

1 Global priorities for conservation of reptilian 2 phylogenetic diversity in the face of human impacts

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4 Rikki Gumbs^{1,2,3*}, Claudia L. Gray³, Monika Böhm⁴, Michael Hoffmann⁵, Richard Grenyer⁶, Walter Jetz⁷,

5 Shai Meiri^{8,9}, Uri Roll¹⁰, Nisha R. Owen¹¹, James Rosindell¹

6 1. Department of Life Sciences, Imperial College London, Silwood Park Campus, Ascot, Berkshire, SL5

7 7PY, United Kingdom

8 2. Science and Solutions for a Changing Planet DTP, Grantham Institute, Imperial College London,

9 South Kensington, London

10 3. EDGE of Existence Programme, Zoological Society of London, Regent's Park, London, United

11 Kingdom

12 4. Institute of Zoology, Zoological Society of London, Regent's Park, London, United Kingdom

13 5. Conservation and Policy, Zoological Society of London, Regent's Park, London, United Kingdom

14 6. School of Geography and the Environment, University of Oxford, Oxford, OX1 3QY, United Kingdom

15 7. Ecology and Evolutionary Biology Department, Yale University, 165 Prospect Street, New Haven, CT

16 06511, USA

17 8. School of Zoology, Tel Aviv University, 6997801, Tel Aviv, Israel

18 9. Steinhardt Museum of Natural History, Tel Aviv University, 6997801, Tel Aviv, Israel

19 10. Mitrani Department of Desert Ecology, Ben-Gurion University of the Negev, Midreshet Ben-Gurion

20 8499000, Israel

21 11. On The EDGE Conservation, London, United Kingdom

22 *r.gumbs@imperial.ac.uk

23 Abstract

24 Phylogenetic Diversity (PD) is increasingly recognised as an important measure that can provide
25 information on evolutionary and functional aspects of biodiversity for conservation planning that are
26 not readily captured by species diversity. Here we develop and analyse two new metrics that combine
27 the effects of PD and human encroachment on species range size — one metric valuing regions and
28 another enabling species prioritisation. We evaluate these metrics for reptiles, which have been
29 largely neglected in previous studies, and contrast these results with equivalent calculations for all
30 terrestrial vertebrate groups. We find that high human impacted areas unfortunately coincide with
31 the most valuable areas of reptilian diversity, more than expected by chance. We also find that, under
32 our species-level metric, the highest priority reptile species score far above the top mammal and bird
33 species, and they include a disproportionate number of species with insufficient information on
34 potential threats. Such Data Deficient species are, in terms of our metric, comparable to Critically
35 Endangered species and may require urgent conservation attention.

36

37 Introduction

38 We are in the midst of a global biodiversity crisis^{1,2} with severely limited resources for conservation
39 action³. At current extinction rates, we are set to experience unprecedented losses of species and
40 their Phylogenetic Diversity (PD). PD is the sum of the phylogenetic branch lengths connecting a set of
41 species to each other across their phylogenetic tree, and measures their collective contribution to the
42 tree of life^{4,5}. PD is increasingly recognised as an important component of global biodiversity^{6,7} with
43 value for human well-being^{4,8,9}. As PD extends beyond the simple counting of species to quantify the
44 amount of variation across a set of species⁴, it is a valuable tool for differentiating among species and
45 regions for conservation prioritisation^{5,10-12}.

46 A large body of literature has explored how PD can be conserved across mammals and birds^{5,7,10,13–16}
47 but reptiles remain poorly studied in global conservation schemes¹⁷, despite comprising ~30% of
48 terrestrial vertebrate species richness¹⁸. Almost one in five reptile species are threatened with
49 extinction¹⁹ and reptile populations have suffered average global declines of around 55% between
50 1970 and 2012²⁰. Existing protected areas and global conservation schemes represent reptiles poorly
51 compared with birds and mammals²¹. Consequently, there is a pressing need to assess all reptiles to
52 enable targeted conservation and allow the incorporation of reptiles into global analyses of
53 conservation priorities.

54 There are several methods available for mapping imperilled PD^{7,12,13,22,23} and, in lieu of explicit
55 extinction risk data, small range size has often been used to identify regions of high conservation
56 value^{12,13}. However, whilst these methods prioritise highly irreplaceable regions, they do not
57 incorporate spatial measures of vulnerability, such as human impact, thus limiting their potential
58 practical application in conservation planning^{24,25}. Unfortunately, while range data to roughly 100 km
59 scale are now available for 99% of reptiles²¹, up-to-date extinction risk data (i.e. published in the past
60 ten years^{26,27}) are available for less than half of reptile species²⁷. In the absence of comprehensive
61 extinction risk assessments for all reptiles, range data must be combined with existing environmental
62 data to determine spatial vulnerability^{28–30}.

63 The Human Footprint index (HF)^{30,31} is the most comprehensive and high-resolution dataset of human
64 pressures on global environments. It combines eight variables—including crop and pasture land,
65 extent of built environments, human population density and night-time lights—which measure direct
66 and indirect impacts of humans on the environment³⁰. Such comprehensive global maps of
67 cumulative human pressures have been shown to be better predictors of species distributions than
68 biological traits³² and are a strong predictor of species extinction risk³³. However, to our knowledge,
69 no measure of human impact—such as the Human Footprint—has previously been explicitly
70 incorporated into methods to value and prioritise the conservation of global vertebrate PD. Here, we

71 present two new metrics combining human encroachment (to measure vulnerability), and range size
72 (to measure irreplaceability), to identify high value regions and high priority species for conserving
73 reptile PD. For comparison, we also calculate these metrics at the global scale for all tetrapod clades.

74 Methods

75 Data

76 We used updated reptile distribution polygons from the Global Assessment of Reptile Distributions
77 (GARD)²¹. We used published phylogenies for lepidosaurs (lizards, snakes and the tuatara)³⁴,
78 crocodilians³⁵ and turtles³⁶. The crocodilian and turtle phylogenies used were single, consensus, fully-
79 resolved phylogenies. To capture phylogenetic uncertainty around the taxonomically imputed
80 lepidosaur phylogenies, we randomly sampled 100 fully-resolved phylogenies from a distribution of
81 10,000 trees³⁴ and used each phylogeny in our analyses to generate median values of PD and PD-
82 based metrics for each grid cell using a Mollweide equal area projection at 96.5 x 96.5 km grid cell
83 resolution²¹. We matched the species in each phylogeny to the distribution data using the taxonomy
84 from the July 2018 version of the Reptile Database¹⁸. For our spatial analyses we included only species
85 with both phylogenetic and distribution data (9,862 species or 91% of total reptilian diversity;
86 Supplementary Table 1).

87 We extracted a random sample of 100 phylogenetic trees from published phylogenies for
88 amphibians³⁷, birds¹³ and mammals³⁸ and spatial data, as polygon shapefiles, for amphibians and
89 mammals from IUCN²⁷ and for birds from BirdLife International³⁹. These distribution data were subset
90 to contain only native and resident or breeding ranges. As with reptiles, for our spatial analyses we
91 included only species with both phylogenetic and distribution data (5,786 amphibians (75.5% of
92 species); 9,274 birds (84.5%); 4,386 mammals (77%) - ~84% of all tetrapods, including reptiles;
93 Supplementary Table 1) and calculated median values of PD and PD-based metrics for each grid cell.

94 We used the 2009 Human Footprint index (HF)³⁰—the most up-to-date HF dataset—to designate
95 spatial patterns of human pressure. The HF index evaluates each grid cell based on the intensity of
96 eight measures of human pressure (built environments, crop land, pasture land, human population
97 density, night-time lights, railways, roads, navigable waterways), weighted according to estimates of
98 their relative levels of human pressure^{30,31}, and assigns an HF value between 0 (lowest human

99 pressure) and 50 (greatest human pressure) to each cell³⁰. We resampled the HF data from its original
100 1 x 1 km resolution to our 96.5 x 96.5 km grid.

101

102 Spatial value metric for conserving PD

103 As small range size is linked to elevated extinction risk^{29,40}, if small-ranged reptiles are clumped
104 together on the tree of life, with no shared branches also subtended by a wide-ranging species, a
105 disproportionately large amount of PD may be at risk of extinction. To examine whether small range
106 size is phylogenetically conserved in this manner, we calculated Pagel's lambda⁴¹ for crocodylians,
107 turtles, and lepidosaurs separately and—within lepidosaurs—for lizards, amphisbaenians, and the
108 tuatara (hereafter collectively 'lizards') and for snakes independently, to remove the biased caused by
109 large range sizes of snakes from the analysis of lizard distributions²¹. Pagel's lambda provides an
110 estimate of how phylogenetically conserved a trait is across a phylogeny, with scores close to 1
111 indicating a trait is extremely clumped on the phylogeny, whereas scores close to 0 indicate a trait to
112 be randomly dispersed throughout the phylogeny⁴¹.

113 To map global patterns of reptilian PD, for each grid cell occupied by at least one species, we summed
114 the lengths of all branches between root and tips for each species in the grid cell. As the branch
115 lengths are time-calibrated, the resulting values represent the PD, as units of time, present in each
116 grid cell. To account for the internal branches connecting crocodylians, turtles and lepidosaurs when
117 mapping PD for all reptiles, we used published divergence estimates between each clade pair⁴².

118 We summed the branch lengths of the turtle and crocodylian phylogenies, and combined these with
119 the additional inferred PD and the median summed branch lengths from the 100 lepidosaur
120 phylogenies to estimate total global reptilian PD. Though crocodylians were included in analyses of all
121 reptiles, we do not report their individual results because they comprise of only 25 species¹⁸.

122 We explored the relationship between PD and richness for each reptile group using Pearson's
123 correlation corrected for spatial autocorrelation in the R package 'Spatialpack'^{43,44}, with conservative
124 Bonferroni correction for multiple testing. To identify global variation in the relationship between PD
125 and richness, we calculated the residuals from a linear regression of richness against PD for all grid
126 cells. We consider grid cells harbouring more PD than expected for the observed richness to
127 represent regions of disproportionately phylogenetically diverse species compositions.

128 For later comparison with our own PD-based spatial metric, we calculated three additional metrics:
129 the species-based metric Weighted Endemism (WE), which provides a measure of range-size-
130 weighted species richness^{12,21}, and two PD-based extensions of Weighted Endemism: Evolutionary
131 Distinctness Rarity (EDR)¹³ and Phylogenetic Endemism (PE)¹² (Supplementary Table 2).

132 A key difference between the two PD-based metrics, Evolutionary Distinctness Rarity and
133 Phylogenetic Endemism, is in their treatment of species ranges: Evolutionary Distinctness Rarity treats
134 all species ranges as spatially independent whereas Phylogenetic Endemism accounts for the spatial
135 overlap of species. We suggest that Evolutionary Distinctness Rarity and Phylogenetic Endemism
136 therefore better represent the potential loss due to differing drivers. Evolutionary Distinctness Rarity
137 represents the amount of Evolutionary Distinctiveness imperilled by *species*-specific threats (e.g.
138 targeted hunting); the losses are species focused because only range size (and not range overlap with
139 other species) is accounted for. In contrast, Phylogenetic Endemism represents the amount of
140 phylogenetic diversity attributed to a particular unit of *space*, reflecting the impact of landscape-level
141 threats (e.g. habitat loss); having additional descendent species in the same size region makes no
142 difference to extinction risk of phylogenetic branches because loss of the region would impact all
143 those species together. As most threats to tetrapod species are present at the landscape-level (e.g.
144 agriculture, logging and livestock production)⁴⁵⁻⁴⁷, we hereafter report and develop analyses based on
145 the Phylogenetic Endemism metric.

146

147 To assess the overlap between regions of high Phylogenetic Endemism and high human pressure, we
148 identified the grid cells in the top 10% of all grid cells for reptilian Phylogenetic Endemism (hereafter
149 “high value grid cells”) and calculated the proportion of the high value grid cells that are also deemed
150 to be under ‘high’ or ‘very high’ human pressure (Human Footprint ≥ 6)³⁰. As Human Footprint value
151 of 4 equates to the human pressure of pasture lands^{48,49}, ours is a conservative estimate of intense
152 human pressure³⁰. We randomised the distribution of grid cells under high or very high human
153 pressure across all terrestrial cells and recalculated the proportion of high value grid cells now
154 considered to be under high or very high human pressure. We repeated this randomisation 1,000
155 times to generate a distribution of randomised scores for comparison with the observed proportion
156 of overlap.

157 Whilst Phylogenetic Endemism incorporates the intrinsic threat of small range size into the calculation
158 of grid cells for conservation of unique evolutionary history, it does not measure the myriad extrinsic
159 threats present. We therefore incorporated the Human Footprint (HF) index^{30,31} as a measure of
160 vulnerability.

161 To calculate an adjusted range size value for each species in relation to HF we first linearly scored
162 each terrestrial grid cell between 0 and 1 according to which of the five approximately equally
163 distributed classes of HF it belonged: HF-adjusted range size of 1 = ‘no pressure’ (HF = 0), the entire
164 grid cell is retained; 0.8 = ‘low pressure’ (HF = 1-2); 0.6 = ‘moderate pressure’ (HF = 3-5); 0.4 = ‘high
165 pressure’ (HF = 6-11); 0.2 = ‘very high pressure’ (HF = 12-50)³⁰. A ‘very high pressure’ grid cell is
166 therefore equivalent to 0.2 of a complete grid cell, to reflect the high human pressure and therefore
167 likely greatly reduced remaining suitable habitat within that cell for species to persist. Though the
168 true proportion of remaining suitable habitat will differ across grid cells of equal Human Footprint and
169 will also be species-specific, our scoring of grid cells based on Human Footprint provides a relative
170 scale representing human pressure under the assumption that increased human pressure equates to
171 less remaining suitable habitat. The new “HF-adjusted range size” of a species is given by the sum of

172 HF-adjusted grid cell size for all cells across which a species is distributed. It can be thought of as an
173 effective range size, which will be much smaller than the true range if large parts of it coincide with
174 high levels of human pressure. Previous analyses have used fine-scale environmental data to estimate
175 range loss across species under scenarios of change⁵⁰, and combined these with phylogenetic data on
176 a regional scale for a relatively small clade⁵¹. However, such fine-scale habitat association and
177 environmental requirement data are lacking for the majority of reptiles and preclude such an analysis
178 at this time.

179 We used these HF-adjusted range sizes to calculate a new spatial PD metric, derived from PE, which
180 we term Human Impacted Phylogenetic Endemism (HIPE). This approach apportions the PD of each
181 branch of the phylogeny according to each grid cell's contribution to the total adjusted range of the
182 species (Supplementary Table 2). When a branch is found either in one grid cell or in multiple grid
183 cells of the same HF-adjusted grid cell size, HIPE is equivalent to Phylogenetic Endemism in
184 apportioning PD. However, when a branch occurs in grid cells of variable human impacts, PD is
185 apportioned by the relative contribution of the Human Footprint-adjusted grid cells, so that those
186 with lower human impact (higher HF-adjusted grid cell size) receive a greater proportion of PD to
187 reflect their higher present value. Consequently, branches which are entirely distributed across grid
188 cells of high human impact contribute a greater proportion of PD to highly impacted grid cells than
189 branches which also occur in grid cells under low human impact.

190 Consider a grid cell under high human impact (HF-adjusted range size = 0.2) where only two branches
191 are present, both comprising 10 MY of PD. Both branches also occur in one other grid cell, branch A in
192 a low impact grid cell with a HF-adjusted range size of 1 (for a total HF-adjusted range of 1.2 grid cells)
193 and branch B in a high impact grid cell with a HF-adjusted range size of 0.2 (total HF-adjusted range of
194 0.4 grid cells). Under traditional Phylogenetic Endemism, the grid cell receives 50% of the PD from
195 each branch (5 MY) as it comprises 50% of the total distribution of the branch (one of two grid cells).
196 Under HIPE, however, branch A would apportion only 1/6th (1.667 MY) of its PD to the grid cell as it

197 comprises only 1/6th of the total HF-adjusted range (0.2 of total 1.2 range), with the remaining 5/6th
198 of the PD being apportioned to the grid cell with a HF-adjusted range size of 1. Conversely, as branch
199 B occurs only in two grid cells of HF-adjusted range size 0.2, the grid cell comprises 50% of the HF-
200 adjusted range of the species (0.2 of total 0.4 range) and is apportioned 50% of the PD of the branch
201 (5 MY) (Supplementary Table 2; Supplementary Figure 1).

202 HIPE increases the relative importance of grid cells under low human impact as well capturing cells
203 with high endemic PD. It is therefore important for conservation planning to highlight which of the
204 high value regions (based on HIPE) are driven by endemic PD in areas of high vs. low human impact,
205 as the two extremes are likely to require different conservation action. We partitioned global patterns
206 of HIPE by human impact, highlighting regions of high HIPE and high human impact ($HF \geq 6$) and
207 regions of high HIPE and low human impact ($HF < 3$).

208 We mapped HIPE for all reptile groups individually and for all reptiles combined. To determine the
209 regions where reptiles provide the greatest contributions to global patterns of tetrapod HIPE, we also
210 calculated HIPE for mammals, birds, amphibians and for tetrapods as a whole. We then calculated the
211 proportions of observed HIPE for all tetrapods that were contributed by each tetrapod clade. We
212 present HIPE scores in MY/km^2 , where the adjusted range size represents the area across which the
213 scores are divided (e.g. a 96.5×96.5 km grid cell with a HF-adjusted grid cell size of 0.2 is considered
214 to comprise 1/5th of the area of an entire grid cell).

215 We ran spatially-corrected correlations between HIPE, Phylogenetic Endemism and Evolutionary
216 Distinctness Rarity to test the extent to which these measures capture the same global patterns. We
217 also ran a spatially-corrected correlations test for relationships between global HIPE patterns among
218 reptile groups and between reptiles and other tetrapods, all with Bonferroni correction for multiple
219 testing.

220

221 Species prioritisation metric for conserving PD

222 We estimated the total PD of reptiles by summing the branch lengths of the crocodylian and turtle
223 phylogenies and adding these to the summed branch lengths for each of the 100 lepidosaur
224 phylogenies to generate a distribution of 100 total reptilian PD values. We compared this distribution
225 with that for other tetrapod classes, which we generated by summing the branch lengths of the 100
226 random phylogenies for amphibians, birds and mammals. We compared the distributions of PD scores
227 using ANOVA and applied Tukey's HSD test to identify pairwise differences between tetrapod classes.
228 The branch lengths were summed for all phylogenies prior to the removal of species with no spatial
229 data to limit the impact of differing availability of spatial data across the different classes.

230 To identify species that should be prioritised to preserve unique evolutionary history, we devised a
231 new metric built around the main component common to both PE and EDR: terminal branch length
232 (TBL). Terminal branches are those which connect the species (tips) to the internal branches of the
233 phylogeny and are the only component of a phylogeny unique to each species. The length of these
234 terminal branches represents the divergence time (in millions of years for time-calibrated
235 phylogenies) between a species and their closest relatives.

236 We defined Terminal Endemism (TE) as the terminal branch length of a species multiplied by 1/the
237 number of grid cells occupied by the species. If a species is found in only one grid cell then its loss
238 from that grid cell would result in the loss of its entire terminal branch. The TE of a species is implicitly
239 calculated when calculating both Evolutionary Distinctness Rarity and Phylogenetic Endemism and
240 represents the unique contribution of the species to the total for each metric. We posit that, as a
241 species focused measure, TE circumvents the differences between Evolutionary Distinctness Rarity
242 and Phylogenetic Endemism and retains the most essential component of each.

243 To incorporate HF, we developed a counterpart to TE, 'Human Impacted Terminal Endemism' (HITE).

244 This metric is given by the terminal branch length of a species divided by its Human Footprint-

245 adjusted range size (see above). For example, a species with a terminal branch length of 10 MY that is

246 found in two grid cells, with HF-adjusted grid cell sizes of 0.2 and 1 would receive a HITE score of
247 $10 \cdot (1/(1+0.2)) = 8.34$. Under standard Terminal Endemism the same species would receive a lower
248 score of 5: ($10 \cdot (1/2)$). HITE therefore increases in response to terminal branches occurring in grid
249 cells under high human impact.

250 We calculated the terminal branch lengths, HF-adjusted range size and HITE for all tetrapods and
251 ranked the species from each clade to identify the species with the highest HITE scores. We highlight
252 tetrapod species which are either unassessed or listed as Data Deficient by the IUCN, but have a high
253 HITE score. These are species that, due to their high irreplaceability and extremely restricted and
254 human-impacted range, are priorities for conservation assessment. Finally, we compared HITE scores
255 for tetrapods across IUCN Red List categories, using ANOVA and Tukey's HSD test, to determine the
256 relationship between HITE scores, data deficiency, and extinction risk across reptiles and all tetrapods.

257 To estimate how much reptilian PD may be lost if all threatened species were to become extinct, we
258 dropped all species listed in threatened categories on the IUCN Red List (i.e. Vulnerable, Endangered
259 and Critically Endangered) from their respective phylogenies and calculated the reduction in total PD.
260 For lepidosaurs we did this for all 100 phylogenies to generate a distribution of values. To determine
261 whether this potential loss of PD was greater than if extinction risk was randomly distributed across
262 the reptilian tree of life, we then selected 100 random sets of species corresponding to an equal
263 number of species as those observed to be threatened and dropped them from their respective
264 phylogenies. We then compared the distribution of potential PD loss from species observed to be
265 threatened with the distribution generated from randomised extinction using a paired t-test.

266 As it is likely that a significant proportion of unassessed and Data Deficient species are also
267 threatened with extinction^{52,53}, these estimates of loss of PD are conservative. To explore how data
268 deficiency affects potential losses of PD across data-poor regions of the tree of life, we selected a
269 poorly-known squamate genus as a case study. We estimated the amount of PD lost under different
270 scenarios of phylogenetic relationships and extinction risk for *Dibamus*, one of the least-known

271 reptilian genera (and the sister clade to all other squamates). First, we estimated the amount of PD
272 represented by the *Dibamus* species included in the phylogeny despite lacking genetic data across our
273 random selection of 100 lepidosaur phylogenies. Second, we estimated how much PD would be lost
274 under three extinction scenarios for *Dibamus*: 1) only a single unassessed or Data Deficient species
275 becomes extinct; 2) a random number and selection of unassessed or Data Deficient species become
276 extinct; and 3) all unassessed and Data Deficient species become extinct.

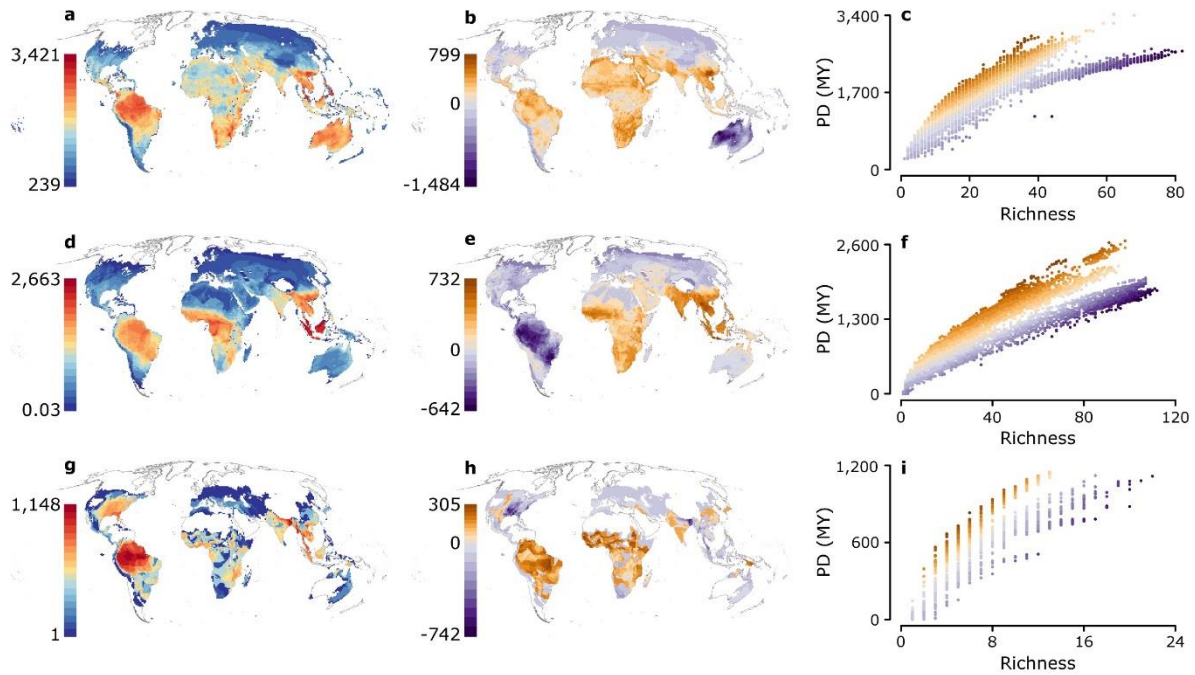
277 Results

278 Spatial value metric for conserving PD

279 Range size is weakly phylogenetically conserved across lepidosaurs ($\lambda = 0.373$, $p \ll 0.0001$;
280 Supplementary Figure 2), and in lizards and snakes independently (lizards: $\lambda = 0.485$, $p \ll 0.0001$;
281 snakes: $\lambda = 0.345$, $p \ll 0.0001$). However, range size is not significantly conserved across turtles ($\lambda =$
282 0.12 , $p = 0.03$) or crocodylians ($\lambda = 0.048$, $p = 0.815$), following Bonferroni correction for multiple
283 testing (adjusted p-value threshold = 0.01), likely due to the low species richness of both clades.

284 Reptilian PD is largely concentrated throughout the tropics (Figure 1, Supplementary Figure 3), and is
285 strongly correlated with species richness on a global scale for all reptiles ($r = 0.948$, e.d.f. = 23.7, $p \ll$
286 0.0001), lizards ($r = 0.920$, e.d.f. = 21.1, $p \ll 0.0001$), snakes ($r = 0.899$, e.d.f. = 24.4, $p \ll 0.0001$) and
287 turtles ($r = 0.873$, e.d.f. = 28.1, $p \ll 0.0001$). Lizard PD is high across Southeast Asia, the Amazon basin
288 and Australia (Figure 1a). Large concentrations of snake PD are found in Malaysia and Indonesia
289 (Figure 1d), whereas the greatest concentrations of turtle PD are found across the Amazon Basin
290 (Figure 1g), despite turtle richness peaking in the Ganges Delta.

291 The greatest levels of high lizard PD, compared with species richness (residuals of PD vs. richness), are
292 in mainland Southeast Asia, whereas regions with the lowest levels of residual PD occur across
293 Australia, where richness is highest (Figure 1b-c). The largest accumulations of snake PD for a given
294 richness occur in mainland Southeast Asia, and the lowest coincide with the species-rich Amazon
295 Basin and Atlantic coast of Brazil (Figure 1e-f). The greatest accumulations of turtle PD for a given
296 richness occur across subtropical West and Central Africa and the Amazon Basin, with lowest
297 accumulations occurring where species richness is highest: the Ganges Delta and Eastern USA (Figure
298 1h-i).



299

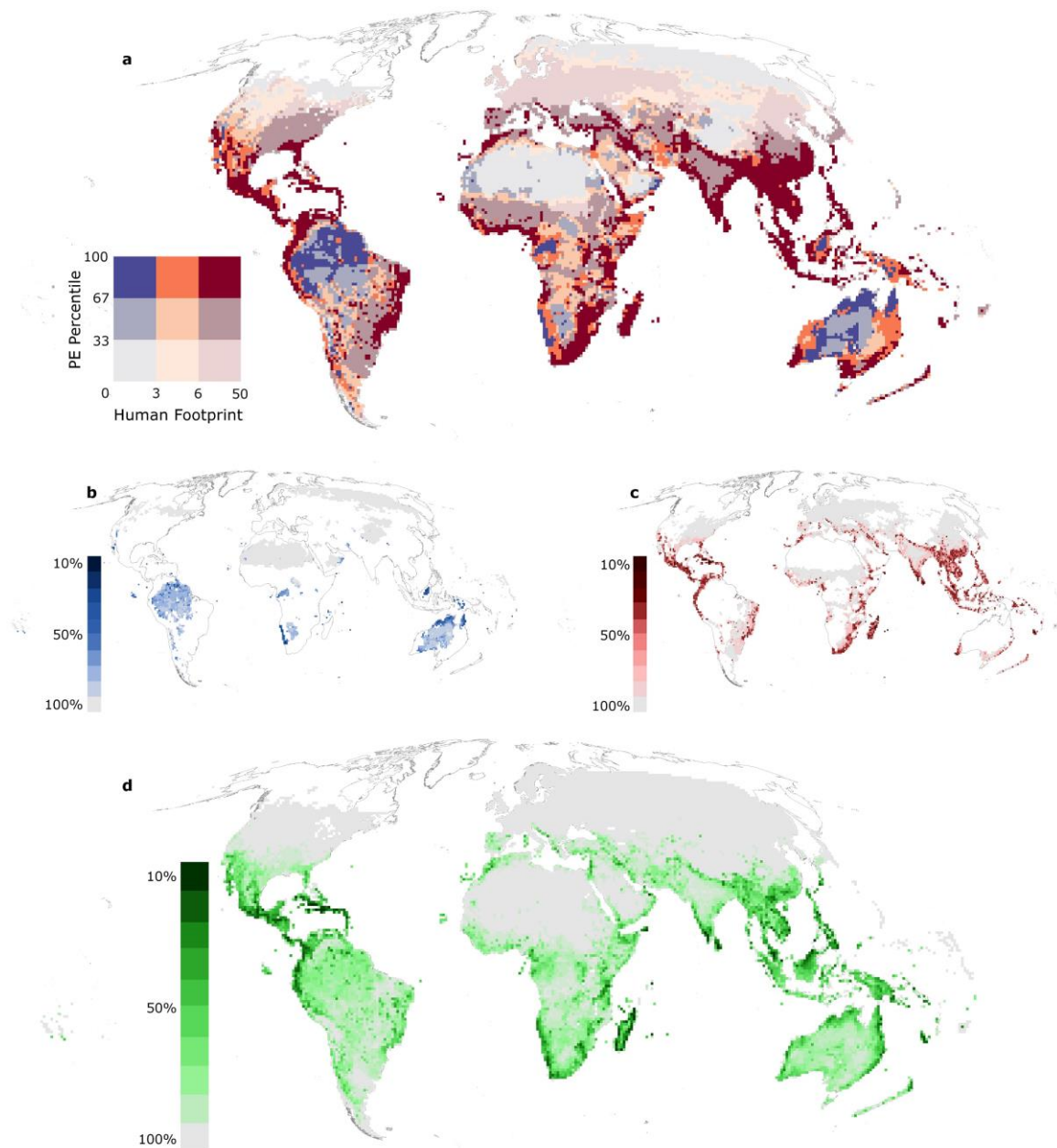
300 **Figure 1: Global patterns of reptilian phylogenetic diversity (PD).** Cumulative PD, in millions of years
301 (MY) (left), Middle: residual PD per grid cell, in MY, (warm colours: more than expected given
302 richness, cold colours: less than expected given richness), Right: the relationship between richness
303 and PD across all grid cells for lizards (a-c), snakes (d-f), and turtles (g-i).

304

305 Phylogenetic Endemism (PE) and Evolutionary Distinctness Rarity (EDR) for reptiles are highly
306 correlated at the global scale ($r = 0.975$, e.d.f. = 537, $p \ll 0.0001$) and both are highly correlated with
307 the non-phylogenetic measure of Weighted Endemism (WE; both $r > 0.93$; Supplementary Figure 4).

308 Almost three-quarters (74%) of high-value grid cells of PE (i.e. top 10% ranking grid cells) are in
309 regions of high or very high human pressure (Human Footprint ≥ 6), whereas just 5% of high PE grid
310 cells coincide with regions of low or no human pressure (HF < 3). The strong association of regions of
311 high PE with those of high human impact is surprising, considering the two are, in theory,
312 independent. Indeed, when we randomise human pressure across grid cells, less than half (49%) of
313 high-value grid cells coincide with high or very high human pressure, and 20% coincide with regions of
314 low or no human pressure. High reptilian PE coincides with very high human pressure (HF > 11) across

315 the tropics—particularly in India, Caribbean islands, the Atlantic Coast of Brazil, and Southeast Asia—
316 and the Mediterranean coast and areas of the Middle East (bold red regions, Figure 2a). Regions of
317 high PE and very low human pressure (HF < 1) are largely restricted to the Amazon Basin and central
318 Australia (bold blue regions, Figure 2a).
319



320

321 **Figure 2: Reptilian Phylogenetic Endemism (PE) and Human Footprint (HF).** a) The global relationship
322 between reptilian PE and HF. The colour of the grid cell is determined by HF value and the intensity of

323 the colour by PE percentile. In panels b-d) grid cells are coloured by the cumulative amount of global
324 HIPE captured; darkest blue (b), red (c), and green (d), indicate the highest-scoring grid cells which
325 together capture 10% of global HIPE, whereas the lowest-scoring grid cells also capturing 10% of
326 global HIPE are coloured light grey. Panel b) shows HIPE for low Human Footprint (< 3) grid cells.
327 Panel c) shows HIPE for high Human Footprint cells (≥ 6), and panel d) shows overall global patterns of
328 reptilian HIPE.

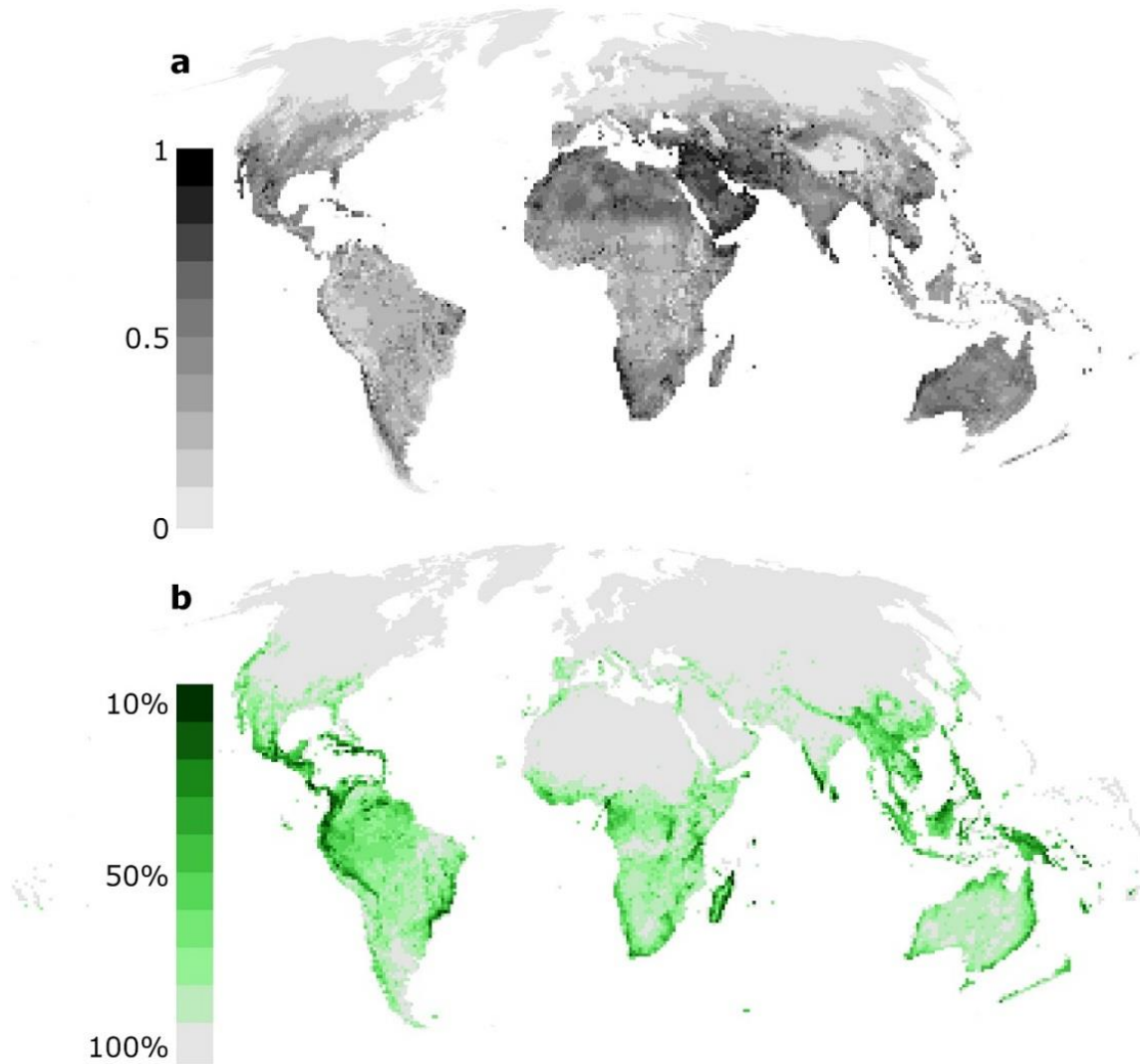
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330 Human-Impacted Phylogenetic Endemism (HIPE), is correlated with standard PE for reptiles ($r = 0.978$,
331 e.d.f. = 448, $p \ll 0.0001$; Supplementary Figure 4), despite individual grid cell values differing from PE
332 by up to 1,500% (median = 21%). Highest HIPE value regions (grid cells comprising top 10% of global
333 reptilian HIPE scores) which also coincide with high human pressure ($HF \geq 6$) span Southeast Asia,
334 Central America and the Caribbean, Madagascar and Sri Lanka (Figure 2b). Conversely, highest HIPE
335 value regions which also coincide with low human pressure ($HF < 3$) are restricted to the coast of
336 Namibia, northern Australia and the highlands of Borneo (Figure 2c).

337 Globally, reptilian HIPE is greatest in Madagascar, Central America and the Caribbean, the Western
338 Ghats of India, Sri Lanka, Socotra, peninsular Malaysia and northern Borneo (Figure 2d). Global
339 patterns of lizard HIPE largely reflect those of all reptiles (Supplementary Figure 5), whereas those for
340 snakes emphasise Central Africa and Southeast Asia (Supplementary Figure 5). High levels of turtle
341 HIPE are concentrated in the Amazon Basin, Central America, southern USA, Southeast Asia, New
342 Guinea, and northern Australia (Supplementary Figure 5).

343 Grid cells have much greater median and maximum HIPE scores for reptiles than for other tetrapod
344 classes (median = 9.1×10^{-4} MY/km² vs amphibians = 4.2×10^{-4} MY/km², birds = 4.3×10^{-4} MY/km²,
345 mammals = 3.6×10^{-4} MY/km²; maximum = 0.33 MY/km² vs amphibians = 0.30 MY/km², birds = 0.05
346 MY/km², mammals = 0.03 MY/km²). Reptiles contribute a median of 31.1% to tetrapod HIPE scores
347 across all grid cells in which they are present, more than any other class (amphibians = 16.6%, birds =

348 29.7%, mammals = 18%; Supplementary Figure 6). The greatest reptilian contributions (>90% of
349 tetrapod HIPE) occur across the Middle East and North Africa (Figure 3a). The lowest non-zero
350 contributions of reptiles (<10%) occur across northern North America and Europe, the Andes and the
351 Himalayas, where reptiles are scarce.



352
353 **Figure 3: Global patterns of tetrapod HIPE and reptilian contributions.** The global patterns of a) the
354 proportion of tetrapod HIPE contributed by reptiles, from 1 (100% of HIPE contributed by reptiles;
355 black) to 0 (0% of HIPE contributed by reptiles; light grey); and b) tetrapod HIPE, where grid cells are
356 coloured by the cumulative amount of global HIPE captured; darkest green cells comprise the highest-
357 scoring grid cells which together capture 10% of global HIPE, whereas the lowest-scoring grid cells
358 which together capture 10% of global HIPE are coloured light grey.

359

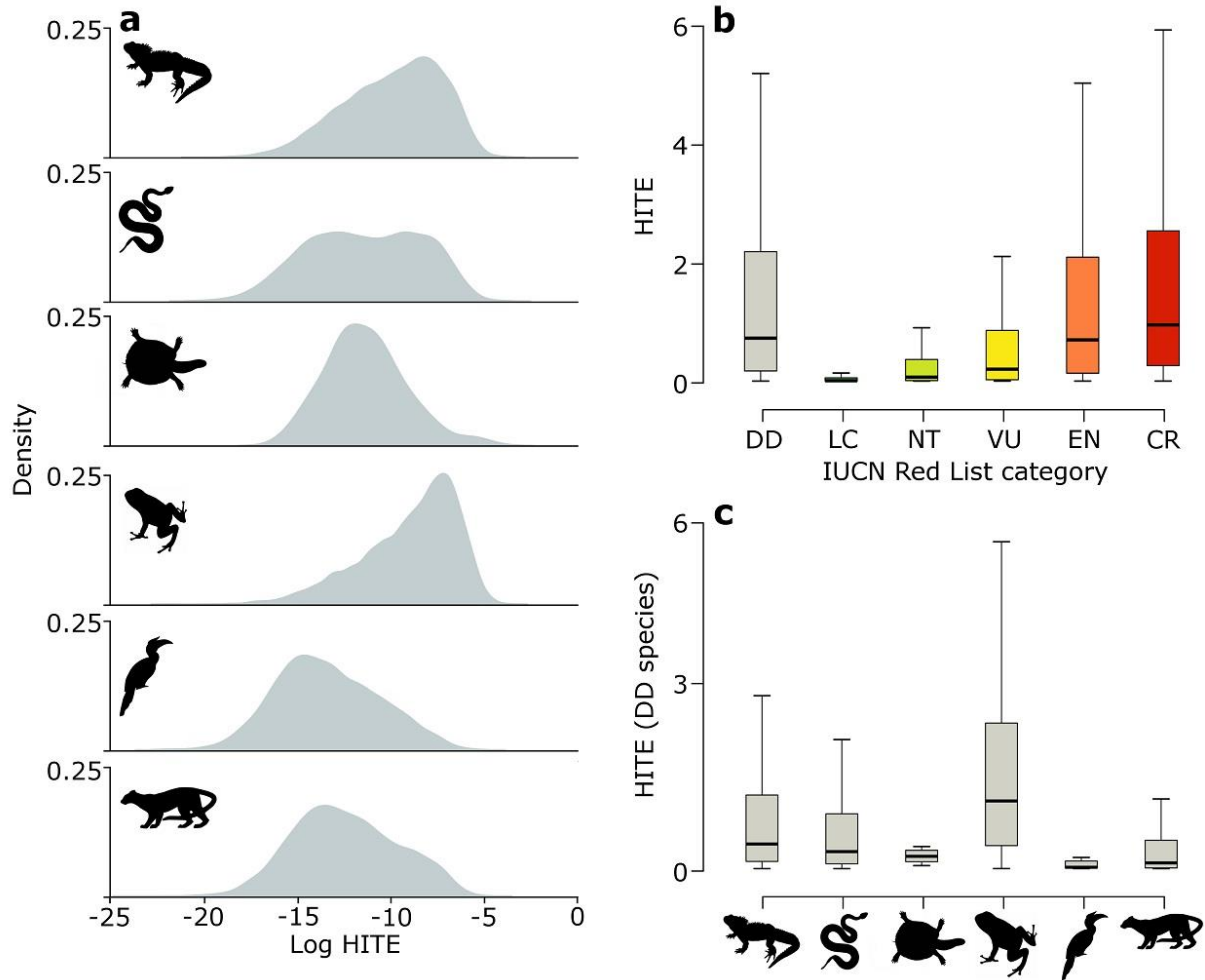
360 Reptilian HIPE is only moderately correlated with HIPE patterns for other tetrapod classes in each cell
361 across the globe, and inter-correlations are moderate between all classes (Supplementary Figure 7).
362 Turtle HIPE is consistently weakly correlated with that of other reptilian orders and tetrapod classes (r
363 < 0.25 , Supplementary Figure 7). Global patterns of tetrapod HIPE are broadly congruent with those
364 for reptiles, but place further emphasis on the importance of the Atlantic coast of Brazil, the
365 Caribbean, Central Africa and New Guinea (Figure 3b). The variation in patterns of clade-specific
366 contributions to global tetrapod HIPE (Figure 3a, Supplementary Figure 6) further highlights the
367 importance of including all tetrapod classes in analyses designed to represent the entire clade.

368

369 Species prioritisation metric for conserving PD

370 Globally, the 91% of reptiles with phylogenetic data comprise approximately 137 billion years of
371 phylogenetic diversity (PD), significantly more than any other tetrapod class (adjusted p-values from
372 Tukey Honest Significant Differences < 0.0001 ; amphibians = 130 BY (93% of species), birds = 85 BY
373 (74% of species), mammals = 47 BY (83.5% of species); Supplementary Table 2).

374 Turtles have the greatest median terminal branch length (TBL) of any tetrapod clade (14.1 MY),
375 whereas lepidosaurs have the greatest maximum TBL (238.7 MY – *Sphenodon punctatus*). Under our
376 new species-level metric, Human-Impacted Terminal Endemism (HITE), lepidosaurs have the second-
377 highest median score (9.9×10^{-5} MY/km²; lizards = 1.7×10^{-4} MY/km², snakes = 2.8×10^{-5} MY/km²;
378 Figure 4a). This is greater than both birds (3.0×10^{-5} MY/km²) and mammals (8.5×10^{-5} MY/km²), with
379 only amphibians scoring higher (median = 5.1×10^{-4} MY/km², maximum = 6.3×10^{-2} MY/km²; Figure
380 4a).



381

382 **Figure 4: Distributions of Human Impacted Terminal Endemism (HITE) for tetrapods. a) Density**

383 distributions of log-transformed HITE scores for tetrapods. Species with long terminal branches

384 occurring in very few grid cells under high human pressure score highly and fall on the right of the x-

385 axis, whereas species with short terminal branches and large ranges encompassing regions of low

386 human pressure fall on the left of the x-axis. Y-axis indicates density of species in each clade with a

387 given HITE value. b) Distribution of HITE scores (in 10^{-3} MY/km²) across tetrapods for each IUCN Red

388 List category (excluding Extinct, Extinct in the Wild and unassessed species). c) Distribution of HITE

389 scores (in 10^{-3} MY/km²) for Data Deficient (DD) tetrapod species for key tetrapod groups.

390

391 Data Deficient tetrapods tend to have longer terminal branches (median = 5.4 MY) than those listed

392 as Least Concern (4.3 MY), Near Threatened (4.3 MY) and Vulnerable (4.8 MY; adjusted p-values from

393 Tukey HSD test < 0.001) and not significantly different from Endangered (5.2 MY) and Critically
394 Endangered (5.5 MY) species (adjusted p-values > 0.05). HITE scores are greater for Data Deficient
395 tetrapods (median = 7.2×10^{-4} MY/km²) than those listed as Least Concern (6.3×10^{-6} MY/km²), Near
396 Threatened (6.7×10^{-5} MY/km²) and Vulnerable (2.0×10^{-4} MY/km²; adjusted p-values < 0.001), and
397 are comparable to those of Endangered (6.9×10^{-4} MY/km²) and Critically Endangered species ($9.5 \times$
398 10^{-4} MY/km²; adjusted p-values > 0.05 ; Figure 4b).

399 Within Data Deficient species, amphibians have the highest HITE scores (median = 1.5×10^{-3} MY/km²),
400 followed by lepidosaurs (4.7×10^{-4} MY/km²; lizards = 5.5×10^{-4} MY/km², snakes = 3.8×10^{-4} MY/km²;
401 Figure 4c). Worryingly, four of the ten highest ranking lizards and eight of the top ten snakes are listed
402 as Data Deficient by the IUCN Red List (ten highest-ranking HITE species for each clade:
403 Supplementary Table 3).

404 If all reptiles currently listed as threatened by the IUCN Red List were to become extinct (1,196 spp.
405 with phylogenetic data), we stand to lose more than 13.1 billion years of PD (mean; range = 12.3 –
406 14.3), or around 10% of total reptile PD. This is 1.36 billion years more PD than if extinction risk was
407 randomly distributed across the reptilian phylogeny (paired t-test; $t = 20.32$, d.f. = 99, $p < 0.0001$).

408 Given the large proportion of Data Deficient and unassessed reptiles (~10% and ~34% of all species,
409 respectively), and their potentially high extinction risk, such loss of PD may be much greater,
410 especially where data deficiency for both extinction risk and phylogenetic relationships intersect.

411 For example, the lizard genus *Dibamus* is represented by 22 species in our study (of the 24 species
412 recognised globally), 16 of which are either unassessed or listed as Data Deficient by the IUCN Red List
413 (as of December 2018). Fifteen of these 22 species are included in the phylogeny despite having no
414 genetic data available, and 12 are known only from their type locality⁵⁴. The amount of PD
415 represented by the 15 species without genetic data is highly uncertain, and ranges from 260 - 1,340
416 MY across 100 phylogenies (median = 560 MY). Accordingly, estimates of the amount of PD loss due
417 to extinction of unassessed or Data Deficient species range from 0.1 MY (a single species lost with the

418 shortest terminal branch length across 100 phylogenies – 0.00001% additional PD loss) to 1,010 MY
419 (all 16 unassessed/Data Deficient species lost with maximum branch lengths from 100 phylogenies –
420 7.8% additional PD loss), with a median loss of 230 MY (1.8% additional PD loss).

421 Discussion

422 Globally, reptiles comprise significantly more phylogenetic diversity (PD) than any other tetrapod
423 class. The distribution of reptilian PD largely reflects global richness patterns²¹, though our analysis
424 suggests that extremely high richness in snakes and lizards is achieved through shallow diversification
425 within clades (Figure 1). Our results highlight a large overlap between regions of high human impact
426 and irreplaceable reptilian PD, which is much greater than expected if the two were independent. We
427 therefore incorporated Human Footprint data into our spatial and species-level analyses to capture its
428 potential impact on globally significant concentrations of range-restricted PD. Our metrics represent
429 the first integration of data on environmental pressure affecting terrestrial vertebrates into global
430 prioritisations of imperilled PD.

431 Reptiles have the highest scores of our spatial metric, Human Impacted Phylogenetic Endemism
432 (HIPE), meaning they are faring worse than amphibians, birds and mammals, and contribute the
433 highest levels of imperilled PD per grid cell. Reptilian contributions to global patterns of tetrapod HIPE
434 are greatest in arid and semi-arid regions, particularly in the Middle East and Southern, North and the
435 Horn of Africa (Figure 2d, Figure 3a)—areas often overlooked in global prioritisations of terrestrial
436 conservation importance for other tetrapod classes^{7,13,14,22,25}. Thus, the inclusion of reptiles in global
437 analyses of this kind is crucial to improve accuracy when attempting to value terrestrial vertebrate
438 diversity for conservation at national, regional and global scales.

439 Global patterns of tetrapod HIPE emphasise the importance of regions where large amounts of PD are
440 wholly restricted to areas under high human impact; particularly Central America and the Caribbean,
441 Madagascar, the Western Ghats and large swathes of Southeast Asia (Figure 2c), and echo general
442 patterns of Biodiversity Hotspots⁵⁵. These grid cells represent areas of high urgency for conservation
443 of global PD. As HIPE alters the effective range of each species under the assumption that a greater
444 proportion of the range persists in grid cells under lower human impact, it also increases the relative
445 importance of these grid cells. We therefore also highlight areas of the Amazon Basin, the Namib

446 coast of Africa, Central Africa, Northern Australia—regions not captured by existing Biodiversity
447 Hotspots—and the highlands of Borneo (Figure 2b) as long-term conservation priorities, where
448 activities to limit future human impact are more pertinent.

449 At the species level, reptiles embody more unique evolutionary history than amphibians, birds or
450 mammals. Turtles tend to have particularly long terminal branches, indicating that each turtle species
451 tends to represent large amounts of unique evolutionary history. It is troubling to note that, across
452 tetrapods, Data Deficient and threatened species also generally comprise more unique evolutionary
453 history than non-threatened species. Our species-level metric, Human Impacted Terminal Endemism
454 (HITE), prioritises species with long terminal branches restricted to small ranges under high human
455 impact. Large numbers of small-ranged amphibians and lizards tend to be on long terminal branches
456 and occur in areas of high human impact, and our metric highlights these groups as of major
457 conservation concern.

458 Many of the highest-ranking HITE tetrapods which have also been classified by the IUCN Red List as
459 Endangered or Critically Endangered are also recognised as priority Evolutionarily Distinct and
460 Globally Endangered (EDGE) species⁵⁶. However, as HITE does not consider IUCN Red List extinction
461 risk data, and uses only phylogeny, range size and Human Footprint, we also identify species of
462 conservation importance which are currently unassessed or listed as Data Deficient by the IUCN.
463 Indeed, we found that Data Deficient tetrapods tend to have HITE scores comparable to those of
464 species listed as Endangered or Critically Endangered. This pattern is particularly pronounced in
465 lizards, snakes and amphibians, where considerably greater proportions of the highest-ranking HITE
466 species for these groups are Data Deficient than either birds or mammals. This suggests that many of
467 the poorly-known amphibians and reptiles are likely to be highly evolutionarily distinct and restricted
468 to regions of intense human pressure. Although such prevalence of high-ranking Data Deficient HITE
469 species is likely driven by higher proportions of data deficiency in amphibians (22%) and reptiles (15%)

470 compared with birds (0.5%) and mammals (14%)²⁷, it also highlights the urgent need to assess the
471 extinction risk facing these species in areas of high human impact.

472 Our case study of the poorly-known lizard genus *Dibamus* underlines the amount of uncertainty we
473 currently face when identifying conservation priorities and estimating impacts of species loss across
474 the tree of life. Our estimation of potential loss of reptilian phylogenetic diversity in this clade varies
475 across four orders of magnitude depending on our assumptions of uncertainty in both phylogeny and
476 extinction risk. Although this is an extreme example, our lack of knowledge of extinction risk and
477 phylogenetic relationships across the reptilian tree of life mean any estimations of potential loss of
478 diversity may be significant underestimates.

479 It is likely that, without conservation action, we will face losses of billions of years of unique
480 amphibian and reptilian evolutionary history worldwide. While greater research efforts are needed to
481 elucidate the phylogenetic relationships, distribution and population status of poorly known reptiles
482 and amphibians, current and future conservation efforts also need to focus on regions, lineages and
483 species that hold or represent disproportionate amounts of imperilled PD.

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- 597

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605 Author Contributions

606 R.Gumbs, C.L.G., J.R., N.R.O. conceived the study. R.Gumbs, C.L.G., J.R., M.H., S.M., U.R., W.J.

607 designed the analyses. R.Gumbs conducted the analyses. R.Grenyer, M.B., S.M., U.R. provided

608 reptile spatial data. C.L.G., J.R., M.B., M.H., N.R.O, S.M., U.R., W.J. provided technical support and

609 conceptual advice. C.L.G., J.R., N.R.O. supervised the study. R.Gumbs wrote the paper, with

610 substantial contributions from J.R, C.L.G., M.B., M.H , N.R.O., S.M., U.R., W.J.

611 Competing Interests statement

612 The authors have no competing interests to declare.