

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

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34 **Abstract**

35 **Aim**

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

43

44 **Location**

45 Global.

46

47 **Methods**

48 We collected data on biological traits and environmental factors of a representative sample of
49 1,139 species of squamate reptiles. We used phylogenetically controlled regression models to
50 identify: general correlates of extinction risk; threat-specific correlates of risk; and realm-
51 specific correlates of risk. We also assessed the relative importance of range size versus other
52 factors through multiplicative bivariate models, partial regressions and variance partitioning.

53

54 **Results**

55 Range size was the most important predictor of extinction risk, reflecting the high frequency
56 of reptiles assessed under range-based IUCN criteria. Habitat specialists occupying accessible
57 ranges were at a greater risk of extinction: although these factors never contributed more than
58 10% to the variance in extinction risk, they showed significant interactions with range size.
59 Predictive power of our global models ranged between 23 and 29%. The general overall
60 pattern remained the same among geographic, taxonomic and threat-specific data subsets.

61

62 **Main conclusions**

63 Proactive conservation requires shortcuts to identify species at high risk of extinction.
64 Regardless of location, squamate reptiles that are range-restricted habitat specialists living in
65 areas highly accessible to humans are likely to become extinct first. Prioritising species that
66 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 & Cowlshaw, 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 al.*
94 *et 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 (km²) 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/m²/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 km²; 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

172 **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

192 **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

203 extinction risk, confirming that range size was the most significant predictor of risk (dated
204 phylogeny: $t = -16.2$, d.f. = 664, $r^2 = 0.28$, $p < 0.001$; non-dated phylogeny: $t = -25.0$, d.f. =
205 1,136, $r^2 = 0.35$, $p < 0.001$). Next, we conducted bivariate additive pGLS of each explanatory
206 variable in turn on extinction risk, including range size as the second variable to control for
207 its effect. Finally, we carried out stepwise multiple regressions, in which variables that caused
208 the most significant increase in explanatory power of the model were added one at a time to
209 produce minimum adequate models (MAMs). To test whether spatial effects remained within
210 our model, possibly contributing to variation within the data, we checked our model residuals
211 for spatial autocorrelation using Moran's I in the package 'spdep' (Bivand *et al.*, 2015) by
212 defining spatial location of each residual as the range mid-point of the corresponding species.

213 To disentangle the influence of range size on extinction risk in MAMs, we carried out
214 three additional analyses (Figure 1B). First, we reconstructed MAMs of extinction risk
215 excluding range size, to compare model performance and determine most significant
216 predictors in the absence of our range size metric. Second, we performed partial regressions
217 of extinction risk using two sets of explanatory variables: range size, and all other significant
218 explanatory variables remaining in the MAMs. The resulting variance partitioning (Legendre
219 & Legendre, 1998) for each MAM shows the shared variance between range size and other
220 explanatory variables, as well as independent contributions of range size and other
221 explanatory variables to extinction risk. Variance partitioning was run in the R package
222 'vegan' (Oksanen *et al.*, 2015). Third, for each variable remaining in the MAM, we tested for
223 interactions with range size using multiplicative bivariate pGLS to check whether the
224 relationship between each significant variable changed with range size (i.e. whether once a
225 species is range-restricted, additional factors increase in importance to decide whether a
226 range-restricted species is threatened or not).

227 Finally, to investigate the predictive ability of our global MAM, we re-ran our
228 analysis on a calibration data set consisting of the world minus one biogeographical realm
229 (e.g. creating a calibration data set containing all but Afrotropical species, a second
230 calibration data set containing all but Australasian species, etc.). Using these calibration data
231 sets, we then used the global MAM (minus the realm) to predict the outcome for the
232 remaining biogeographical realm. We diagnosed predictive performance of the MAM versus
233 observed values using four metrics: mean squared error of prediction ($MSEp = \Sigma((O -$
234 $P)^2/N)$), bias (mean of the difference between observed and predicted extinction risk
235 squared), percentage bias ($\%bias = 100 \times bias/MSEp$) and percentage error of prediction

236 ($\%error = 100 * \sqrt{MSEp} / \text{mean}_{EX}$, 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 km². 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 autocorrelated (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.

304

305 *Predictive ability of global models*

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

310

311 **Taxonomic, geographic and threat variation in correlates of extinction risk**

312 *Geographical realm*

313 Habitat specialism significantly correlated with high extinction risk in the Afrotropics and
314 Neotropics, while accessibility was an important factor in the Afrotropics, Australasia and the
315 Nearctic (Table 3). Explanatory power of MAMs varied greatly between biogeographical
316 realms, from 70% of variation explained in the Australasian realm to 29% in both Nearctic
317 and Palearctic realms. Threat type was significant in the Indomalayan and Australasian
318 MAMs, with overharvesting increasing extinction risk in both realms, and invasive species
319 increasing extinction risk in the Australasian realm. In the Afrotropical realm, snakes had a
320 higher extinction risk than lizards. The Palearctic MAM only contained range size as a
321 predictor. Geographical subsetting of the data helped to remove spatial autocorrelation in
322 some of the subsets (Australasia: Moran $I = -0.6$, $p = 0.72$; Indomalayan: Moran $I = 1.3$, $p =$
323 0.10 ; Nearctic: Moran $I = 0.01$, $p = 0.50$; Palearctic: Moran $I = 0.7$, $p = 0.23$), but not all
324 (Afrotropical: Moran $I = 4.0$, $p < 0.001$; Neotropical: Moran $I = 6.0$, $p < 0.001$).

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

332

333 *Taxonomic subsets*

334 The MAM for lizards accounted for 41% of the total variance. Lizards were at a greater risk
335 of extinction if they were habitat specialists ($t = -5.4$, d.f. = 653, $p < 0.001$), had accessible
336 range areas ($t = -4.1$, d.f. = 653, $p < 0.001$) and large maximum SVLs ($t = 2.4$, d.f. = 653,
337 $p < 0.05$) (Table 3). There was no significant MAM for snakes.

338

339 *Threat type*

340 Number of habitat types ($t = -4.5$, d.f. = 360, $p < 0.001$), maximum SVL ($t = 3.3$, d.f. = 360,
341 $p < 0.001$) and accessibility ($t = -3.5$, d.f. = 360, $p < 0.001$) were significant factors in the MAM
342 for species affected by habitat loss, which accounted for 51% of the total variance (Table 3).
343 For species threatened by habitat loss with additional threats of overexploitation or invasive
344 species, none of the traits were significant.

345

346 **DISCUSSION**

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

354

355 **IUCN Red List assessments and the importance of range size**

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

365 Small range size alone is insufficient to class a species as threatened, so that range-
366 based IUCN criteria incorporate additional symptoms of threat (criterion B: severe
367 fragmentation, occurrence in only few locations, continuing decline in population
368 size/habitat/range or extreme fluctuations; criterion D2: presence of a plausible future threat)
369 (Mace *et al.*, 2008). Factors influencing extinction risk in addition to range size may explain
370 why one range-restricted species is at a higher risk of extinction than another. In this study,
371 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

375 **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

393 **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.

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

420

421 **Threat-specific correlates and spatial pattern of extinction risk**

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

426 In mammals, high extinction risk in species threatened by processes directly affecting
427 survival (e.g., overexploitation) was associated with large body sizes and small litters, whilst
428 high risk in species threatened by habitat-modifying processes was associated with habitat
429 specialization (Gonzalez-Suarez *et al.*, 2013). In our study, habitat specialization was
430 significantly correlated with extinction risk in species threatened by habitat loss, although
431 body size and accessibility of species range were also significant. The addition of other
432 threats (overhunting, invasive species) did not yield any significant correlates of extinction
433 risk. The high frequency of habitat loss compared to other threats within our sample
434 overwhelmed the results, making it difficult to provide any insights into threat-specific
435 extinction risk correlates.

436 Because threats are not evenly distributed across space [e.g. habitat loss/exploitation
437 in reptiles, Böhm *et al.* (2013); forest loss, Hansen *et al.* (2013)], where a species occurs
438 geographically may be as relevant to determining extinction risk as its specific biological

439 traits. Although we found that extinction risk correlates for squamates varied among
440 biogeographical realms, the same two traits were consistently correlated with extinction risk.
441 Habitat specialists were at higher risk of extinction throughout the tropics, a pattern
442 consistent with other studies (e.g., butterflies; Steffan-Dewenter & Tschardtke, 2000) and
443 attributed to the prevalence of anthropogenic habitat loss in tropical regions (Devictor *et al.*,
444 2008). Most of our models retained significant spatial autocorrelation suggesting that
445 unexplained variation in our data may stem from underlying spatial processes.

446

447 **Improving extinction risk assessments**

448 With Red Listing of species often using qualitative rather than quantitative data on threats,
449 discerning the cause of species declines presents a complicated task, with assessors likely to
450 list the most pervasive or obvious threats. Identifying causal factors of species declines is
451 fraught with difficulties and requires greater research attention in order to elicit the most
452 appropriate conservation response. With increased research attention on species-independent
453 threat mapping, future assessments of extinction risk may rely on objective and readily
454 available data sources on threats affecting our natural world [e.g., forest loss (Hansen *et al.*,
455 2013), climate change (IPCC, 2013), human encroachment via human footprint (CIESIN,
456 2005a, b) etc.].

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

464

465 **Conclusions**

466 Comparative studies can contribute to conservation prioritization by identifying species that
467 possess extinction-promoting traits. Areas of relatively intact habitat are likely to be degraded
468 in the near future, through increased accessibility and demand for natural resources. It is in
469 these areas that currently non-threatened species may become threatened with extinction. Our
470 global analysis of extinction risk in squamates revealed that biological (habitat specialism)
471 and environmental factors (accessibility of species range to humans) are key to predicting
472 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.

486

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491

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639 **Supporting Information**

640 Additional supporting information may be found in the online version of this article at the
641 publisher's web-site. The data and composite phylogeny used in these analyses will be
642 archived in the Dryad digital repository.

643 **Appendix S1.** Species data

644 **Appendix S2.** Building the composite reptile phylogeny

645 **Appendix S3.** Additional results and discussion of extinction risk correlates

646 **Appendix S4.** Additional references in Supplementary Materials

647 **Table S1.** Species trait data included in the models of extinction risk

648 **Table S2.** Habitat and threat classification used by the IUCN

649 **Table S3.** Results from univariate phylogenetic generalized linear models of the effect of trait
650 variables on extinction risk

651 **Table S4.** Significant correlations from bivariate phylogenetic generalized linear model of
652 extinction risk, taking range size into account

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

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

657 **Table S7.** Results from bivariate phylogenetic generalized linear model of extinction risk in
658 six different geographical realms

659 **Table S8.** Minimum adequate models explaining extinction risk in squamates using the dated
660 phylogeny

661 **Table S9.** Diagnostics of predictive performance of global minimum adequate model
662 predicted versus observed values (dated phylogeny)

663 **Table S10.** Diagnostics of predictive performance of global minimum adequate model
664 predicted versus observed values (dated phylogeny)

665 **Table S11.** Full model output for all six holdout models to test minimum adequate model of
666 extinction risk using the non-dated phylogeny

667 **Table S12.** Full model output for all six holdout models to test minimum adequate model of
668 extinction risk using the dated phylogeny

669 **Table S13.** Bivariate phylogenetic generalized linear model of extinction risk, including
670 interactions with range size

671 **Table S14.** Minimum adequate models of extinction risk in squamates excluding range size

672

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
<i>Intrinsic factors</i>					
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 <i>et al.</i> , 2000; Cardillo <i>et al.</i> , 2008)
Island endemism	Categorical: Island- or mainland-dwelling	+	Island endemics have smaller ranges & populations	Invasive species	(Purvis <i>et al.</i> , 2000)
Habitat specialism	Number of habitats occupied	-	Habitat specialists are at higher risk of extinction	Habitat loss	(Owens & Bennett, 2000; Gonzalez-Suarez <i>et al.</i> , 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 <i>et al.</i> , 2008; Gonzalez-Suarez <i>et al.</i> , 2013; Tingley <i>et al.</i> , 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 <i>et al.</i> , 2013)
Reproductive mode (viviparity)	Categorical: Viviparous vs oviparous	+	Viviparous species tend to be larger than oviparous species	Overexploitation, invasive species	(Durnham <i>et al.</i> , 1988)
Diet (trophic level)	Categorical: Omnivore, herbivore, carnivore	+	Higher trophic levels (carnivores) more vulnerable to disturbance		(Crooks & Soule, 1999)

4

5

1 **Table 1.** continued.

Factor	Variables in analysis	Prediction	Justification	Interaction with threats	References
<i>Extrinsic factors</i>					
Precipitation	Annual average precipitation	+	Areas experiencing high levels of precipitation have higher productivity & potentially higher human disturbance		(Tingley <i>et al.</i> , 2013)
Temperature	Annual average temperature	-	Reptiles are solar ectotherms, with slower life histories (hence reproduction) in areas of lower temperatures		(Scharf <i>et al.</i> , 2015)
Elevation	Minimum elevation (in m)	+	High minimum elevations suggest smaller, more restricted ranges		(Davies <i>et al.</i> , 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 <i>et al.</i> , 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.

<i>Non-dated phylogeny</i>							
	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		

4
 5
 6

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

A) Biogeographic realm

<i>Afrotropical</i>	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		
<i>Australasian</i>	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		
<i>Indomalayan</i>	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		
<i>Nearctic</i>	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		
<i>Neotropical</i>	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
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<i>Palearctic</i>	Coefficient	S.E.	t	p	Model r ²	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

<i>Lizards</i>	Coefficient	S.E.	t	p	Model r ²	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		

<i>Snakes</i>	Coefficient	S.E.	t	p	Model r ²	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

<i>Habitat loss</i>	Coefficient	S.E.	t	p	Model r ²	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

2

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

1 **Figure legends**

2 **Figure 1.** Explanation of analyses carried out to (A) build predictive models of extinction
3 risk in reptiles and (B) evaluate the importance of range size versus other explanatory
4 variables (biological traits and environmental factors). We followed this schematic to carry
5 out our analyses using both the non-dated and dated phylogeny.

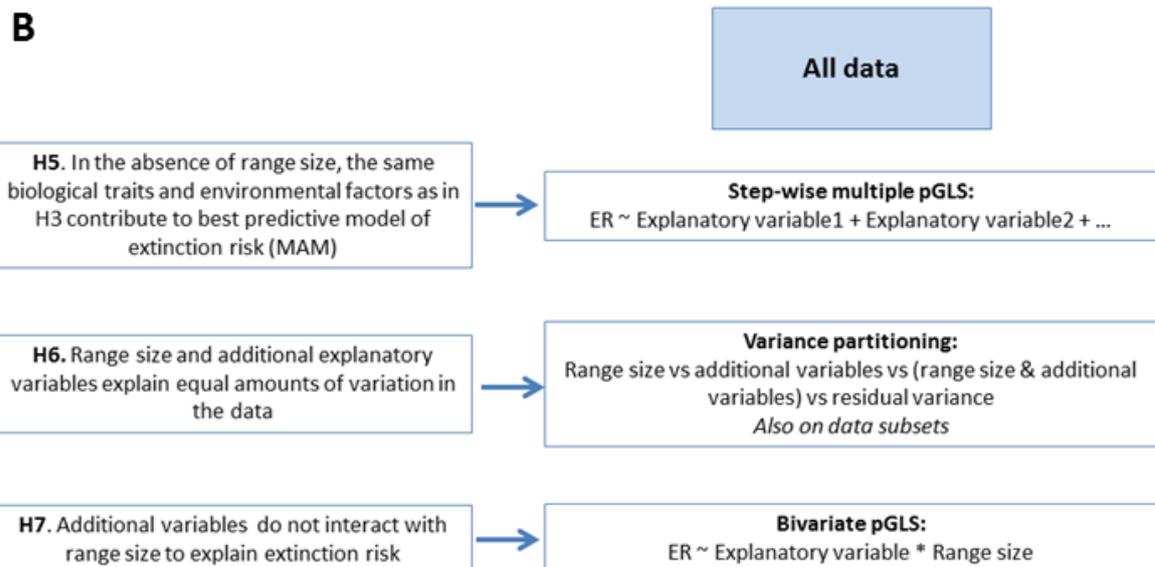
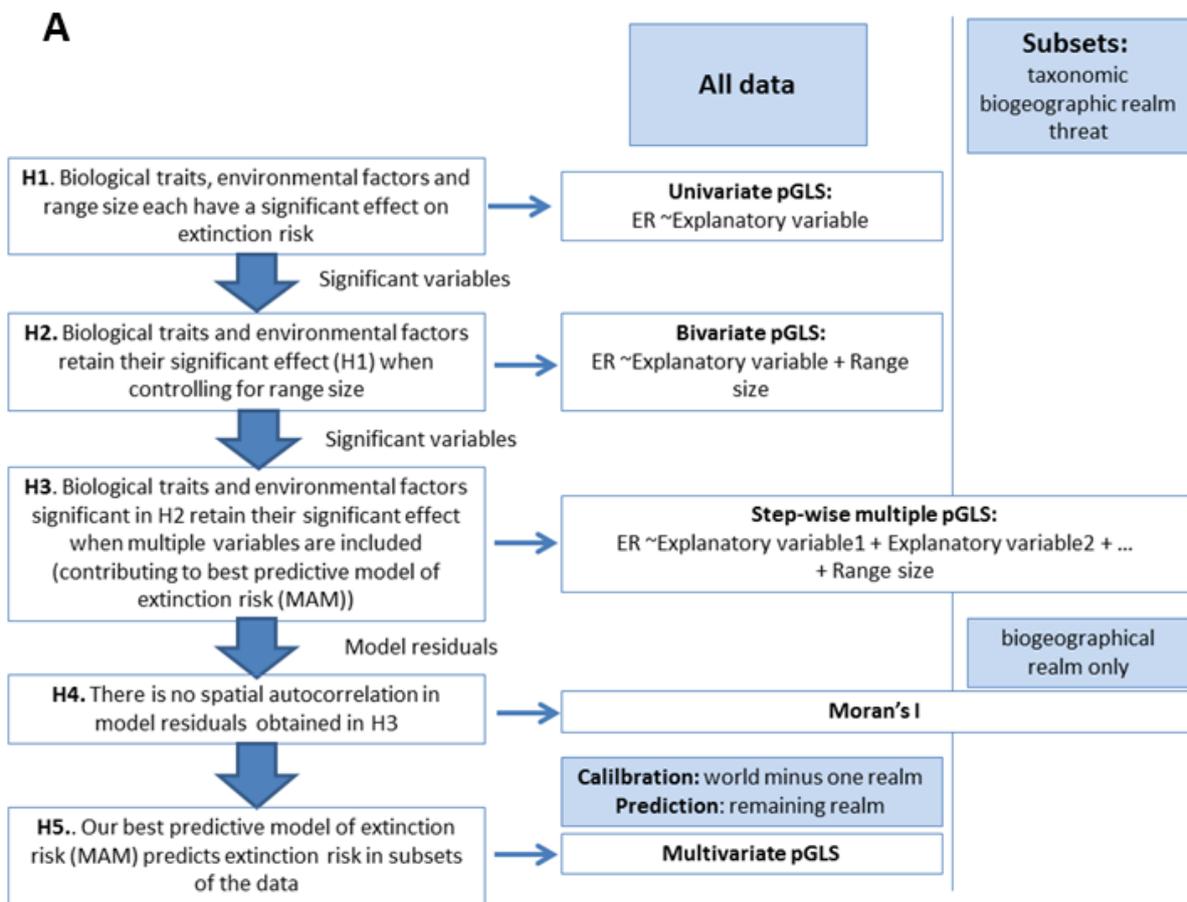
6
7 **Figure 2.** Variance partitioning for all minimum adequate models (MAM) of extinction risk
8 (global, and by geographical, taxonomic and threat type subsets), showing the different
9 contributions of variables retained as significant within the respective MAM, as well as their
10 shared contribution, to extinction risk: a) combined independent contribution of all variables
11 retained in MAM excluding range size (solid line); b) shared contribution of all MAM
12 variables including range size (thick dashed line); c) independent contribution of range size
13 only (thin dashed line); d) unexplained (residual) variance in the model (dotted line). The
14 variables for each figure were selected based on the outcomes of the MAMs using the non-
15 dated phylogeny only (see Tables 2 and 3). Biogeographical subsets: AFR – Afrotropical;
16 AUS – Australasian; IND – Indomalayan; NE – Nearctic; NEO – Neotropical.

17
18 **Figure 3.** Observed versus predicted log Red List status derived from holdout models (the
19 global model containing all species minus those from the stated biogeographical realm)
20 predicting Red List status for the remaining (held out) biogeographical realm: A –
21 Afrotropical (%error of prediction = 23.6); B – Australasian (%error = 23.6); C –
22 Indomalayan (%error = 29.0); D – Nearctic (%error = 27.6); E – Neotropical (%error = 25.7);
23 F – Palearctic (%error = 27.1). Full diagnostics for each model are given in the
24 Supplementary Materials (Table S9).

25
26 **Figure 4.** Global distribution maps for significant species traits in our analyses: (A) The
27 number of habitats occupied (as a measure of habitat specialism); (B) accessibility of species'
28 geographical ranges (travel time in minutes of land-based travel to cities of more than 50,000
29 people). Grid cell values are the average weighted mean for trait values, for species' ranges
30 intersecting the grid cell.

31

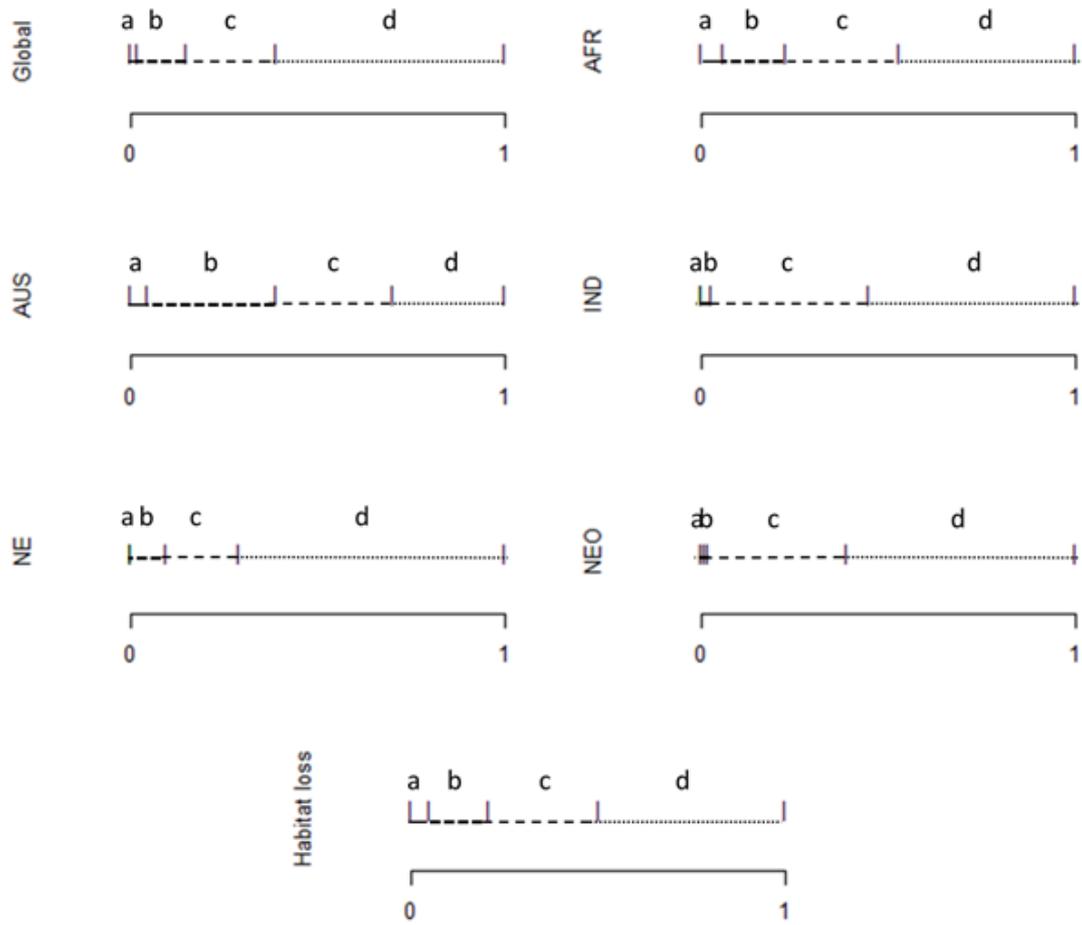
1 **Figure 1.**



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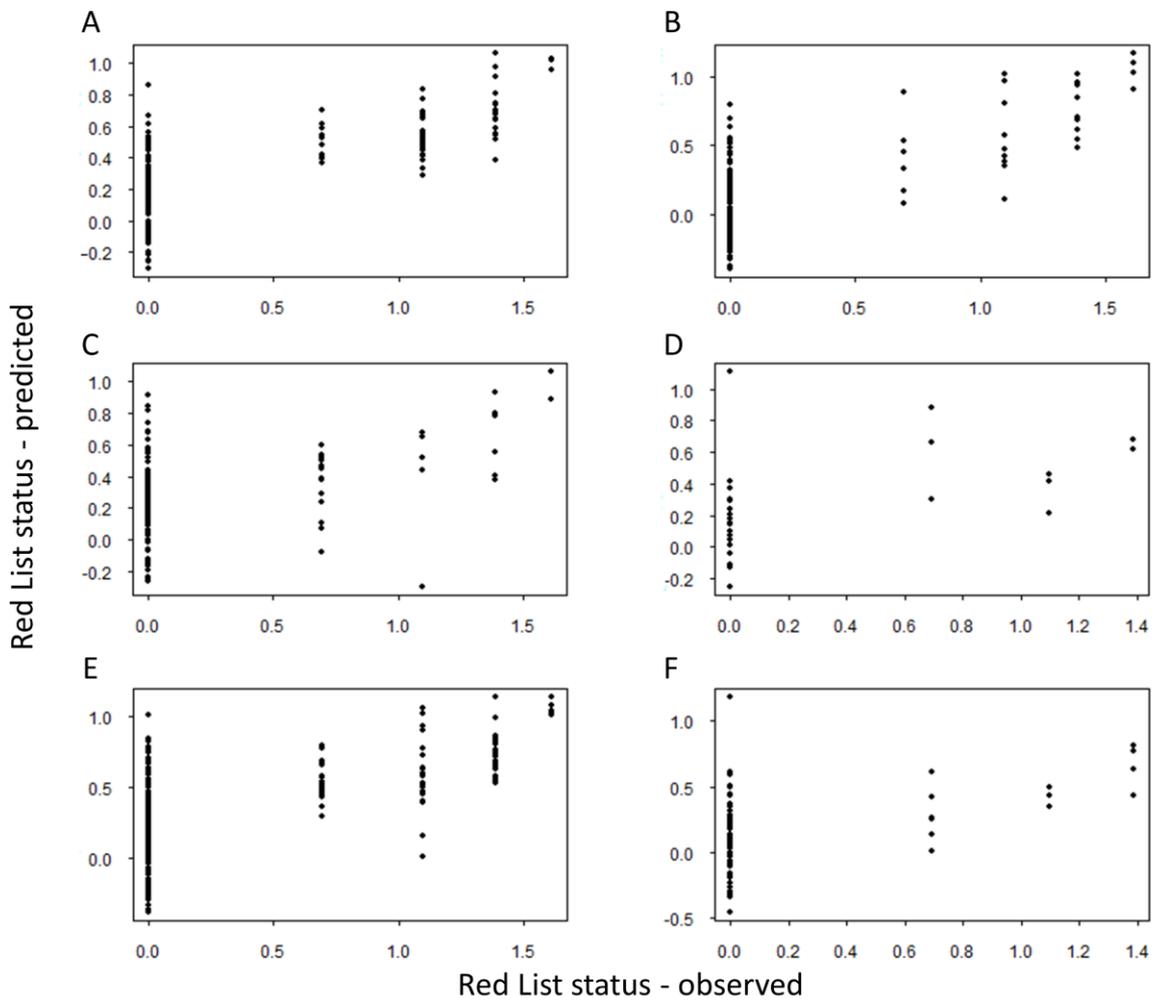
1 **Figure 2.**



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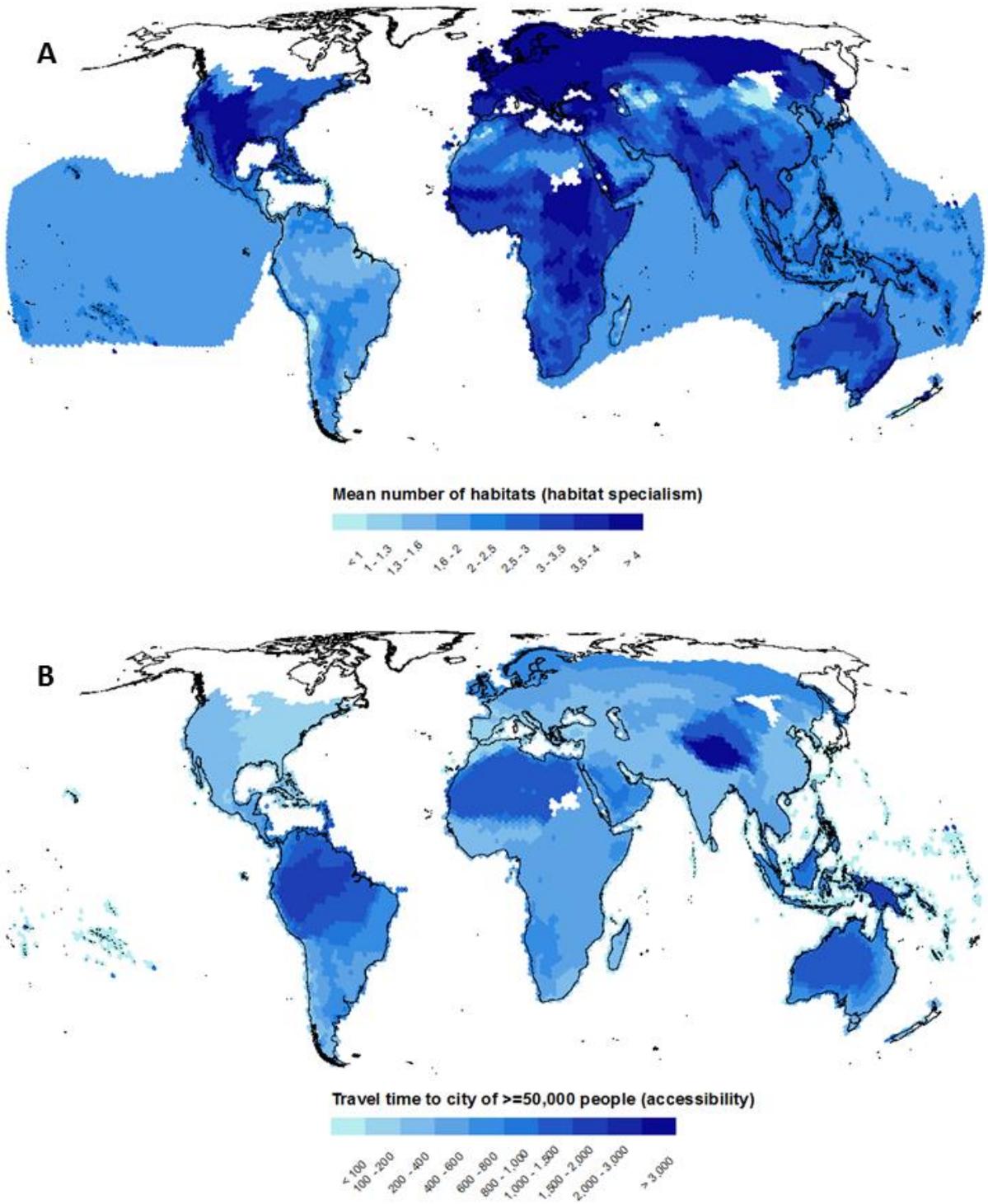
1 **Figure 3.**



2

3

1 **Figure 4.**



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