Threat type: overharvest | 0.202 | 0.113 | 1.8 | 0.077 | | |
| Threat type: invasives | −0.328 | 0.176 | −1.9 | 0.065 | | |
| Nearctic | | | | | | |
| Intercept | 3.186 | 0.880 | 3.6 | <0.001 | 0.292 | 0.000 |
| Range size | −0.099 | 0.026 | −3.9 | <0.001 | | |
| Accessibility | −0.764 | 0.321 | −2.4 | 0.023 | | |
| Neotropical | | | | | | |
| Intercept | 1.378 | 0.077 | 17.9 | <0.001 | 0.386 | 0.000 |
| Range size | −0.099 | 0.007 | −14.1 | <0.001 | | |
| No. of habitats | −0.106 | 0.045 | −2.3 | 0.020 | | |
| Palaearctic | | | | | | |
| Intercept | 1.107 | 0.169 | 6.6 | <0.001 | 0.288 | 0.000 |
| Range size | −0.081 | 0.014 | −5.9 | <0.001 | | |

(b) Taxonomy

| | Coefficient | SE | *t* | *P* | Model $r^2$ | λ |
|---|---|---|---|---|---|---|
| Lizards | | | | | | |
| Intercept | 1.652 | 0.167 | 9.9 | <0.001 | 0.411 | 0.000 |
| Range size | −0.103 | 0.006 | −16.5 | <0.001 | | |
| Accessibility | −0.082 | 0.020 | −4.1 | <0.001 | | |
| No. of habitats | −0.168 | 0.031 | −5.4 | <0.001 | | |
| Maximum SVL | 0.071 | 0.030 | 2.3 | 0.019 | | |
| Snakes | | | | | | |
| Intercept | 0.904 | 0.196 | 4.6 | <0.001 | 0.372 | 0.012 |
| Range size | −0.091 | 0.007 | −13.7 | <0.001 | | |
| Maximum SVL | 0.059 | 0.032 | 1.8 | 0.066 | | |

(c) Threat type

| | Coefficient | SE | *t* | *P* | Model $r^2$ | λ |
|---|---|---|---|---|---|---|
| Habitat loss | | | | | | |
| Intercept | 2.031 | 0.180 | 11.3 | <0.001 | 0.506 | 0.000 |
| Range size | −0.128 | 0.009 | −14.7 | <0.001 | | |
| No. of habitats | −0.196 | 0.043 | −4.5 | <0.001 | | |
| Maximum SVL | 0.074 | 0.022 | 3.3 | <0.001 | | |
| Accessibility | −0.096 | 0.027 | −3.5 | <0.001 | | |

SVL, snout–vent length; λ, Pagel's lambda.

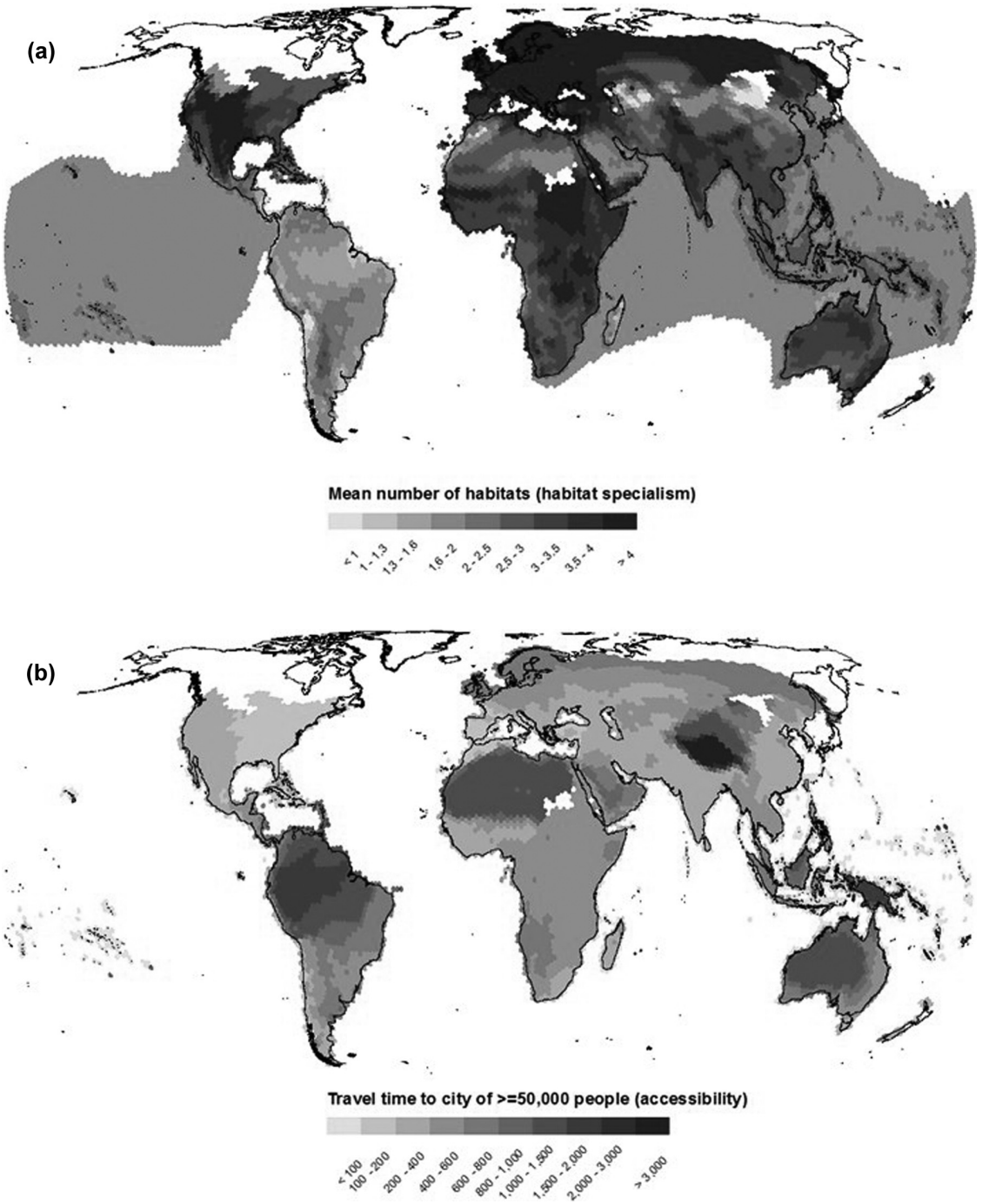


Figure 4 Global distribution maps for significant species traits in our analyses: (a) the number of habitats occupied (as a measure of habitat specialism); (b) accessibility of species geographical ranges (travel time in minutes of land-based travel to cities of more than 50,000 people). Grid cell values are the average weighted mean for trait values, for species ranges intersecting the grid cell.

were significant for species threatened by habitat loss with additional threats of overexploitation or invasive species.

## DISCUSSION

Despite being one of the largest vertebrate species groups (10,038 species described to date; Uetz & Hošek, 2015), knowledge of the factors predisposing certain reptile species to a high risk of extinction lags behind other species groups (Böhm *et al.*, 2013). Understanding how biological traits and environmental factors interact with threats may help predict the extinction risk of species and fill knowledge gaps. Our study suggests that squamate reptiles with small range size, habitat specialism and ranges that are accessible to humans are at high risk of extinction.

### IUCN Red List assessments and the importance of range size

A species' range size is important in shaping its potential extinction risk: restricted-range species are generally at a higher risk of extinction, and this is reflected in two of the five IUCN criteria for assessing the extinction risk of species (criteria B and D2; IUCN, 2001). Since little is known about the population status of most of the world's reptiles, range-based criteria are predominantly used to estimate extinction risk in reptiles (Böhm *et al.*, 2013). Our finding that most of the variation in extinction risk is explained by range size is therefore a reflection of the Red List assessment process. However, relationships between a species' abundance and distribution have been found to vary in strength across systems and at different spatial scales (Gaston *et al.*, 2000).

Small range size alone is insufficient to class a species as threatened, so that range-based IUCN criteria incorporate additional symptoms of threat (criterion B, severe fragmentation, occurrence in only a few locations, continuing decline in population size/habitat/range or extreme fluctuations; criterion D2, presence of a plausible future threat) (Mace *et al.*, 2008). Factors influencing extinction risk in addition to range size may explain why one range-restricted species is at a higher risk of extinction than another. In this study, accessibility and habitat specialism specifically were found to have an increased effect on extinction risk towards smaller range sizes, and may help inform future assessments of extinction risk and models.

### Biological traits: habitat specialization and body size

Habitat specialists were consistently at a higher risk of extinction. This relationship between habitat specialism and extinction risk has previously been observed in birds (Owens & Bennett, 2000), mammals (Gonzalez-Suarez *et al.*, 2013) and New Zealand lizards (Tingley *et al.*, 2013). Habitat specialists are likely to be at higher risk of extinction as they are less able to adapt to habitat changes or persist outside of their preferred habitat type (Reed & Shine, 2002) and due to the synergistic effects of narrow niche and small range size (Slayter *et al.*, 2013).

Larger species also had a higher risk of extinction, corroborating similar findings in mammals (Cardillo *et al.*, 2006), birds (Owens & Bennett, 2000) and New Zealand lizards (Tingley *et al.*, 2013). Large body size is correlated with traits related to slow life histories (e.g. low reproductive rates, late maturity in mammals; Bielby *et al.*, 2007) and low population densities and large home ranges, all of which have been shown to increase the risk of extinction (e.g., Davidson *et al.*, 2009). That few of the fecundity-related factors had any effects on extinction risk may relate to the fact that the vast majority of species were assessed under range-based criteria, rather than the more demographically related decline criteria of the IUCN.

### Environmental factors: accessibility of species ranges to humans

Accessibility of species range to humans was the best and most consistent environmental predictor of extinction risk. Species with ranges that are more accessible to humans have a greater risk of extinction because these regions are more likely to be affected by anthropogenic threats, such as habitat loss and exploitation. Alternatively, measures of accessibility may be negatively correlated with extinction risk, because higher accessibility may already have caused species susceptible to anthropogenic threats to become extinct. Because IUCN Red List assessments are likely to lag behind species declines, due to difficulties documenting declines in a timely fashion, this latter relationship is unlikely to be observed in our dataset. Instead, information on range accessibility may aid the assessment process by providing information on a number of the subconditions contained within criteria B and D2, namely the presence of continuing declines through anthropogenic pressures.

It has been argued that the inclusion of measures of human pressure would improve Red List assessments. Our results suggest that species experts may already incorporate some impression of human pressure into the assessment process, albeit in an unquantified manner. Accessibility, here estimated as travel time to cities of more than 50,000 people, appears to be a preferred measure to gauge human pressure on reptile species, while human population density performed worse overall. Accessibility also outperformed human population density in characterizing human pressures on the distribution of terrestrial vertebrates (Torres-Romero & Olalla-Tárraga, 2015). Explicitly incorporating quantitative data on human pressure into the IUCN Red List assessment process is likely to improve our judgement of the exposure of species to threats and hence better categorize their extinction risk, specifically given that the effect of human pressure becomes more important at smaller range sizes. Such data could be based on variables that are likely to covary with threats (e.g. distance to roads), directly measure habitat change for species threatened by habitat loss (e.g. deforestation; Hansen *et al.*, 2013) or measure changes in ecosystem condition (e.g. the IUCN Red List of Ecosystems; Rodriguez *et al.*, 2015).

### Threat-specific correlates and spatial pattern of extinction risk

Recent studies have highlighted the impact of threat types on the relationship between species traits and extinction risk (Gonzalez-Suarez *et al.*, 2013). Failing to take into account threat type may lead to a relatively low explanatory power of models in correlative studies of extinction risk (Cardillo *et al.*, 2008; Murray *et al.*, 2014).

In mammals, high extinction risk in species threatened by processes that directly affect survival (e.g. overexploitation) was associated with large body size and small litters, whilst high risk in species threatened by habitat-modifying processes was associated with habitat specialization (Gonzalez-Suarez *et al.*, 2013). In our study, habitat specialization was significantly correlated with extinction risk in species threatened by habitat loss, although body size and accessibility of species range were also significant. The addition of other threats (overhunting, invasive

species) did not yield any significant correlates of extinction risk. The high frequency of habitat loss compared with other threats within our sample overwhelmed the results, making it difficult to provide any insights into threat-specific correlates of extinction risk.

Because threats are not evenly distributed across space (e.g. habitat loss/exploitation in reptiles, Böhm *et al.*, 2013; forest loss, Hansen *et al.*, 2013), where a species occurs geographically may be as relevant to determining extinction risk as its specific biological traits. Although we found that extinction risk correlates for squamates varied among biogeographical realms, the same two traits were consistently correlated with extinction risk. Habitat specialists were at higher risk of extinction throughout the tropics, a pattern consistent with other studies (e.g. butterflies; Steffan-Dewenter & Tscharntke, 2000) and attributed to the prevalence of anthropogenic habitat loss in tropical regions (Devictor *et al.*, 2008). Some of our models retained significant spatial autocorrelation, suggesting that unexplained variation in our data may stem from underlying spatial processes.

### Improving assessments of extinction risk

With Red Listing of species often using qualitative rather than quantitative data on threats, discerning the cause of species declines is a complicated task, with assessors likely to list the most pervasive or obvious threats. Identifying causal factors of species declines is fraud with difficulties and requires greater research attention in order to elicit the most appropriate conservation response. With increased research attention on species-independent threat mapping, future assessments of extinction risk may rely on objective and readily available data sources on threats affecting our natural world (e.g. forest loss, Hansen *et al.*, 2013; climate change, IPCC, 2013; human encroachment via human footprint, CIESIN, 2005a,b).

While our results suggest a complex relationship between extinction-promoting factors, geographical location and threat processes, we have highlighted certain factors which act as correlates of extinction risk in addition to range size. Consolidating this information into extinction risk assessments and future modelling processes is paramount in order to make predictions of species status. Specifically, the additional factors highlighted in this study may help in the prediction of whether range-restricted species (and thus potential candidates for assessment under criteria B and D2) may ultimately be classed as threatened.

## CONCLUSIONS

Comparative studies can contribute to conservation prioritization by identifying species that possess extinction-promoting traits. Areas of relatively intact habitat are likely to be degraded in the near future, through increased accessibility and demand for natural resources. It is in these areas that currently non-threatened species may become threatened with extinction. Our global analysis of extinction risk in squamates revealed that biological (habitat specialism) and environmental factors (accessibility of a species' range to humans) are key to predicting high extinction risk in species assessed under range-based extinction risk criteria.

While it has been suggested that small-scale analyses may be more useful than global analyses for conservation (Fritz *et al.*, 2009), the general overall pattern remained the same among geographical, taxonomic and threat-specific data subsets. Predictive models of extinction risk have been proposed as a cost-effective solution for prioritizing and steering conservation compared with the current, often lengthy, assessment process (Bland *et al.*, 2015). There is a need for increased volume and accessibility of data on threats (particularly spatial data), which can inform extinction risk analyses and identify species at risk. This is particularly important for species groups such as reptiles for which adequate population information is traditionally lacking, and which greatly rely on knowledge of their distribution and the threats within their ranges. Additionally, we need to test quantitative approaches for predicting extinction risk on a wider number of squamate species, including DD species, in order to complement current efforts aimed at producing extinction risk assessments for the world's reptiles.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Species data.
**Appendix S2** Building the composite reptile phylogeny.
**Appendix S3** Additional results and discussion of extinction risk correlates.
**Appendix S4** Additional references in Supplementary Materials.
**Table S1** Species trait data included in the models of extinction risk.
**Table S2** Habitat and threat classification used by the IUCN.
**Table S3** Results from univariate phylogenetic generalized linear models of the effect of trait variables on extinction risk.
**Table S4** Significant correlations from bivariate phylogenetic generalized linear models of extinction risk, taking range size into account.
**Table S5** Results from bivariate phylogenetic generalized linear models of extinction risk for lizards and snakes.
**Table S6** Results from bivariate phylogenetic generalized linear models of extinction risk for species affected by habitat loss only.
**Table S7** Results from bivariate phylogenetic generalized linear models of extinction risk in six different geographical realms.
**Table S8** Minimum adequate models explaining extinction risk in squamates using the dated phylogeny.
**Table S9** Diagnostics of predictive performance of global minimum adequate model predicted versus observed values (non-dated phylogeny).

**Table S10** Diagnostics of predictive performance of global minimum adequate model predicted versus observed values (dated phylogeny).
**Table S11** Full model output for all six holdout models to test the minimum adequate model of extinction risk using the non-dated phylogeny.
**Table S12** Full model output for all six holdout models to test the minimum adequate model of extinction risk using the dated phylogeny.
**Table S13** Bivariate phylogenetic generalized linear model of extinction risk, including interactions with range size.
**Table S14** Minimum adequate models of extinction risk in squamates excluding range size.

## BIOSKETCH

The researchers involved in this analysis [the Indicators and Assessments Unit at the Zoological Society of London (http://www.zsl.org/indicators) and their collaborators at University College London, Stony Brook University, Universidad Nacional Autónoma de México and the University of Melbourne] share a common interest in understanding global change in biodiversity using extinction risk analyses, monitoring of global population trends and ecosystem-level studies.

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