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 those 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 of a representative sample of 1,139 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. Predictive power of our global models ranged between 23 and 29%. The general overall pattern remained the same among geographic, 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. Prioritising species that exhibit such traits could forestall extinction. Integration of data sources on human pressures,

67 such as accessibility of species ranges, may aid robust and time-efficient assessments of

68 species' extinction risk.

69

70 **INTRODUCTION**

71 To combat decline in biodiversity and prioritize conservation action, there is an urgent need

72 to identify species at risk of extinction. Identifying key correlates of risk and evaluating how

73 they vary across time, species and space is a central goal of conservation research, having

74 focussed on all vertebrate groups (e.g. Olden *et al.*, 2007; Sodhi *et al.*, 2008; Davidson *et al.*,

75 2009; Lee & Jetz, 2011), with the exception of reptiles.

76 What makes one species more prone to extinction than another is likely to vary

77 depending on biological traits and environmental factors. Habitat specialization, large body

78 size and small geographical range frequently correlate with increased extinction risk (Owens

79 & Bennett, 2000; Cardillo *et al.*, 2006). Higher annual precipitation, higher minimum

80 elevation and increased human population density can predict the susceptibility of species to

81 extinction (Cardillo *et al.*, 2004; Davies *et al.*, 2006; Luck, 2007; Tingley *et al.*, 2013). Such

82 analyses can help identify high-risk species and regions, thus establishing conservation

83 priorities (Murray *et al.*, 2014).

84 Certain traits may render species vulnerable to some threat processes but not others

85 (Murray *et al.*, 2014). Ignoring the identity and severity of threats acting on a species may

86 lead to relatively low explanatory power of models in correlative studies of extinction risk

87 (Isaac & Cowlishaw, 2004; Murray *et al.*, 2014). Bird species with high extinction risk

88 caused by overexploitation and invasive species had long generation times and large body

89 sizes, whilst extinction risk in species threatened by habitat loss was associated with habitat

90 specialization and small body sizes (Owens & Bennett, 2000).

91 Correlates of extinction risk may also vary across space. For example, the importance

92 of traits can vary among geographical scales: human population density is a significant

93 predictor of risk at a global scale, but is less consistent within geographical realms (Davies *et*

94 *al.*, 2006). It has been suggested that both regional and global analyses are required to

95 contribute to a better understanding of extinction risk patterns and their drivers (Davies *et al.*,

96 2006; Fritz *et al.*, 2009).

97 Reptiles have been neglected in global conservation prioritization due to the relative

98 paucity of data on their extinction risk. Some smaller-scale, regional studies have identified

99 correlates of heightened extinction risk in squamate reptiles (lizards, snakes and

100 amphisbaenids), such as small geographic range (Tingley *et al.*, 2013), ambush foraging and

101   lack of male-male combat (Reed & Shine, 2002), and large body size, habitat specialization

102   and high annual precipitation (Tingley *et al.*, 2013). However, a global analysis of extinction

103   risk correlates had so far not been possible due to a lack of consolidated data on reptile

104   extinction risk, distribution and life history. Recently, a global assessment of extinction risk

105   in a representative sample of 1,500 reptile species established that one-fifth of reptiles are

106   threatened with extinction, with proportion of threat highest in freshwater environments,

107   tropical regions and on oceanic islands (Böhm *et al.*, 2013).

108   Given the lack of population data for squamates, their extinction risk is primarily

109   based on restricted geographical range; for example, 82% of squamates were assessed under

110   IUCN Red List Criterion B (restricted geographic range) and 13% under Criterion D2 (very

111   restricted population) (Böhm *et al.*, 2013). This introduces circularity into correlative studies,

112   since geographic range size is likely to have the strongest effect on extinction risk. Previous

113   studies have dealt with this issue by producing an analysis of species not classified under the

114   two range-based criteria (e.g. Purvis *et al*., 2000; Cardillo *et al*., 2004). However, given the

115   lack of population and trend data for squamates, and thus the lack of extinction risk

116   assessments under population decline criteria, assessments of extinction risk correlates

117   greatly rely on establishing the significance of contributing factors in relation to range size.

118   Here, we build on this sampled assessment of reptile extinction risk to conduct the

119   first global phylogenetic comparative study of squamate extinction risk. We first identify

120   biological traits and environmental factors that correlate with elevated extinction risk. We

121   hypothesize that, in addition to a negative effect of range size: 1) biological traits such as

122   large body size and increased habitat specialisation are positively correlated with high

123   extinction risk; 2) environmental factors relating to increased human influence positively

124   correlate with extinction risk (Table 1). We conduct further analyses on the effects of threat

125   type, taxonomy and geography on extinction risk, and investigate the explanatory power of

126   extinction risk correlates relative to range size. We find range-restricted habitat specialists in

127   areas highly accessible to humans at a higher extinction risk, with practical implications for

128   the Red List assessment process and reptile conservation.

129

130   **METHODS**

131   **Data**

132   We obtained extinction risk data from a representative sample of 1,500 randomly selected

133   reptile species (Böhm *et al.*, 2013). We included all 1,139 non-Data Deficient squamate

134   species in our analyses [i.e. excluding species too data poor to allow an estimate of extinction

135   risk, an approach followed by previous authors (e.g. Purvis *et al.*, 2000; Cardillo *et al.*,

136   2004)]. Since Data Deficient (DD) species are likely to have traits which make their detection

137   difficult (e.g. small body/ range size, habitat specialism; Bland, 2014; Vilela *et al.*, 2014),

138   excluding DD species may bias our parameters towards the opposite end of the spectrum, i.e.

139   larger-bodied habitat generalists in more expansive ranges. However, because of existing data

140   gaps, it is beyond the scope of this paper to address issues of data deficiency.

141   IUCN Red List category (IUCN, 2001) provided our response variable of extinction

142   risk, a five-point scale from lowest (Least Concern = 1) to highest extinction risk (Critically

143   Endangered = 5) (e.g. Cardillo *et al.*, 2004). No species were classified as Extinct or Extinct

144   in the Wild.

145   Geographic range size (km^2) was calculated from freely available distribution maps

146   produced as part of the IUCN Red List assessment process (Böhm *et al.*, 2013). The

147   following biological traits were chosen as additional predictor variables based on hypotheses

148   derived from the literature (Table 1): degree of habitat specialisation (calculated as number of

149   habitat types a species occupies), body size/mass [maximum snout-vent-length (SVL, in

150   mm)], number of offspring per year, reproductive mode (viviparous, oviparous) and diet

151   (omnivore, herbivore, carnivore). Data were collected via literature searches, museum

152   specimens and input from species experts (Supplementary Materials). IUCN Red List

153   assessments record the habitats occupied by each species using a classification scheme of 103

154   habitat types, which we combined into 15 broader habitat categories (Supplementary

155   Materials). From this, we calculated number of habitats occupied by each species.

156   We tested the following environmental predictor variables, based on hypotheses

157   derived from the literature (Table 1): annual precipitation (in mm), annual temperature (˚C),

158   minimum elevation (Hijmans *et al.*, 2005), and Net Primary Productivity (NPP;

159   grams/m^2/year; Imhoff *et al.*, 2004). We also tested the following aggregate measures of the

160   level of human influence within a species range: human appropriation of NPP (HANPP,

161   measured as % of NPP; Imhoff *et al.*, 2004), mean human population density (HPD,

162   measured as people per km^2; CIESIN, 2005a), accessibility (measured as travel time to city

163   with more than 50,000 people; Nelson, 2008), and mean human footprint (Human Influence

164   Index, normalised per region and biome; CIESIN, 2005b). All extrinsic predictor variables

165   were extracted using ArcGIS 9.3, as the mean value across each species' range. We also

166   divided threat types recorded as part of the Red List assessments into five categories

167   (Salafsky *et al.*, 2008): habitat loss or disturbance, overexploitation, invasive species

168   introductions, climate change and pollution (Supplementary Material). We included threat

169 type, biogeographic realm and taxonomy (lizards, snakes) as additional variables in our

170 analyses.

171

Reptile phylogeny

173 We primarily relied on the dated phylogeny from Pyron *et al.* (2013), which contained 666 of

174 the species in our dataset (hereafter referred to as 'dated phylogeny'). From this, we built a

175 composite non-dated phylogeny (hereafter referred to as 'non-dated phylogeny') including all

176 1,139 species in our dataset, using Phylowidget (Jordan & Piel, 2008). We set all branch

177 lengths in our non-dated phylogeny to unity.

178   Most of the relationships between genera and families within our non-dated

179 phylogeny were derived from the molecular phylogeny by Pyron *et al.* (2013) and revised

180 using a more recent phylogeny on the origin of viviparity (Pyron & Burbrink, 2014).

181 Literature searches on phylogenetic relationships were carried out for species not included in

182 Pyron *et al.* (2013). Polytomies were assumed where relationships could not be resolved.

183 Studies based on morphological evidence were used only if phylogenies based on molecular

184 methods were unavailable. The final tree had 1,005 nodes and included a species of

185 *Sphenodon* as an out-group. The higher-level relationships were: (1) *Dibamidae* and

186 *Gekkonidae* near the base of the tree, (2) Scincoidea (*Scincidae*, *Cordylidae*, *Gerrhosauridae,*

187 *Xantusiidae*) as a sister group to all other squamates (except *Dibamidae* and *Gekkonidae*), (3)

188 Lacertoidea (*Lacertidae, Amphisbaenidae, Teiidae, Gymnophthalmidae*) as a sister group to

189 Toxifera (*Anguimorpha*, *Iguanidae,* Serpents). Lower-level relationships are detailed in the

190 Supplementary Materials.

191

Statistical analysis

193 Statistical analyses were carried out in R version 3.1.2 (R Core Team, 2014). Variables were

194 log-transformed to achieve normality. Phylogenetic relationships between species may

195 violate assumptions about independence of character traits, so that trait-based models of

196 extinction risk need to control for shared ancestry (Freckleton *et al.*, 2002). We followed

197 Revell (2010) and simultaneously estimated phylogenetic signal (Pagel's λ, using maximum

198 likelihood) and regression model, an approach which has been shown to outperform

199 equivalent non-phylogenetic approaches. We implemented this using phylogenetic

200 generalized linear models (pGLS) in the R package 'caper' (Orme *et al.*, 2012).

201   To overcome circularity in our data introduced by range size, we ran a number of

202 analyses, summarised in Figure 1A. 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. = 1,136, 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 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 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 (Figure 1B). First, we reconstructed MAMs of extinction risk excluding range size, to compare model performance and determine 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 of range size and other explanatory variables to extinction risk. 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 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 data set consisting of the world minus one biogeographical realm (e.g. creating a calibration data set containing all but Afrotropical species, a second calibration data set containing all but Australasian species, etc.). Using these calibration data sets, 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 (MSEp = $\Sigma((O - P)^2/N)$), bias (mean of the difference between observed and predicted extinction risk squared), percentage bias (%bias = 100 x bias/MSEp) and percentage error of prediction

236 (%error = $100*\text{sqrt}(MSEp)/\text{mean}_{EX}$, where mean_{EX} is the average extinction risk in the

237 predicted dataset).

238   We conducted further pGLS on subsets of data, based on biogeographical realm,

239 taxonomy and threats, to assess the robustness of trends detected in the complete dataset

240 (Figure 1A). For biogeographical realms, we created six subsets, containing species solely

241 present in one of six realms (following Olson *et al.*, 2001): Afrotropical, Australasian,

242 Indomalayan, Nearctic, Neotropical and Palearctic. We excluded the Oceanian realm from

243 the analysis as only seven species in our sample were from that region. We analysed two

244 taxonomic groups separately: lizards (702 species) and snakes (423 species). We split the

245 data into three threat categories: species affected by habitat loss alone (405 species), species

246 affected by habitat loss and overexploitation (56 species), and species affected by habitat loss

247 and invasive species (49 species). Threats of invasive species and overexploitation were

248 considered in conjunction with habitat loss, because too few species were affected by

249 invasive species or overexploitation alone to allow for meaningful statistical analysis. We

250 conducted bivariate pGLS accounting for range size and MAMs separately for each data

251 subset, as well as variance partitioning as described above.

252   All analyses were run using both the dated and non-dated phylogeny to assess

253 whether the results obtained from the two phylogenies were sufficiently similar. Where

254 multiple hypotheses were tested simultaneously, i.e. in MAMs, we corrected for possible

255 inflation of Type I errors using Bonferroni corrections of *p* values.

256

257 **Species trait mapping**

258 To investigate the spatial distribution of risk-promoting traits, we used an assemblage-based

259 approach (Olalla-Tarraga *et al.*, 2006) to produce global distribution maps for variables

260 significantly correlated with extinction risk. For each trait, we overlaid a hexagonal grid onto

261 the stacked species' distributions and calculated for each grid cell the average trait value for

262 species present in the cell. The grid used was defined on an icosahedral, projected to the

263 sphere using the inverse Icosahedral Snyder Equal Area (ISEA) projection to account for the

264 Earth's spherical nature. Each grid cell was approximately 23,000 km^2. We conducted the

265 analysis using Hawth's Tools for ArcGIS 9.3 (Beyer, 2004).

266

267 **RESULTS**

268 Because results are broadly similar between analyses, here we only report results using the

269 non-dated phylogeny (to maximise sample size), primarily focussing on MAMs as these

270   models best account for shared content among variables. All other results are reported in the

271   Supplementary Materials.

272

273   **Global correlates of squamate extinction risk**

274   The MAM accounted for 39% of the total variance (Table 2), suggesting that species were at

275   a greater risk of extinction if they were habitat specialists ($t = -4.5$, d.f. = 951, p<0.001), had

276   large maximum SVLs ($t = 2.2$, d.f. = 951, p<0.05) and occupied more accessible range areas

277   ($t = -3.8$, d.f. = 951, p<0.001). Maximum SVL was no longer significant after Bonferroni

278   correction, and model residuals remained significantly spatially autorcorrelated (Moran $I =$

279   7.2, p < 0.001).

280

281   *Effect of range size*

282   When excluding range size from MAM construction, accessibility and number of habitats

283   remained the most significant effects in addition to body size, with NPP also contributing

284   (Table S13). The model only explained 14.6% of variation in the data compared to 39%

285   explained by the full MAM.

286   Range size was the largest contributing factor to extinction risk in reptiles (Figure 2).

287   Range size (c in Figure 2) contributed between 24 and 47% of variation in extinction risk to

288   our models. Additional variables within MAMs (a in Figure 2) never contributed more than

289   10% independently to extinction risk, and had the greatest contribution of nearly 10% in the

290   Nearctic model (accessibility is the sole explanatory variable). The combined contribution (b

291   in Figure 2) of range size and other explanatory variables varied between models, and was

292   particularly large for the Australasian MAM. Unexplained variance was largest in nearly all

293   models, with the exception of the Australasian realm model, where range size (c), combined

294   variables (b), and unexplained variation (d) contributed to nearly equal parts.

295   Range size interacted significantly with all other factors, with the most significant

296   interactions with accessibility, number of habitats, and number of threats (Table 4).

297   Accessibility lost its negative effect slowly as range size increased (i.e. closer proximity to

298   population centres causes higher extinction risk at smaller range sizes). Similarly, habitat

299   specialism was negatively related with extinction risk when range size was very small

300   (species occupying fewer habitats have higher extinction risk), though again this effect

301   diminished as range area increased. Interestingly, at low NPP, range area had a positive effect

302   on extinction risk though this effect diminished as NPP increased, suggesting a complex

303   interplay between NPP and range area.

9

Predictive ability of global models

Mean square error of prediction ranged from 0.11 to 0.18, bias from <0.001 to 0.003 and percentage bias from 0.02 to 1.55 for our MAM. Percentage error of prediction was broadly similar across realms, ranging between 23% and 29% (Figure 3). Prediction error was highest for the Indomalayan realm and lowest for the Australasian realm.

Taxonomic, geographic and threat variation in correlates of extinction risk

Geographical realm

Habitat specialism significantly correlated with high extinction risk in the Afrotropics and Neotropics, while accessibility was an important factor in the Afrotropics, Australasia and the Nearctic (Table 3). Explanatory power of MAMs varied greatly between biogeographical realms, from 70% of variation explained in the Australasian realm to 29% in both Nearctic and Palearctic 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 Palearctic 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 I = -0.6, p = 0.72; Indomalayan: Moran I = 1.3, p = 0.10; Nearctic: Moran I = 0.01, p = 0.50; Palearctic: Moran I = 0.7, p = 0.23), but not all (Afrotropical: Moran I = 4.0, p<0.001; Neotropical: Moran 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 (Figure 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 (Figure 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 3). There was no significant MAM for snakes.

338

Threat type

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 3). For species threatened by habitat loss with additional threats of overexploitation or invasive species, none of the traits were significant.

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 high extinction risk lags behind other species groups (Böhm *et al.*, 2013). Understanding how biological traits and environmental factors interact with threats may help predict extinction risk of species and fill knowledge gaps. Our study suggests 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 to assess 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 reptile extinction risk (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 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

372 extinction risk towards smaller range sizes, and may help inform extinction risk assessments
373 and models in future.

374

Biological traits: habitat specialization and body size

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

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

392

Environmental factors: accessibility of species ranges to humans

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

It has been argued that 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 overall worse. Accessibility also outperformed human population density to characterize 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 assessments process is likely to improve our judgement of the exposure of species to threats and hence better categorise 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 co-vary 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., 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 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 directly affecting survival (e.g., overexploitation) was associated with large body sizes 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 to other threats within our sample overwhelmed the results, making it difficult to provide any insights into threat-specific extinction risk correlates.

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). Most of our models retained significant spatial autocorrelation suggesting that unexplained variation in our data may stem from underlying spatial processes.

Improving extinction risk assessments

With Red Listing of species often using qualitative rather than quantitative data on threats, discerning the cause of species declines presents 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) etc.].

While our results suggest a complex relationship between extinction-promoting factors, geographic 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 species range to humans) are key to predicting high extinction risk in species assessed under range-based extinction risk criteria.

473   While it has been suggested that small-scale analyses may be more useful than global

474   analyses for conservation (Fritz *et al.*, 2009), the general overall pattern remained the same

475   among geographic, taxonomic and threat-specific data subsets. Predictive models of

476   extinction risk have been proposed as a cost-effective solution for prioritising and steering

477   conservation compared to the current, often lengthy, assessment process (Bland *et al.* 2015).

478   There is a need for increased volume and accessibility of data on threats (particularly spatial

479   data), which can inform extinction risk analyses and identify species at risk. This is

480   particularly important for species groups such as reptiles for which adequate population

481   information is traditionally lacking, and which greatly rely on knowledge of their distribution

482   and the threats within their ranges. Additionally, we need to test quantitative approaches for

483   predicting extinction risk on a wider number of squamate species, including Data Deficient

484   species, in order to complement current efforts aimed at producing extinction risk

485   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 at the

publisher's web-site. The data and composite phylogeny used in these analyses will be

archived in the Dryad digital repository.

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 model of extinction risk, taking range size into account

Table S5. Results from bivariate phylogenetic generalized linear model of extinction risk for lizards and snakes

Table S6. Results from bivariate phylogenetic generalized linear model of extinction risk for species affected by habitat loss only

Table S7. Results from bivariate phylogenetic generalized linear model 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 (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 minimum adequate model of extinction risk using the non-dated phylogeny

Table S12. Full model output for all six holdout models to test 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

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673 **Biosketch**

674 The researchers involved in this analysis (the Indicators and Assessments Unit at the

675 Zoological Society of London (http://www.zsl.org/indicators) and their collaborators at

676 University College London, Stony Brook University, Universidad Nacional Autónoma de

677 México and The University of Melbourne) share their interest in understanding global change

678 in biodiversity using extinction risk analyses, monitoring of global population trends and

679 ecosystem-level studies.

1 **Tables.**

2 **Table 1.** Hypotheses on the relationship between intrinsic and extrinsic factors, and

3 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 & 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 (SVL)	+	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/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 vs 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)

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5

1   **Table 1.** continued.

Factor	Variables in analysis	Prediction	Justification	Interaction with threats	References
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 (NPP)	+	Higher productivity suggests potentially higher human disturbance and impact		(Luck, 2007)
Human impact	1. Human appropriation of net primary productivity (HANPP) 2. Human population density (HPD) 3. Human footprint 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)

1 **Table 2.** Minimally adequate models explaining extinction risk in squamates using the non-
2 dated phylogeny. No.: number of; SVL: snout-vent length; λ: Pagel's lambda. Uncorrected
3 (p) and Bonferroni adjusted (p corr) *p* values are shown.

Non-dated phylogeny							
	Coefficient	S.E.	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. habitats	-0.110	0.025	-4.4	<0.001	<0.001		
Maximum SVL	0.028	0.013	2.2	0.026	0.105		

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Table 3. Minimally adequate models explaining extinction risk in squamates using subsets of
the data based on A) biogeographic realm, B) taxonomy, C) threat type. Note that predictors
of extinction risk vary among biogeographic realms, and between lizards and snakes. No.:
number of; SVL: snout-vent length; λ: Pagel's lambda. Non-dated phylogeny only.

A) Biogeographic realm

Afrotropical	Coefficient	S.E.	t	p	Model r^2	λ
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. habitats	-0.130	0.055	-2.4	0.020		
Taxonomy: snake	0.145	0.064	2.3	0.025		
Australasian	Coefficient	S.E.	t	p	Model r^2	λ
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		
Invasives	0.231	0.099	2.3	0.023		
Indomalayan	Coefficient	S.E.	t	p	Model r^2	λ
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		
Invasives	-0.328	0.176	-1.9	0.065		
Nearctic	Coefficient	S.E.	t	p	Model r^2	λ
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	Coefficient	S.E.	t	p	Model r^2	λ
Intercept	1.378	0.077	17.9	<0.001	0.386	0.000
Range size	-0.099	0.007	-14.1	<0.001		

No. habitats	-0.106	0.045	-2.3	0.020		
Palearctic	Coefficient	S.E.	t	p	Model r²	λ
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

Lizards	Coefficient	S.E.	t	p	Model r²	λ
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. habitats	-0.168	0.031	-5.4	<0.001		
Maximum SVL	0.071	0.030	2.3	0.019		
Snakes	Coefficient	S.E.	t	p	Model r²	λ
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

Habitat loss	Coefficient	S.E.	t	p	Model r²	λ
Intercept	2.031	0.180	11.3	<0.001	0.506	0.000
Range size	-0.128	0.009	-14.7	<0.001		
No. 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		

1

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1 **Table 4.** Bivariate phylogenetic generalized linear model of extinction risk, including
2 interactions of predictors with geographical range size. Here we show results of the three
3 most significant variables: accessibility, number of habitat types and net primary productivity
4 (NPP) (for all results, see Supplementary Materials). λ: Pagel's lambda. Non-dated
5 phylogeny only.

Accessibility

	Coefficient	S.E.	t	p	Model r^2	λ
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		

Number of habitats

	Coefficient	S.E.	t	p	Model r^2	λ
Intercept	1.730	0.062	27.9	<0.001	0.412	0.000
Range size	-0.130	0.006	-22.5	<0.001		
No. habitats	-0.835	0.085	-9.9	<0.001		
Range size * no. habitats	0.065	0.007	9.1	<0.001		

NPP

	Coefficient	S.E.	t	p	Model r^2	λ
Intercept	-6.410	1.419	-4.5	<0.001	0.316	0.012
Range size	0.464	0.121	3.8	<0.001		
NPP	0.291	0.053	5.4	<0.001		
Range size * NPP	-0.021	0.005	-4.6	<0.001		

6

7

Figure legends

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 phylogeny.

Figure 2. Variance partitioning for all minimum adequate models (MAM) of extinction risk (global, and by geographical, taxonomic 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 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 and 3). Biogeographical subsets: AFR – Afrotropical; AUS – Australasian; IND – Indomalayan; NE – Nearctic; NEO – Neotropical.
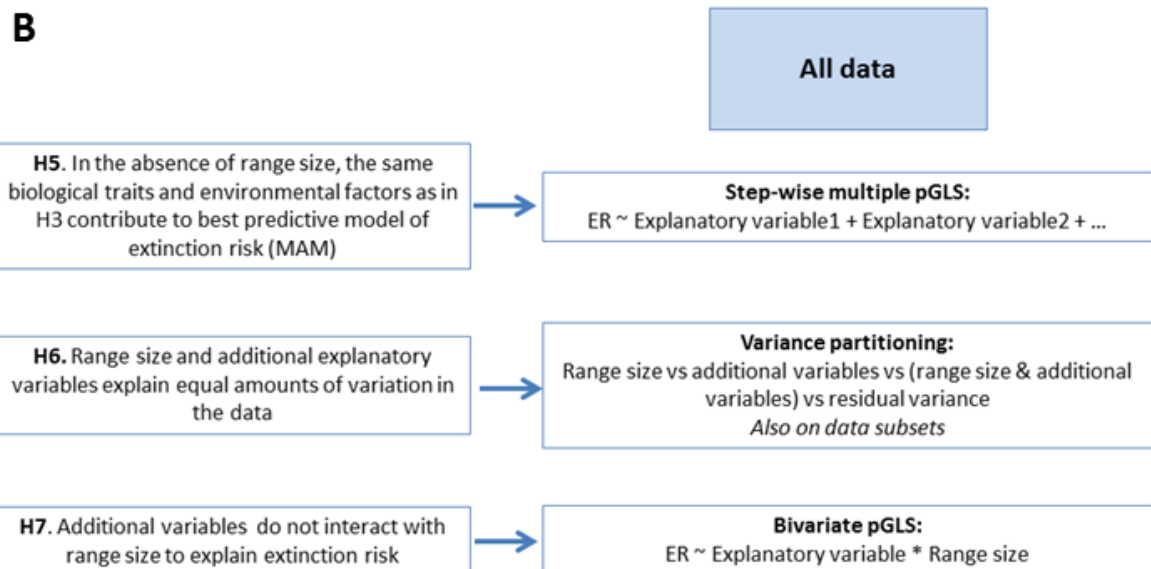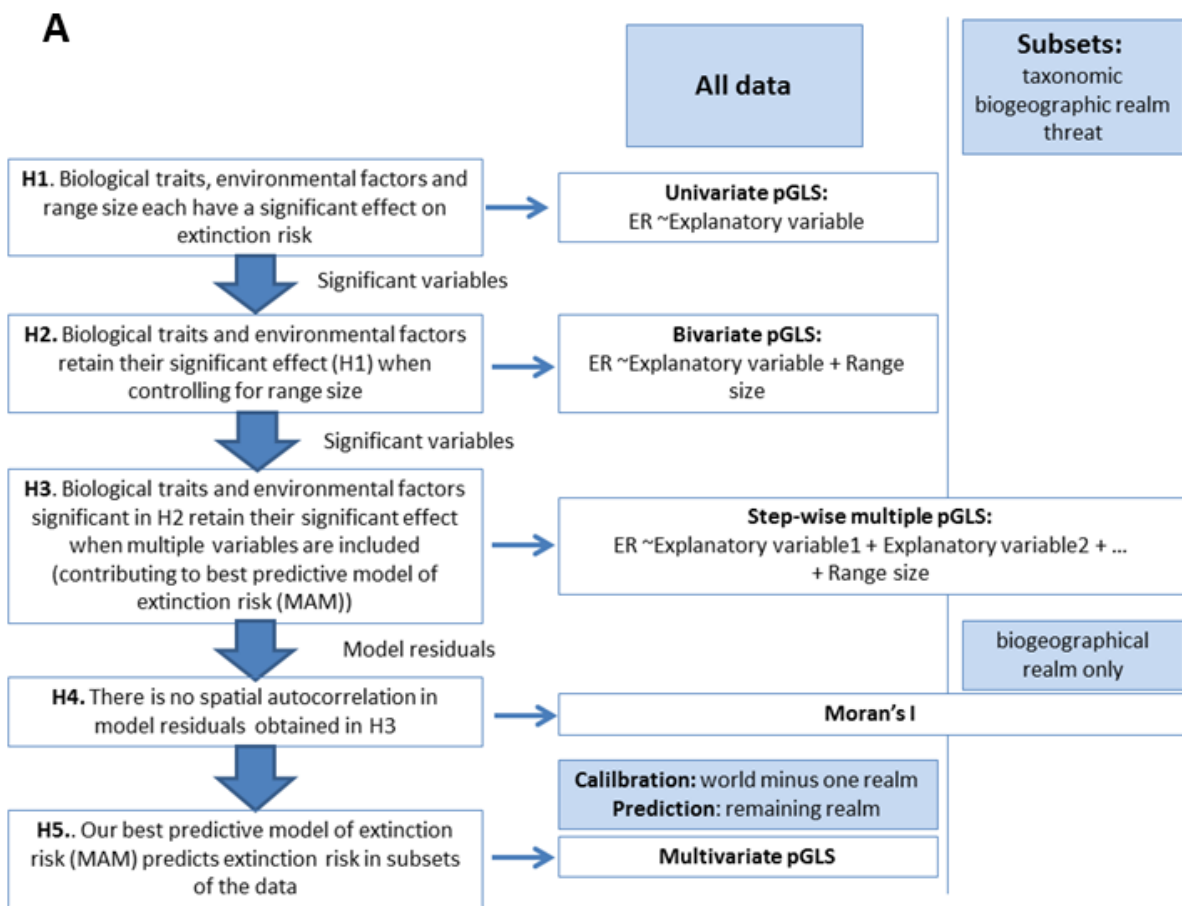
Figure 3. Observed versus predicted log Red List status derived from holdout models (the global model containing all species minus those from the stated biogeographical realm) predicting Red List status for the remaining (held out) biogeographical realm: A – Afrotopical (%error of prediction = 23.6); B – Australasian (%error = 23.6); C – Indomalayan (%error = 29.0); D – Nearctic (%error = 27.6); E – Neotropical (%error = 25.7); F – Palearctic (%error = 27.1). Full diagnostics for each model are given in the Supplementary Materials (Table S9).

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.
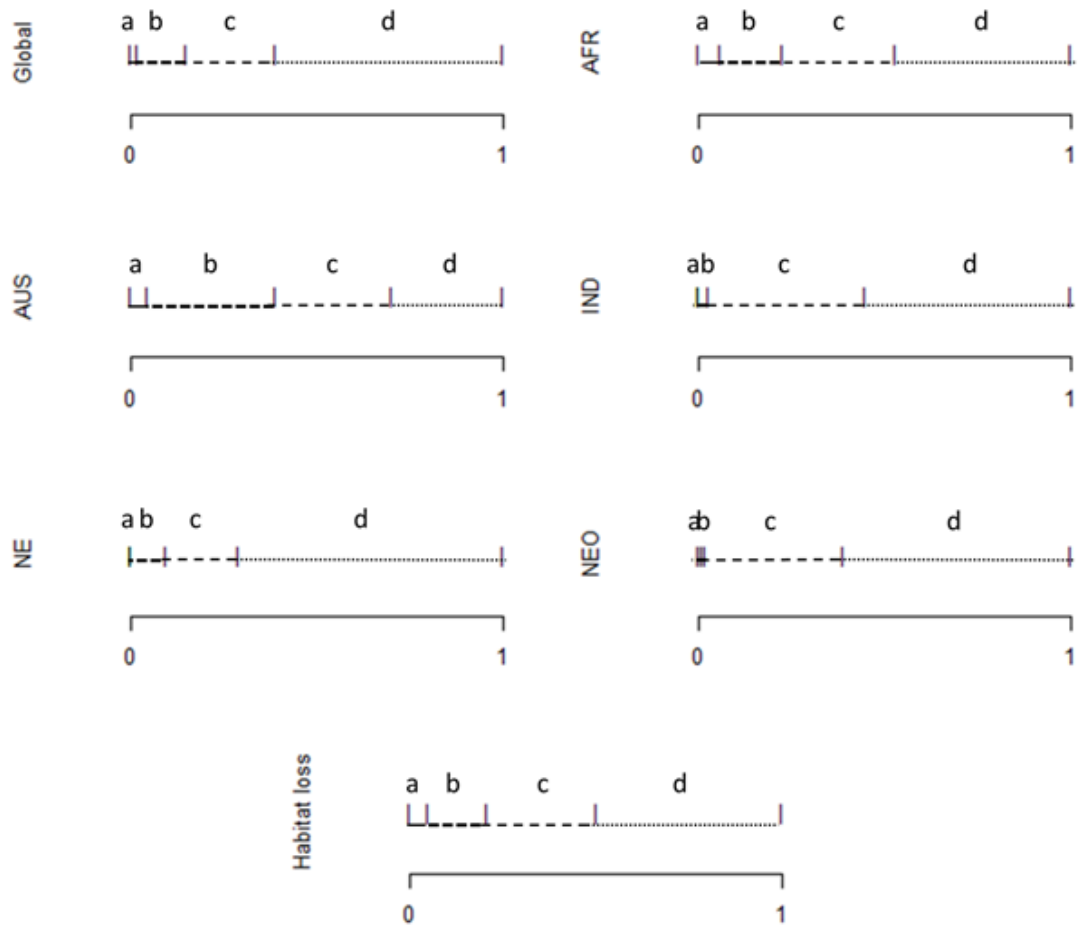
Figure 1.

1   **Figure 2.**
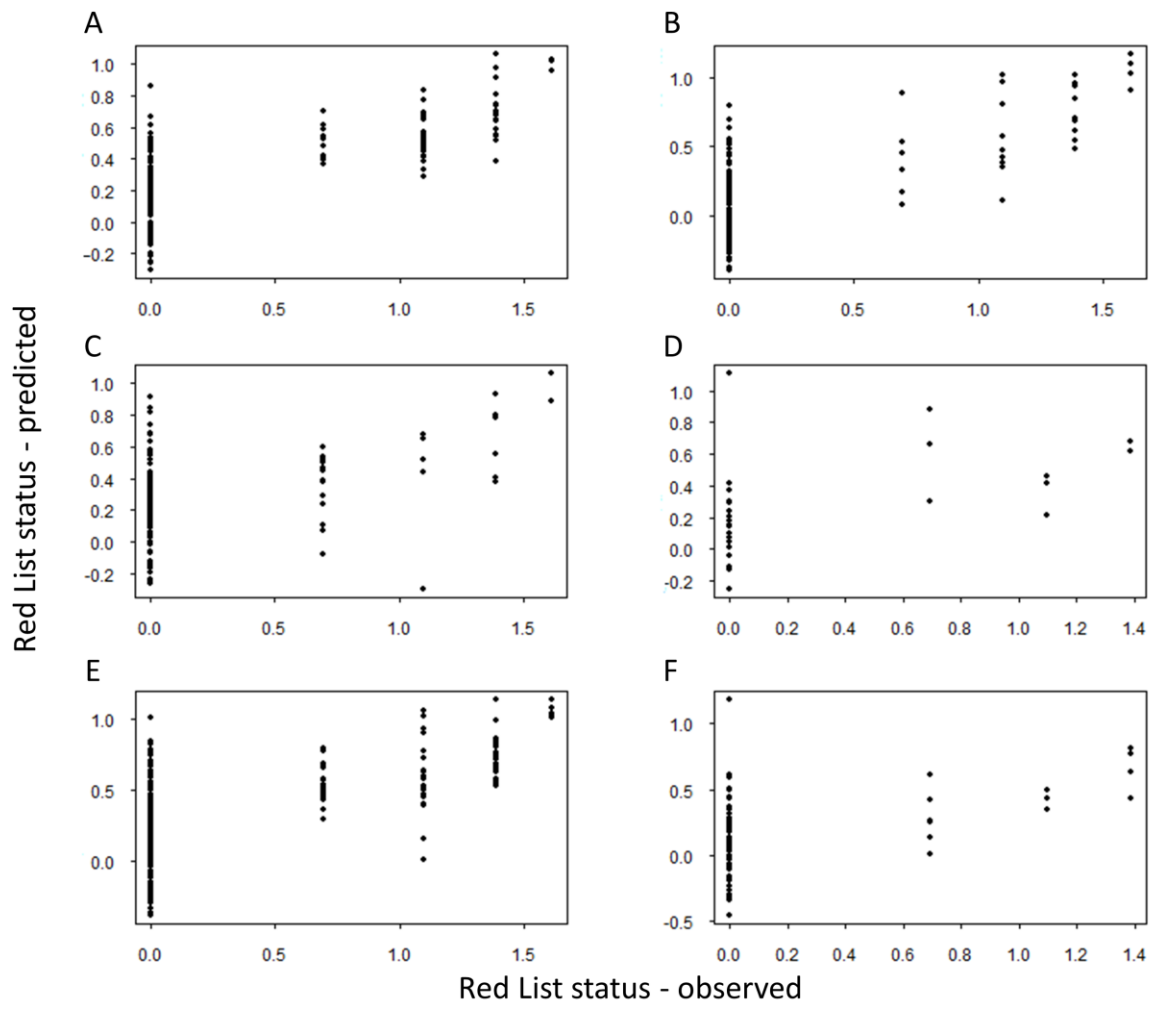

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1   **Figure 3.**
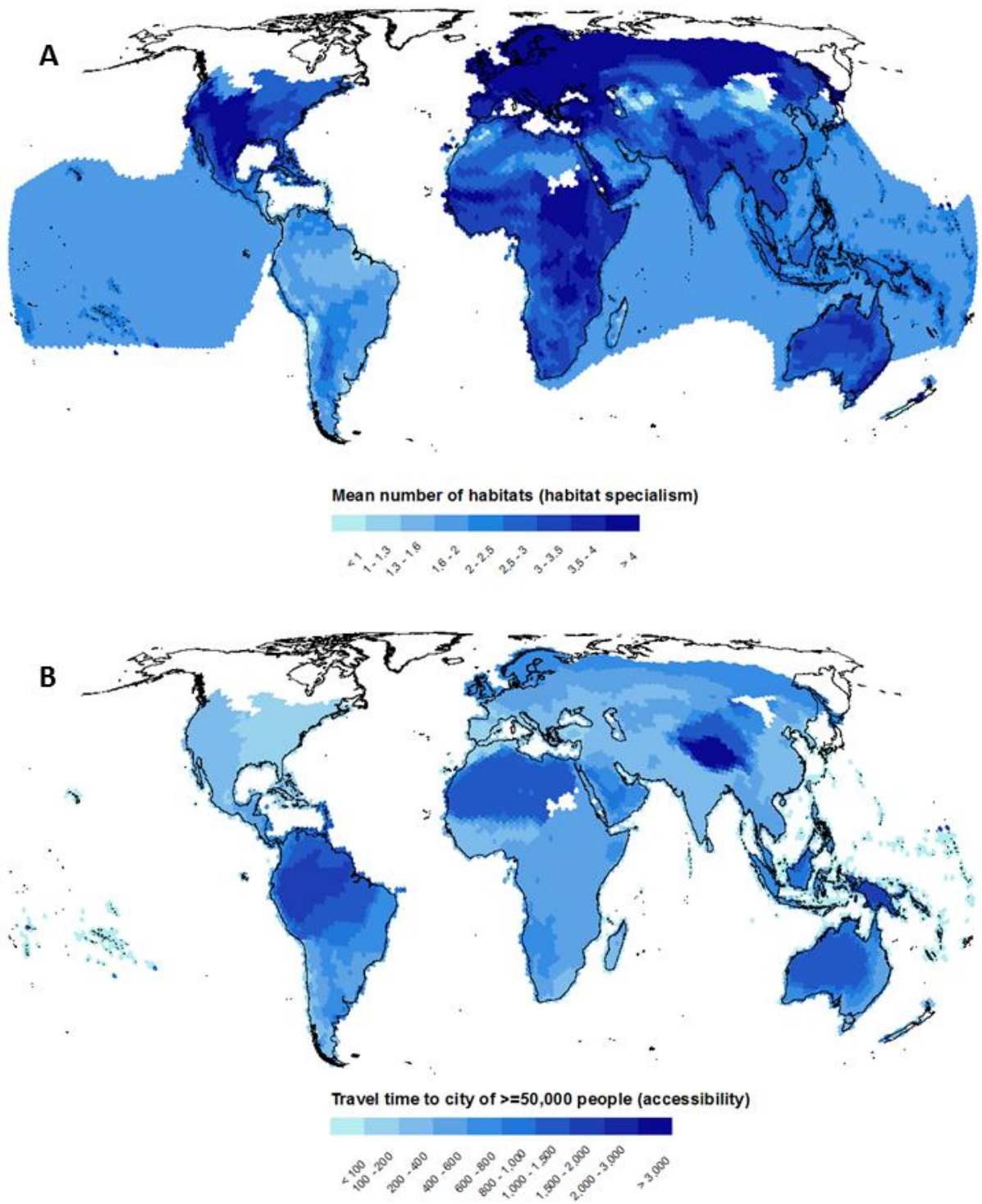
Figure 4.

Mean number of habitats (habitat specialism)

<1 1 - 1.3 1.3 - 1.6 1.6 - 2 2 - 2.5 2.5 - 3 3 - 3.5 3.5 - 4 > 4

Travel time to city of >=50,000 people (accessibility)

< 100 100 - 200 200 - 400 400 - 600 600 - 800 800 - 1,000 1,000 - 1,500 1,500 - 2,000 2,000 - 3,000 > 3,000

2