



Gumbs, R., Williams, R.C., Lowney, A.M. and Smith, Darrell (2020) Spatial and species-level metrics reveal global patterns of irreplaceable and imperiled gecko phylogenetic diversity. *Israel Journal of Ecology and Evolution*, 66 (3-4). pp. 239-252.

Downloaded from: <http://insight.cumbria.ac.uk/id/eprint/5687/>

Usage of any items from the University of Cumbria's institutional repository 'Insight' must conform to the following fair usage guidelines.

Any item and its associated metadata held in the University of Cumbria's institutional repository Insight (unless stated otherwise on the metadata record) may be copied, displayed or performed, and stored in line with the JISC fair dealing guidelines (available [here](#)) for educational and not-for-profit activities

provided that

- the authors, title and full bibliographic details of the item are cited clearly when any part of the work is referred to verbally or in the written form
- a hyperlink/URL to the original Insight record of that item is included in any citations of the work
- the content is not changed in any way
- all files required for usage of the item are kept together with the main item file.

You may not

- sell any part of an item
- refer to any part of an item without citation
- amend any item or contextualise it in a way that will impugn the creator's reputation
- remove or alter the copyright statement on an item.

The full policy can be found [here](#).

Alternatively contact the University of Cumbria Repository Editor by emailing insight@cumbria.ac.uk.

1 Spatial and species-level metrics reveal global patterns of
2 irreplaceable and imperiled gecko phylogenetic diversity

3 Rikki Gumbs*^{1,2,3}, Rachel C Williams⁴, Anthony M Lowney⁵, Darrell Smith⁶

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

5 7PY, United Kingdom

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

7 South Kensington, London

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

9 Kingdom

10 4. Department of Biology, Duke University, Durham, NC 27708, USA

11 5. Fitzpatrick Institute of African Ornithology, DST-NRF Centre of Excellence, University of Cape Town,

12 South Africa

13 6. Centre for National Parks and Protected Areas, University of Cumbria, Ambleside, United Kingdom

14 *rikki.gumbs@zsl.org

15

16 Abstract

17 Phylogenetic Diversity (PD) is increasingly recognised as a useful tool for prioritising species and
18 regions for conservation effort. Increased availability of spatial and phylogenetic data for reptiles now
19 facilitates their inclusion in conservation initiatives. Geckos are a highly divergent and diverse clade
20 that comprises almost 20% of global reptile diversity. Their global distribution is coincident with
21 numerous anthropogenic threats, making them worthy of conservation prioritisation. Here, we
22 combine phylogenetic, spatial distribution and extinction risk data for geckos with global human
23 encroachment data, to identify both regions and species representing irreplaceable gecko diversity at
24 risk from human pressure. We show that high levels of irreplaceable gecko diversity are restricted to
25 regions under intense human pressure, such as India, Sri Lanka and the Caribbean. There is a lack of
26 extinction risk data for the western regions of Angola and Namibia, and yet these regions harbour
27 high levels of irreplaceable diversity. At the species level, geckos display more unique PD than other
28 lizards and snakes, and are of greater conservation concern under our metric. The PD represented by
29 Data Deficient geckos is at comparable risk to that of Endangered species. Finally, estimates of
30 potential gecko diversity loss increase by up to 300% when species lacking extinction risk data are
31 included. Our analyses show that many evolutionarily unique gecko species are poorly known and are
32 at an increased risk of extinction. Targeted research is needed to elucidate the conservation status of
33 these species and identify conservation priorities.

34

35 Introduction

36 The current extinction crisis threatens unprecedented loss of global biodiversity (Ceballos et al., 2015;
37 Davis et al., 2018; Dirzo et al., 2014). As the financial resources available for conservation action are
38 limited (Mccarthy et al., 2012), we are forced to prioritise amongst species and regions for urgent and
39 effective conservation action. Phylogenetic Diversity (PD; Faith 1992), which measures the total
40 amount of evolutionary history represented by a set of taxa, is increasingly recognised as a critical
41 component of biodiversity for conservation (Mace et al., 2003; Pollock et al., 2017; Rosauer et al.,
42 2017; Weitzman, 1998). PD links evolutionary history with the maintenance of future options for
43 humanity (Faith, 1992; Owen et al., 2019). PD is associated with increased ecosystem productivity
44 (Cadotte, 2013), and has been linked to plants with medicinal uses (Forest et al., 2007). It is
45 recognised as an indicator for “nature’s contributions to people” through the maintenance of options
46 by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES,
47 2018).

48 PD is a useful tool for prioritising species (e.g. Isaac et al. 2007; Faith 2008; Nunes et al. 2015) and
49 regions (e.g. Rosauer et al. 2009; Safi et al. 2013; Pollock et al. 2017) for conservation effort; it can be
50 used to both count the number of units of biodiversity (as units of branch length, e.g. millions of
51 years) and the difference in these units between and amongst taxa (e.g. summed branch lengths
52 spanning different species communities). One notable application of PD in conservation is the
53 Zoological Society of London’s EDGE of Existence programme (www.edgeofexistence.org). The EDGE
54 of Existence programme uses the EDGE metric (Isaac et al., 2007) to identify priority ‘EDGE species’
55 harbouring disproportionate amounts of threatened PD, and funds conservation projects on these
56 species through early-career, in-country conservationists.

57 Effective prioritisation for conservation requires comprehensive data on both the irreplaceability (e.g.
58 endemism, contribution to global PD) and vulnerability (e.g. extinction risk, increased human
59 pressure) of the species or region under consideration (Brooks et al., 2006). The availability of

60 extensive extinction risk data (in the form of IUCN Red List assessments), distribution and
61 phylogenetic data have facilitated comprehensive species-level and spatial phylogenetically-informed
62 prioritisations of birds and mammals (Isaac et al., 2007; Jetz et al., 2014; Pollock et al., 2017; Rosauer
63 et al., 2017; Rosauer and Jetz, 2015) and, to a certain extent, amphibians (Isaac et al., 2012; Safi et al.,
64 2013).

65 Despite comprising more than 11,000 species (Uetz et al., 2016), reptiles have, until recently, been
66 largely overlooked by global conservation prioritisation efforts. Roll et al. (2017) used the first dataset
67 of global distribution data to identify regions of irreplaceable reptilian diversity, and Gumbs et al.
68 (2018) utilised recently-published species-level phylogenetic data (Tonini et al. 2016) to generate the
69 first EDGE prioritisation for reptiles. However, Gumbs et al. (2018) restricted their prioritisation to
70 reptiles with non-Data Deficient IUCN Red List assessments, omitting more than 50% of reptile
71 species. As of October 2019, more than 40% (~4,200 spp.) of described, extant reptile species remain
72 either unassessed or listed as Data Deficient (> 1,100 spp.) by the IUCN Red List (IUCN, 2016; Uetz et
73 al., 2016).

74 The omission of Data Deficient species when assessing the loss of evolutionary history can lead to
75 significant underestimations of potential loss (Veron et al., 2016). Indeed, Gumbs et al. (2019)
76 estimated that, due to lack of both genetic and extinction risk data for the enigmatic squamate genus
77 *Dibamus*, uncertainty around the potential loss of evolutionary history across the genus spanned four
78 orders of magnitude, from 100,000 years to more than 1 billion years of PD. Though analyses
79 identifying highly irreplaceable regions or species are now possible for reptiles, the lack of extinction
80 risk data has generally precluded a truly global assessment of conservation priorities. To circumvent
81 the lack of extinction risk data for the world's reptiles, we can estimate spatial vulnerability using the
82 Human Footprint Index (HF), a terrestrial dataset of cumulative human pressures on the environment
83 (Sanderson et al., 2002; Venter et al., 2016). We can then measure species vulnerability by weighting
84 HF against global patterns of irreplaceable reptilian diversity (Gumbs et al 2019).

85 Despite comprising only 17% of reptilian species richness, geckos account for 50% of the lizard species
86 identified as conservation priorities when ranked by evolutionary uniqueness, range restriction and
87 overlap with regions of high human pressure (Gumbs et al., 2019). Similarly, one in five “Top 100”
88 priority EDGE Reptiles—where Evolutionary Distinctiveness is weighted by extinction risk—are geckos
89 (Gumbs et al., 2018). The prominent presence of geckos in these phylogenetically-informed
90 prioritisations reflects their vast evolutionary heritage, extreme geographical range restriction, and
91 disproportionately low levels of coverage in protected areas (Meiri, this issue).

92 Here, we apply existing spatial and species-level metrics to explore global patterns of irreplaceable
93 and imperiled gecko PD. We highlight regions of low human pressure that represent potential
94 safeguards for otherwise vulnerable PD and centres of gecko diversity that are predominantly
95 restricted to regions of high human pressure. We use species-level metrics to compare gecko diversity
96 and vulnerability to other large lepidosaur clades. Finally, we identify both species and regions
97 comprising large amounts of unassessed and potentially imperiled gecko PD.

98

99 Methods

100 Data

101 We used distribution polygons for geckos (Gekkota) from the Global Assessment of Reptile
102 Distributions (GARD)(Roll et al., 2017), which we mapped at 96.5 km x 96.5 km resolution using a
103 Mollweide equal-area projection. Phylogenetic data were taken from a published distribution of
104 10,000 phylogenetic trees for lepidosaurs (Tonini et al., 2016), from which we randomly sampled 100
105 fully-resolved phylogenetic trees and subset them to contain only gecko species for which we had
106 distribution data. We limited our analyses to species for which both spatial and phylogenetic data
107 were available, accounting for 1,582 species of gecko (85% of all gecko species)(Uetz et al., 2016).
108 Extinction risk data were taken from the IUCN Red List for 1,135 geckos with Red List assessments, of
109 which 992 could be matched to gecko species in the phylogeny (IUCN, 2016)

110 We used the 2009 Human Footprint index (HF)(Venter et al., 2016) to represent broad spatial
111 patterns of human pressure globally. The HF index evaluates grid cells based on multiple metrics of
112 human encroachment (built environments, crop land, pasture land, human population density, night-
113 time lights, railways, roads, navigable waterways), and assigns a HF score between 0 (lowest) to 50
114 (highest) to each cell (Venter et al., 2016).

115 Spatial patterns of irreplaceable gecko diversity

116 There are five defined categories of human pressure which broadly represent equal areas of land
117 worldwide: 'no pressure' (HF = 0), 'low pressure' (HF = 1-2), 'moderate pressure' (HF = 3-5), 'high
118 pressure' (HF = 6-11), and 'very high pressure' (HF = 12-50). We assigned a weighting to each grid cell
119 according to its human pressure category. Grid cells under 'very high' human pressure (HF = 12-50)
120 received a HF-weighted value of 0.2 (i.e. we considered the grid cell to be 'worth' 0.2 of a grid cell
121 experiencing no human pressure), whereas grid cells in the intermediate categories of human
122 pressure were valued at 0.4 ('high pressure'), 0.6 ('moderate pressure') and 0.8 ('low pressure'). Grid

123 cells under 'no pressure' (HF = 0) received a HF-weighted value of 1, to provide a broad linear
124 valuation of global grid cells at a broad scale (see Gumbs et al. 2019).

125 We resampled the categorised HF data from 1 km x 1 km resolution to the same 96.5 km x 96.5 km
126 resolution used for gecko spatial data by taking the average HF-weighted value across all 1 km x 1 km
127 grid cells comprising each 96.5 km x 96.5 km cell. The use of this broad metric of general human
128 pressure across a coarse resolution of grid cells is to provide a measure of value, in terms of human
129 pressure, against which we can weight the coarse resolution gecko distribution data.

130 To identify regions of highly irreplaceable gecko diversity restricted to areas of high human pressure,
131 we used the spatial metric Human Impacted Phylogenetic Endemism (HIPE) (Gumbs et al., 2019). HIPE
132 is an extension of Phylogenetic Endemism (PE) (Rosauer et al., 2009) which incorporates the Human
133 Footprint index (HF) to weight each grid cell globally based on its HF categorisation. Whereas
134 standard PE multiplies each branch of the phylogeny by the number of grid cells across which it is
135 distributed—with each grid cell being equally valued in the calculation—HIPE redistributes PE across
136 grid cells based on their HF-weighted value.

137 When HIPE distributes the length of a branch across grid cells, grid cells with larger HF-weighted
138 values (i.e. lower human pressure) receive a proportionally greater amount of the branch's length.
139 However, when all grid cells across which a branch is distributed have equal HF-weighted values, HIPE
140 distributes the branch lengths evenly and is equal to standard PE (for further details, see Gumbs et al.
141 2019). Therefore, HIPE highlights two phenomena not captured by standard PE: 1) grid cells under
142 high human pressure containing large amounts of PD which is wholly—or largely—restricted to highly
143 impacted grid cells (i.e. regions of high HF with high PE even after PE is redistributed to areas of lower
144 human pressure); 2) grid cells of low human pressure which represent high potential value to
145 branches also present in grid cells under more intense human pressure (i.e. regions of low HF with
146 high PE following the redistribution of PE under HIPE).

147 We calculated both standard PE and HIPE 100 times for geckos—using the distribution of 100 subset
148 phylogenetic trees—across all grid cells in which species occur, and here present the median values
149 for each grid cell. To determine the relationship between global patterns of PE and Human Footprint,
150 we ran an ANOVA of PE values from each grid cell amongst the five categories of Human Footprint
151 outlined above, from ‘very high pressure’ to ‘low pressure’, and applied Tukey’s Honest Significant
152 Difference (HSD) test to identify pairwise differences in PE across the Human Footprint categories.

153 In order to determine regions where the extinction risk of irreplaceable gecko diversity under
154 potential high human impact (i.e. high HIPE grid cells) was least known, we recalculated global HIPE
155 values for geckos which were either unassessed or listed as Data Deficient by the IUCN Red List. We
156 repeated these analyses across all 100 gecko phylogenies and calculated the median value of
157 unassessed or Data Deficient imperiled gecko diversity for each grid cell. We then scaled the value of
158 each grid cell by that of the maximum HIPE grid cell value when all geckos were included. This score,
159 between 0 and 1, provides a composite measure of the amount of HIPE in a grid cell (imperiled
160 diversity) and the extent to which it was unassessed. Values close to 1 represented grid cells with
161 large amounts of poorly-known gecko diversity. We examined the relationships amongst global
162 patterns of HIPE, gecko species richness and richness of unassessed/Data Deficient geckos using
163 Pearson’s correlation corrected for spatial autocorrelation in the R package ‘Spatialpack’ (Dutilleul et
164 al., 1993; Osorio and Vallejos, 2018).

165 Regions of high human impact are likely to require different conservation actions than those under
166 low human impact (e.g. restoration and intervention vs. land protection). We therefore partitioned
167 global HIPE into regions of two extremes: ‘very high’ human pressure (HF \geq 12, HF-weighted grid cell
168 score = 0.2) and ‘no’ pressure (HF = 0, HF-weighted grid cell score = 1) to represent regions likely in
169 need of differing conservation action. To determine the amount of endemic PD restricted to these
170 regions of extreme high or low human pressure, we also calculated standard Phylogenetic Endemism
171 for all global grid cells.

172 For each grid cell under very high human pressure, the proportion of HIPE to PE in the grid cell is a
173 measure of the proportion to which the phylogenetic branches present in the cell are restricted to
174 regions of very high human pressure. As HIPE = PE for a grid cell when all grid cells in which the
175 phylogenetic branches occur have equal HF-weighted distribution scores, grid cells under very high
176 human pressure with proportional HIPE/PE scores close to 1 comprise phylogenetic diversity
177 extremely restricted to regions of very high human pressure, and are therefore both highly
178 irreplaceable and under intense human pressure.

179 Conversely, for each grid cell under 'no' human pressure, the proportional HIPE/PE can never be
180 below 1, as HIPE for grid cells with a HF-weighted distribution score of 1 is equal to PE. Therefore, grid
181 cells under no human pressure with the greatest proportional HIPE/PE scores represent regions
182 where the phylogenetic branches are also distributed across regions of high human pressure,
183 meaning the grid cells of no human pressure receive a greater proportion of the branch length under
184 HIPE. These regions are therefore potential refugia for otherwise imperiled branches of the tree of
185 life.

186 [Species-level priorities for gecko conservation](#)

187 We used our global dataset on gecko distributions and HF-weighted grid cell values to identify gecko
188 species which represent large amounts of unique PD that is restricted to regions under high human
189 pressure. We used terminal branch length (TBL) as a measure of unique PD at the species level. The
190 TBLs in a phylogenetic tree represent the unique PD of each species (or 'tip') in the tree, as each
191 species resides alone on the tip of each terminal branch.

192 Though other metrics exist which assign species-level PD scores from the phylogeny (e.g.
193 'Evolutionary Distinctiveness', Isaac et al. 2007), the partition of internal branches amongst species is
194 either implicitly or explicitly influenced by the perceived extinction risk of the descendant species
195 (Faith, 2008). As we are using a measure of spatial irreplaceability—in the form of range size—and

196 vulnerability—in the form of HF—to weight PD, rather than extinction risk values, the partitioning of
197 internal branches amongst species is more problematic (Gumbs et al., 2019).

198 To identify priority species restricted to small regions under intense human pressure, we used the
199 metric Human Impacted Terminal Endemism (HITE) (Gumbs et al. 2019), which weights the terminal
200 branch length of each species by the summed HF-weighted distribution score of each species. The HF-
201 weighted distribution score is simply the summed HF-weighted values for all grid cells in which the
202 species occurs, and the TBL is divided by this value to calculate HITE. For species restricted to grid
203 cells under high human pressure—or low HF-weighted values—their HITE score is therefore increased
204 relative to species with equal TBLs which are distributed across pristine—or high HF-weighted value—
205 grid cells. We present HITE results in terms of MY/km², where the area of each grid cell has been
206 scaled according to its HF-weighted value.

207 We compared the distribution of TBL and HITE scores between geckos and other major lepidosaur
208 clades: Anguimorpha (anguid lizards, monitor lizards, *Shinisaurus*), Iguania (iguanas, anoles,
209 chameleons and agamid lizards), Lacertoidea (lacertid, teiid, and gymnophthalmid lizards, and
210 amphisbaenians), Scincoidea (skinks), and Serpentes (snakes). We also compared TBL and HITE scores
211 among the gecko families Carphodactylidae, Diplodactylidae, Eublepharidae, Gekkonidae,
212 Phyllodactylidae, Pygopodidae and Sphaerodactylidae. We compared TBL and HITE values across
213 groups using ANOVA, and applied Tukey's Honest Significant Difference (HSD) test to identify pairwise
214 differences between groups.

215 To examine the relationship among extinction risk, TBL and HITE, we compared the distribution of
216 both TBL and HITE in relation to Red List status. We used ANOVA (with Tukey's HSD test) to compare
217 the distributions of TBL and HITE across Data Deficient, Least Concern, Near Threatened, Vulnerable
218 (VU), Endangered (EN) and Critically Endangered (CR) IUCN Red List categories, along with those
219 species Not Evaluated (NE) by the IUCN Red List.

220 The EDGE metric (Isaac et al., 2007) is an existing tool to prioritise species for conservation based on
221 their contribution to PD and their extinction risk. However, EDGE scores do not exist for species which
222 are Data Deficient or unassessed by the IUCN Red List, with priority ‘EDGE Species’ being defined as
223 those with above median phylogenetic scores (Evolutionary Distinctiveness) and in a threatened
224 category of the IUCN Red List (VU, EN, CR). To determine the relationship of priority gecko species
225 identified by the HITE metric with priority species identified by the EDGE metric, we ran a correlation
226 of the HITE rankings of geckos assessed as VU, EN or CR against published EDGE rankings of geckos
227 (Gumbs et al., 2018).

228 Unlike the EDGE metric, the use of spatial vulnerability data to identify priorities, rather than
229 extinction risk data, permits the inclusion of species with no formal extinction risk assessment in our
230 species-level prioritisation. We therefore highlight the highest-ranking geckos—in terms of HITE
231 score—currently unassessed or listed as Data Deficient by the IUCN Red List as priority species for
232 further research. These species represent large amounts of unique PD and are likely to be imperiled
233 by intense human pressure.

234 To determine the potential underestimation of PD loss when unassessed or Data Deficient species are
235 excluded from analyses of biodiversity loss across geckos, we simulated the loss of species from the
236 gecko phylogeny under three scenarios. For the first scenario, under a ‘baseline’ scenario, species in
237 the three threatened categories of the IUCN Red List (VU, EN, CR) became ‘extinct’ and were dropped
238 from the phylogeny, along with their terminal branch lengths (which increase in length by
239 incorporating the shared branch with a sister, should the sister be lost from the phylogeny). For the
240 second scenario, we considered a ‘moderate’ outcome, where—along with all threatened species—
241 we randomly selected 20% of unassessed or Data Deficient species to become extinct, in line with
242 findings that ~20% of Data Deficient reptiles are likely to be threatened (Bland and Böhm, 2016).
243 Finally, we simulated a ‘worst case’ scenario, where all threatened, Data Deficient and unassessed
244 species became extinct and were dropped from the phylogeny. We then summed the PD remaining in

245 each phylogeny following the removal of species and subtracted this from the total PD of the
246 unaltered gecko phylogeny to calculate PD loss and repeated this over each of the 100 phylogenies.

247

248

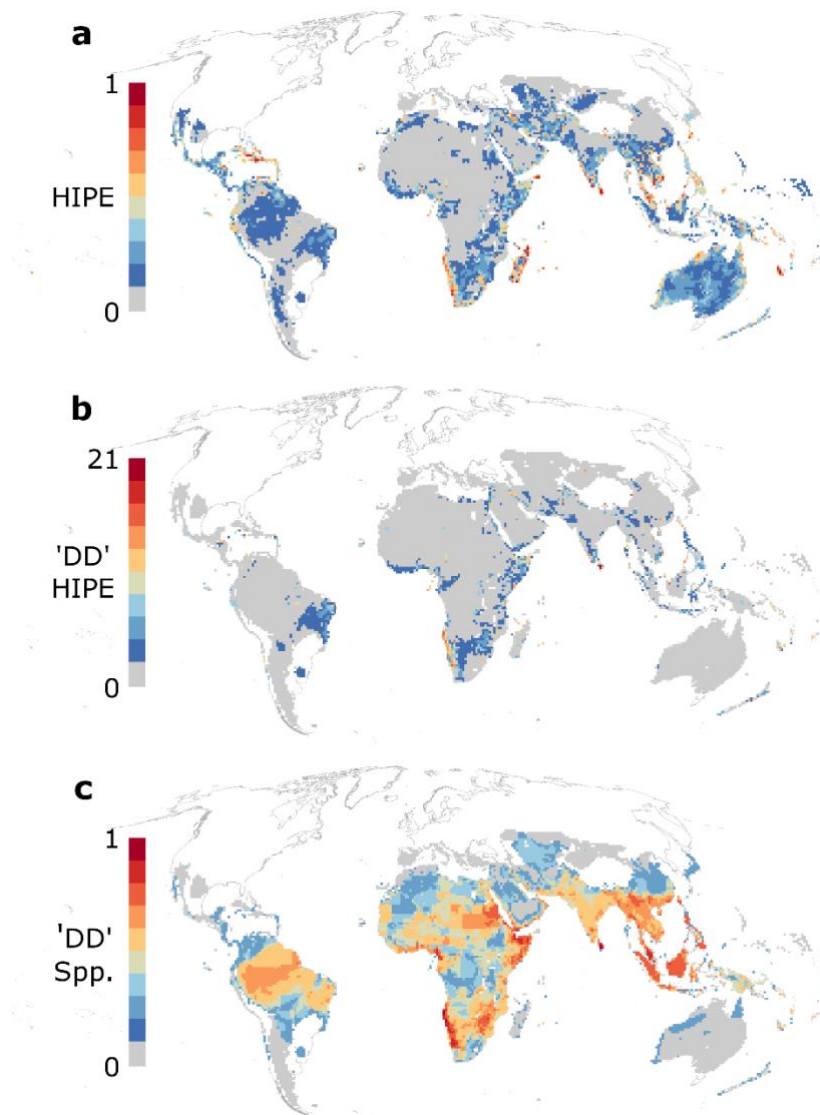
249 Results

250 Spatial patterns of irreplaceable gecko diversity

251 Grid cells under 'high' and 'very high' human pressure ($HF \geq 6$) harbour greater levels of Phylogenetic
252 Endemism (PE; median = 1.0 and 0.99, respectively) than grid cells under 'moderate', 'low' and 'no'
253 human pressure (all adjusted p-values for both 'high' and 'very high' vs. lower human pressure
254 categories from Tukey's Honest Significant Differences < 0.01).

255 Global patterns of Human-Impacted Phylogenetic Endemism (HIPE) for geckos are predominantly
256 concentrated across the tropics and subtropics, particularly across islands and more coastal regions of
257 landmasses (Figure 1a). The regions of highest importance under HIPE include Madagascar, the
258 western coast of southern Africa, Socotra, the Caribbean, the Western Ghats of India, Sri Lanka,
259 peninsular Malaysia, northern Australia and New Caledonia (Figure 1a). There are low levels of
260 irreplaceable and human-impacted gecko PD, relative to all reptiles (Gumbs et al., 2019), throughout
261 Central America.

262 Global patterns of unassessed or Data Deficient gecko species richness are weakly correlated with
263 both overall species richness ($r = 0.25$, e.d.f. = 97.3, $p = 0.01$) and global HIPE ($r = 0.15$, e.d.f. = 534.8,
264 $p < 0.0001$; Figure 1b). Regions with particularly high levels of irreplaceable gecko diversity (i.e. high
265 HIPE values) and also relatively low levels of extinction risk knowledge (i.e. high levels of
266 unassessed/Data Deficient species) are Sri Lanka and the western coast of southern Africa (Figure 1c).
267 High levels of extinction risk knowledge across the Caribbean and Madagascar capture large
268 proportions of high HIPE regions.



269

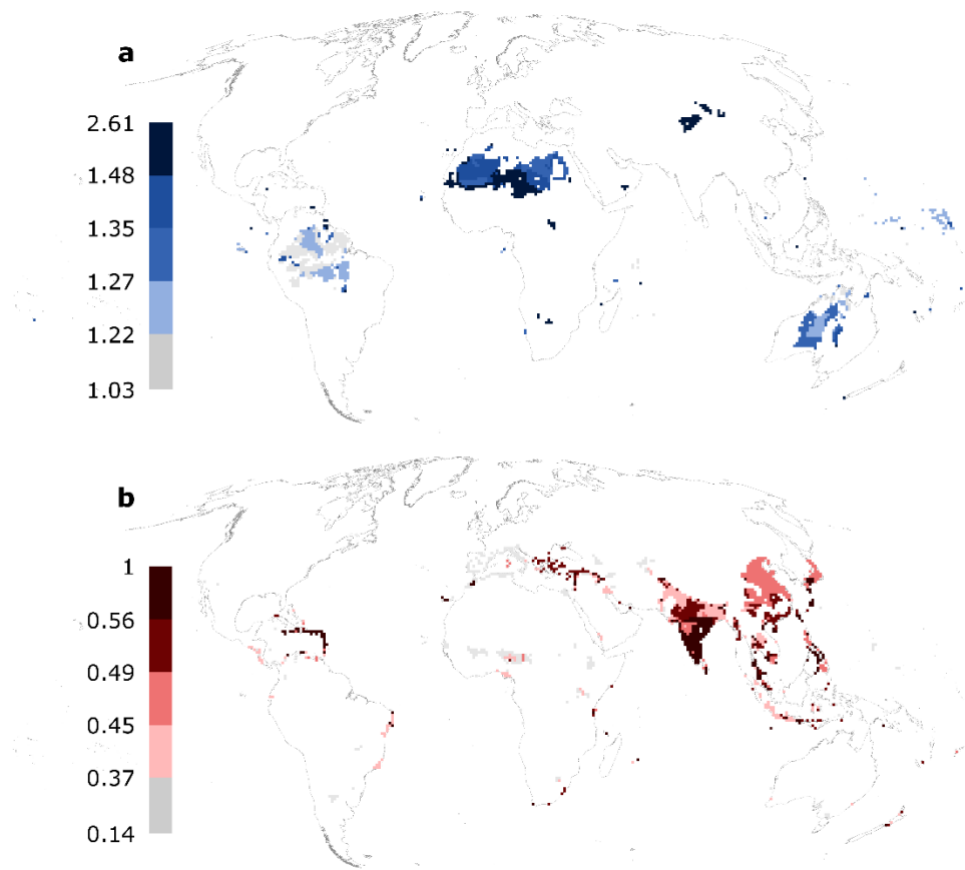
270 **Figure 1: Spatial patterns of total and unassessed gecko diversity.** a) global patterns of gecko Human-
 271 Impacted Phylogenetic Endemism (HIPE), scaled between 1 (max) and 0 (min); b) composite measure
 272 of magnitude of HIPE and proportion of HIPE which is contributed by unassessed or Data Deficient
 273 ('DD') species for each grid cell, scaled between 1 (max) and 0 (min) with values closest to 1
 274 representing regions of high HIPE with high levels of 'DD'; c) richness of 'DD' gecko species present in
 275 each grid cell. Values are for 96.5 × 96.5 km grid cells under Mollweide projection.

276

277 HIPE values for grid cells under 'no' human pressure (HF = 0) increased by a median of 30% from
 278 those for standard PE (range = 3% - 161% increase), due to the redistribution of branch lengths from

279 higher HF-weighted grid cells to those under lower human pressure (Figure 2a). The lowest levels of
280 increase in HIPE scores across no pressure grid cells (HIPE/PE values closest to 1), which indicate grid
281 cells with PD highly endemic to regions of no human pressure, occur across the Amazon Basin,
282 Australia and Oceanic islands (Figure 2a, grey and lightest blue grid cells). The grid cells under no
283 pressure with the highest HIPE/PE ratios represent regions where the phylogenetic branches present
284 are also distributed across regions under higher human pressure, and these are mainly distributed
285 across the Sahara and Central Asia (Figure 2a, darkest blue grid cells).

286 For grid cells under very high human pressure ($HF \geq 12$), HIPE values comprised a median of 46% of
287 the original PE value before redistribution of PD according to HF-weighted grid cell scores. Grid cells
288 under very high human pressure whose PD was also distributed across regions of grid cells of less
289 intense human impact (HIPE/PE values closest to 0) are distributed across the Mediterranean, Sub-
290 Saharan Africa, central and southern Asia, Indonesia and the Atlantic coast of Brazil (Figure 2b, grey
291 and light pink grid cells). Regions of highly irreplaceable gecko PD that is predominantly restricted to
292 grid cells of high human pressure (HIPE/PE values closest to 1) are distributed across the Philippines,
293 Japanese islands, Peninsular Malaysia, Sri Lanka and large swathes of India (Figure 2b, darkest red grid
294 cells).



295

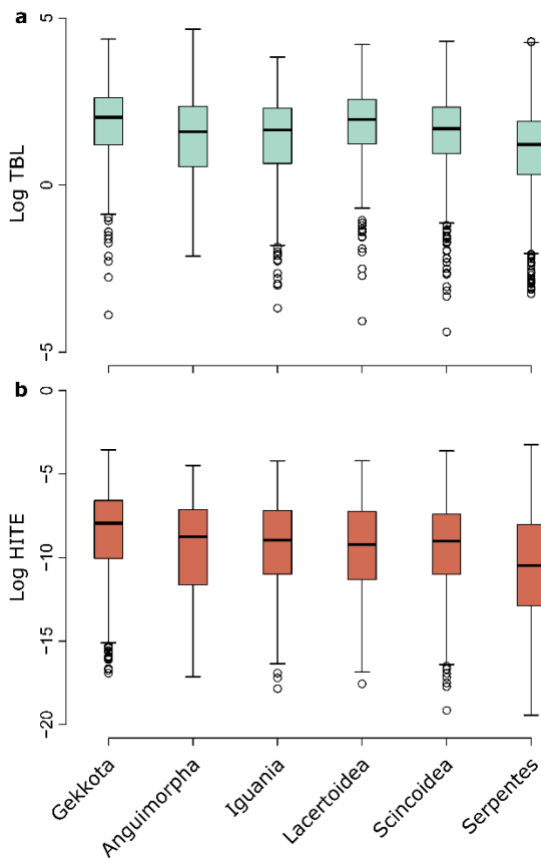
296 **Figure 2: The ratio of grid cell values under Human-Impacted Phylogenetic Endemism (HIPE)**
 297 **compared to standard PE.** a) regions of 'no' human pressure (HF = 0) are highlighted, where values
 298 close to 1 represent grid cells with Phylogenetic Diversity that is highly endemic to no pressure
 299 regions (HF = 0), and values closer to the max represent grid cells with PD also distributed across
 300 regions under high human pressure; b) regions of very high human pressure (HF ≥ 12) are highlighted,
 301 where values close to 0 represent grid cells with PD also distributed in regions under lower human
 302 pressure, and values closest to 1 represent grid cells where the PD is highly endemic to regions under
 303 very high human pressure. Values are for 96.5 × 96.5 km grid cells under Mollweide projection.

304

305 [Species-level priorities for gecko conservation](#)

306 Gecko species tend to represent significantly larger amounts of unique PD (median terminal branch
 307 length = 7.6 MY) than anguimorph (4.9 MY) and iguanid lizards (5.2 MY), skinks (5.3 MY) and snakes

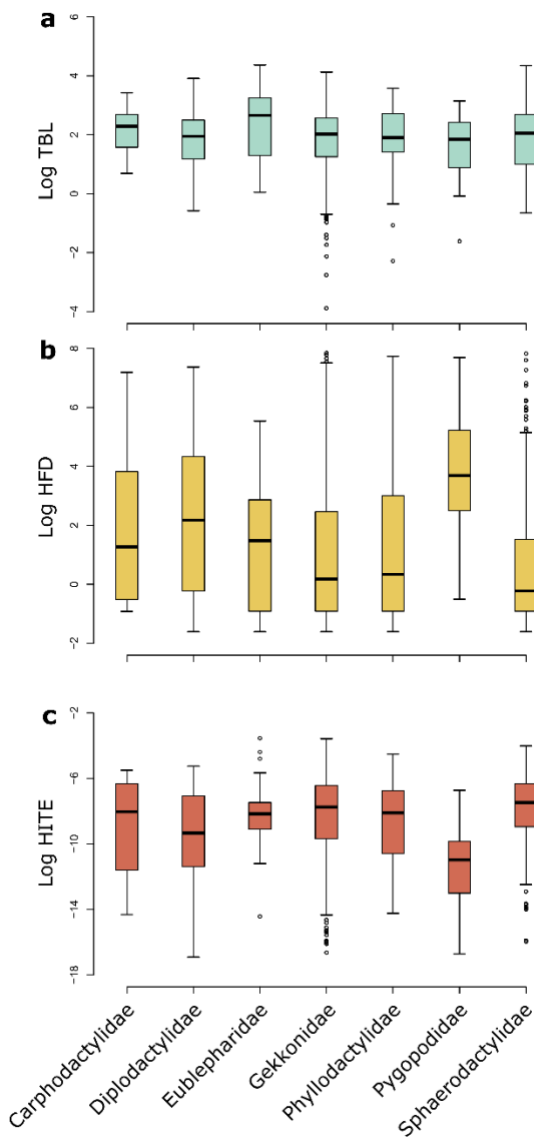
308 (3.4 MY; adjusted p-values from Tukey Honest Significant Differences < 0.005), with lacertoid lizards
 309 having similarly long terminal branches (median = 7.1 MY; adjusted p-value = 0.73; Figure 3a).
 310 Similarly, geckos have significantly higher HITE scores than other lepidosaur groups (median HITE =
 311 3.5×10^{-4} MY/km²; adjusted p-values < 0.05; Figure 3b).



312
 313 **Figure 3: Species-level measures of Phylogenetic Diversity for six major lepidosaur groups.** The
 314 distribution of a) terminal branch lengths (TBL), a measure of the unique contribution of a species to
 315 global Phylogenetic Diversity, and b) Human-Impacted Terminal Endemism scores, which weights the
 316 terminal branch of a species by its Human Footprint-weighted distribution.

317
 318 Within geckos, there is a weak but significant positive correlation between terminal branch length and
 319 range size (no. of grid cells; $\rho = 0.15$, $p < 0.0001$). Eublepharidae have significantly longer terminal
 320 branches (median = 7.6 MY) than other families (adjusted p-values < 0.05; Figure 4a), and are more

321 widely distributed than four of the six other gecko families (median no. of grid cells occupied = 12;
 322 Carphodactylidae = 6, Diplodactylidae = 14.5, Gekkonidae = 3, Phyllodactylidae = 3, Pygopodidae = 40,
 323 and Sphaerodactylidae = 2). Gecko families occur in grid cells under similar human pressure (median
 324 HF-weighted grid cell value = 0.4 for Eublepharidae, Gekkonidae, Phyllodactylidae and
 325 Sphaerodactylidae and 0.6 for Carphodactylidae, Diplodactylidae and Pygopodidae), resulting in the
 326 HF-weighted distribution scores strongly reflecting overall range size ($\rho = 0.9$, $p < 0.0001$). The
 327 positive relationships between 1) terminal branch length and range size, and 2) range size and HF-
 328 weighted distribution score reduces the influence of the longer terminal branches of eublepharid
 329 geckos, and results in HITE scores which are relatively similar across all groups (Figure 4c).



331 **Figure 4: Species-level measures of Phylogenetic Diversity and Human Footprint for the seven gecko**

332 **families.** The distribution of a) terminal branch lengths (TBL); b) HF-weighted distribution (HFD)

333 scores, with lower values indicating a species is range restricted and occurs in regions of high human

334 pressure; and c) Human-Impacted Terminal Endemism (HITE) scores across the seven gecko families.

335

336 Gecko terminal branch lengths do not increase with increased extinction risk ($p = 0.02$, $p = 0.51$;

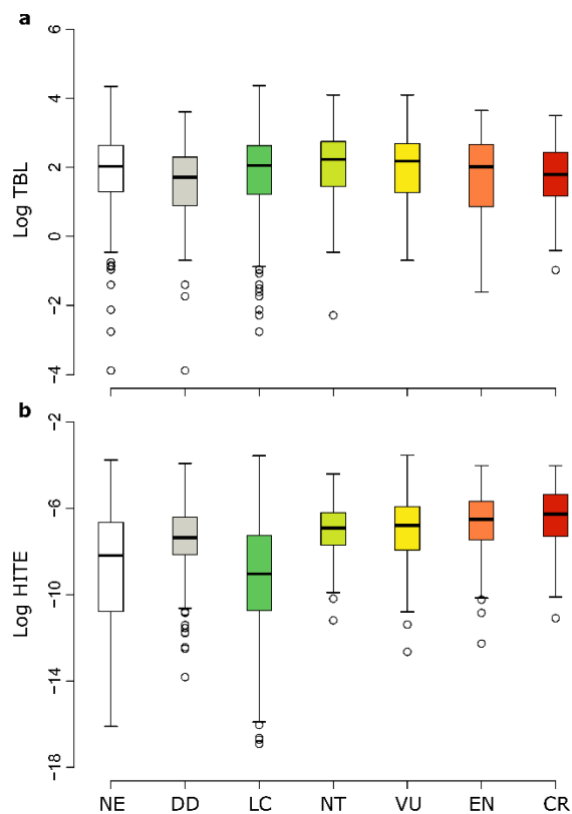
337 Figure 5a), however gecko HITE does increase with increased extinction risk ($p = 0.18$, $p < 0.0001$).

338 Gecko species Not Evaluated by the IUCN Red List have comparable HITE scores to Near Threatened

339 geckos, and Data Deficient (DD) geckos have comparable HITE scores to Endangered geckos (adjusted

340 p -value = 0.51), with only Critically Endangered geckos having significantly greater HITE scores

341 (adjusted p -value = 0.0001; Figure 5b).



342

343 **Figure 5:** Species-level measures of Phylogenetic Diversity for geckos across IUCN Red List categories.

344 The distribution of a) terminal branch lengths (TBL) and b) Human-Impacted Terminal Endemism

345 (HITE) scores. NE = species Not Evaluated, or unassessed, by the IUCN Red List.

346

347 When limited to geckos listed in threatened IUCN Red List categories (VU, EN, CR), HITE rankings are

348 significantly positively correlated with EDGE rankings ($\rho = 0.18$, $p = 0.01$). A large majority (19/20) of

349 the highest-ranking threatened HITE geckos are also priority EDGE gecko species. The top 20 highest-

350 ranking HITE geckos which are unassessed or listed as DD by the IUCN Red List comprise 13 gekkonid,

351 four sphaerodactylid, two phyllodactylid and one eublepharid species (Table 1). The highest ranking

352 unassessed gecko is *Lepidodactylus yami*, known only from its type locality on Lanyu Island, Taiwan

353 (Meiri et al., 2018).

354

355 **Table 1:** Top 20 gecko species, when ranked by their Human-Impacted Terminal Endemism (HITE)

356 score, which are either unassessed (NE) or listed as Data Deficient (DD) by the IUCN Red List. TBL =

357 terminal branch length, a measure of the unique contribution of a species to global Phylogenetic

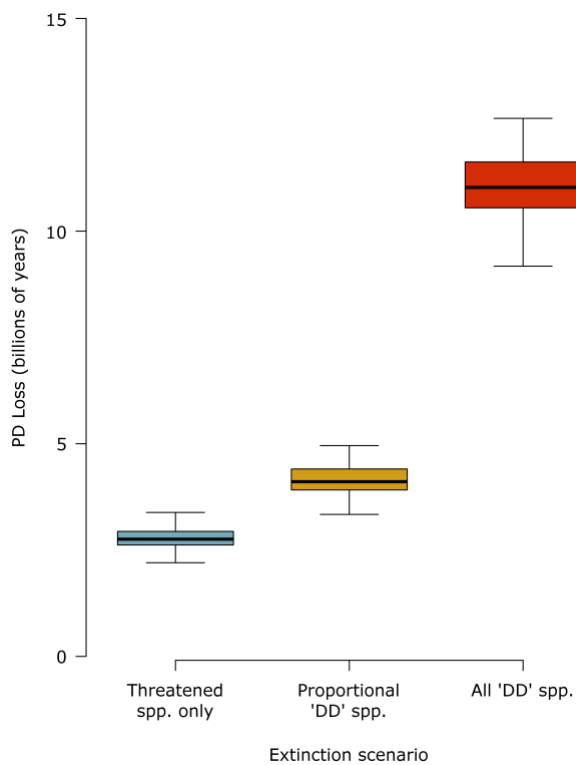
358 Diversity.

Family	Species	Red List Status	HF-weighted		
			distribution score	TBL	HITE
Gekkonidae	<i>Lepidodactylus yami</i>	NE	0.2	42.80	2.30
Gekkonidae	<i>Luperosaurus yasumai</i>	DD	0.2	36.82	1.98
Gekkonidae	<i>Lepidodactylus browni</i>	NE	0.2	27.53	1.48
Gekkonidae	<i>Luperosaurus gulat</i>	NE	0.2	26.76	1.44
Sphaerodactylidae	<i>Coleodactylus natalensis</i>	DD	0.2	24.90	1.34
Sphaerodactylidae	<i>Sphaerodactylus parvus</i>	NE	0.2	23.77	1.28
Eublepharidae	<i>Goniurosaurus toyamai</i>	NE	0.2	23.06	1.24

Phyllodactylidae	<i>Asaccus saffinae</i>	NE	0.2	20.24	1.09
Gekkonidae	<i>Cnemaspis upendrai</i>	NE	0.2	19.82	1.06
Gekkonidae	<i>Cnemaspis samanensis</i>	NE	0.2	19.64	1.05
Phyllodactylidae	<i>Thecadactylus oskrobapreinorum</i>	DD	0.2	15.90	0.85
Gekkonidae	<i>Cyrtodactylus irianjayaensis</i>	DD	0.4	31.63	0.85
Gekkonidae	<i>Cnemaspis scalpensis</i>	NE	0.2	15.70	0.84
Sphaerodactylidae	<i>Gonatodes lichenosus</i>	DD	0.4	30.61	0.82
Gekkonidae	<i>Cnemaspis kallima</i>	NE	0.2	15.08	0.81
Gekkonidae	<i>Nactus soniae</i>	NE	0.2	14.96	0.80
Sphaerodactylidae	<i>Sphaerodactylus shrevei</i>	NE	0.4	29.52	0.79
Gekkonidae	<i>Mediodactylus brachykolon</i>	NE	0.4	28.13	0.76
Gekkonidae	<i>Cnemaspis girii</i>	NE	0.2	13.25	0.71
Gekkonidae	<i>Luperosaurus iskandari</i>	DD	0.4	24.03	0.65

359

360 Estimates of gecko PD loss increase significantly when unassessed and Data Deficient species are
361 included. Under our ‘baseline’ scenario around 2.7 billion years of unique gecko PD is at risk of being
362 lost. This increases to 4.1 billion years under our ‘moderate’ species loss scenario (49% increase in PD
363 loss). Under our ‘worst case’ scenario, we stand to lose a median of 11 billion years of unique gecko
364 PD (300% increase; Figure 6).



365

366 **Figure 6: Loss of gecko PD under three extinction scenarios.** The extent of PD lost, in billions of years,
 367 if we were to lose gecko species under three scenarios: the 'Baseline', where all threatened species
 368 (VU, EN, CR categories on IUCN Red List) become extinct; the 'Moderate' scenario, where all
 369 threatened species and a random selection of 20% (following Bland and Böhm, 2016) of unassessed
 370 or DD species become extinct; and the 'Worst case' scenario, where all threatened, unassessed and
 371 Data Deficient species are lost. Analyses were repeated across 100 phylogenies to capture
 372 phylogenetic uncertainty.

373

374 Discussion

375 Our results reveal that global concentrations of highly irreplaceable gecko Phylogenetic Diversity (PD)
376 often coincide with regions most impacted by human activities. Further, we show that regions under
377 higher human pressure harbour greater levels of irreplaceable gecko PD (measured by Phylogenetic
378 Endemism; PE) than regions under lower human pressure.

379 When PE values are redistributed spatially in relation to levels of human pressure, the resulting
380 patterns of Human-Impacted PE (HIPE) for geckos, are largely congruent with global patterns of
381 endemism previously identified for reptiles (Gumbs et al., 2019; Roll et al., 2017), and biodiversity
382 hotspots in general (Mittermeier et al., 2004; Myers et al., 2000). However, low levels of HIPE
383 throughout mainland Central and South America reflect the overall lower diversity of geckos in the
384 Neotropics in comparison with the Old World and Australasia (Meiri, this issue).

385 Unsurprisingly, the distribution of large concentrations of irreplaceable and potentially imperilled
386 gecko PD (as measured by HIPE) lacking extinction risk data highlight regions of intersect between
387 high levels of both diversity and data deficiency (Figure 1). Particularly important regions for targeted
388 efforts to increase our knowledge of extinction risk are Sri Lanka and the western regions of Namibia
389 and Angola.

390 The temporal pattern of extinction risk assessments (or lack thereof) for geckos mirrors that for
391 amphibians (Tapley et al., 2018). Unassessed geckos are more than likely to be recently described
392 species, with more than 50% of unassessed species having been described since the turn of the
393 century (Meiri and Chapple, 2016; Uetz et al., 2016). We therefore suggest Tapley et al. (2018)'s
394 recommendations to amphibian researchers are also valid for gecko (and reptile) taxonomists, too.
395 Researchers involved in taxonomic descriptions or taxonomic revisions must make greater efforts to
396 include information relevant to IUCN Red List assessments and, wherever possible, take greater
397 responsibility for the assessment of extinction risk of the species they describe.

398 At the species-level, geckos harbour greater levels of unique PD (i.e. terminal branch length; TBL) than
399 other major squamate groups, reflecting both their divergence from other clades early in squamate
400 evolution, and ancient radiations across continents and islands (Tonini et al., 2016; Zheng and Wiens,
401 2016). Geckos, on average, have significantly smaller range sizes than other lepidosaurs (Meiri, this
402 issue; Roll et al. 2017). As a result, our species-level measure of irreplaceable and imperilled gecko PD
403 (Human-Impacted Terminal Endemism; HITE) is significantly larger in geckos than other lepidosaurs.
404 This indicates that significantly greater amounts of unique PD are coincident with regions of high
405 human pressure in geckos than other lepidosaur groups.

406 Within geckos, species of eublepharid geckos harbour the greatest levels of unique PD. However,
407 greater unique PD is linked to greater range size in geckos and this relationship results in all gecko PD
408 being similarly imperilled and irreplaceable at the species-level, once weighted by range size and
409 human pressure (i.e. HITE scores). Worryingly, Data Deficient (DD) geckos have similar range sizes
410 under comparable human pressure to species listed as Endangered by the IUCN Red List. This
411 heightened spatial vulnerability may be an overestimation of imperilment driven by the propensity of
412 poorly-studied lizards known only from their type locality (Meiri et al., 2018). However, as DD species
413 show a trend of greater conservation need than unassessed species—which, by definition, should be
414 similarly poorly-known—their elevated imperilment suggests that considerable amounts of PD are
415 poorly known and restricted to regions under intense human pressure.

416 Almost 50% of the priority unassessed or Data Deficient geckos highlighted here (Table 1) are known
417 only from their original description (Meiri et al., 2018). These nine species alone may account for
418 close to a quarter of a billion years of unique PD, and increased knowledge of their extinction risk—
419 and perhaps continued existence—is a crucial first step to determining the persistence of this
420 irreplaceable evolutionary history. Three-quarters of the priority unassessed and Data Deficient
421 species are island endemics and are predominantly distributed across Asia, including the highest-

422 ranking species, *Lepidodactylus yami*. One priority species, *Nactus soniae*, is suspected to be extinct
423 (Meiri et al., 2018). If so, this signifies an estimated PD loss of around 15 million years.

424 The HITE metric successfully captured 'EDGE' geckos, with 19 of the 20 priority species identified here
425 also being identified as EDGE Species (Gumbs et al. 2018). However, the benefit of the HITE metric is
426 its ability to circumvent the need for formal extinction risk assessments (e.g. IUCN Red List) to identify
427 species likely to be imperiled due to their ranges being restricted to regions facing broad and intense
428 human pressure. Therefore, the metric compliments existing PD prioritisation metrics by
429 incorporating currently unassessed or Data Deficient species with distribution data.

430 Conclusions

431 A globally significant amount of gecko phylogenetic diversity is potentially threatened, and billions of
432 years of additional gecko PD is at risk when we consider species lacking extinction risk data. Our
433 findings highlight the importance of incorporating species lacking extinction risk data into global
434 analyses for taxa with poor data coverage, such as geckos and reptiles more generally. Greater work is
435 required by herpetological researchers and conservationists to determine the extinction risk of
436 potentially vulnerable species and the impact of human encroachment on regions of irreplaceable
437 diversity. The failure to maintain global phylogenetic diversity will not only result in the loss of species
438 but reduced ecosystem function, resilience, and future options for humanity.

439

440 Literature Cited

- 441 Arne O. Mooers, Heard, S.B., Chrostowski, E., 2005. Evolutionary heritage as a metric for
442 conservation. *Phylogeny Conserv.* 120–138.
- 443 Bland, L.M., Böhm, M., 2016. Overcoming data deficiency in reptiles. *Biol. Conserv.* 204, 16–22.
444 <https://doi.org/10.1016/j.biocon.2016.05.018>
- 445 Brooks, T.M., A, M.R., Da Fonseca, G.A.B., Gerlach, J., Hoffmann, M., Lamoreux, J.F., Mittermeier, C. G,
446 Pilgrim, J.D., Rodrigues, A.S., 2006. Global Biodiversity Conservation Priorities. *Sciences (New*
447 *York)*. 313, 58–61. <https://doi.org/10.1126/science.1127609>
- 448 Cadotte, M.W., 2013. Experimental evidence that evolutionarily diverse assemblages result in higher
449 productivity. *Proc. Natl. Acad. Sci.* 110, 8996 LP – 9000.
450 <https://doi.org/10.1073/pnas.1301685110>
- 451 Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated
452 modern human – induced species losses: entering the sixth mass extinction. *Sci. Adv.* 1, 1–5.
453 <https://doi.org/10.1126/sciadv.1400253>
- 454 Davis, M., Faurby, S., Svenning, J.-C., 2018. Mammal diversity will take millions of years to recover
455 from the current biodiversity crisis. *Proc. Natl. Acad. Sci.* 115, 11262–11267.
456 <https://doi.org/10.1073/pnas.1804906115>
- 457 Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B., 2014. Defaunation in the
458 Anthropocene. *Science (80-)*. 345, 401 LP – 406.
- 459 Dutilleul, P., Clifford, P., Richardson, S., Hemon, D., 1993. Modifying the t Test for Assessing the
460 Correlation Between Two Spatial Processes. *Biometrics* 49, 305–314.
461 <https://doi.org/10.2307/2532625>
- 462 Faith, D.P., 2008. Threatened species and the potential loss of phylogenetic diversity: Conservation

463 scenarios based on estimated extinction probabilities and phylogenetic risk analysis. *Conserv.*
464 *Biol.* 22, 1461–1470. <https://doi.org/10.1111/j.1523-1739.2008.01068.x>

465 Faith, D.P., 1992. Conservation evaluation and phylogenetic diversity. *Biol. Conserv.* 61, 1–10.
466 [https://doi.org/10.1016/0006-3207\(92\)91201-3](https://doi.org/10.1016/0006-3207(92)91201-3)

467 Forest, F., Grenyer, R., Rouget, M., Davies, T.J., Cowling, R.M., Faith, D.P., Bank, M. Van Der, Reeves,
468 G., Balmford, A., Manning, J.C., Hedderson, T.A.J., Savolainen, V., 2007. Preserving the
469 evolutionary potential of floras in biodiversity hotspots. *Nature* 445, 757–760.
470 <https://doi.org/10.1038/nature05587>

471 Gumbs, R., Gray, C.L., Böhm, M., Hoffmann, M., Grenyer, R., Jetz, W., Meiri, S., Roll, U., Owen, N.R.,
472 Rosindell, J., 2019. Global priorities for conservation of reptilian phylogenetic diversity in the
473 face of human impacts. *bioRxiv* 723742. <https://doi.org/10.1101/723742>

474 Gumbs, R., Gray, C.L., Wearn, O.R., Owen, N.R., 2018. Tetrapods on the EDGE: Overcoming data
475 limitations to identify phylogenetic conservation priorities. *PLoS One* 13, e0194680.

476 IPBES, 2018. The IPBES regional assessment report on biodiversity and ecosystem services for Asia
477 and the Pacific. Karki, M., Senaratna Sellamuttu, S., Okayasu, S., and Suzuki, W. (eds). Bonn,
478 Germany. <https://doi.org/10.5281/zenodo.3237373>

479 Isaac, N.J.B., Redding, D.W., Meredith, H.M., Safi, K., 2012. Phylogenetically-Informed Priorities for
480 Amphibian Conservation. *PLoS One* 7, 1–8. <https://doi.org/10.1371/journal.pone.0043912>

481 Isaac, N.J.B., Turvey, S.T., Collen, B., Waterman, C., Baillie, J.E.M., 2007. Mammals on the EDGE:
482 Conservation priorities based on threat and phylogeny. *PLoS One* 2.
483 <https://doi.org/10.1371/journal.pone.0000296>

484 IUCN, 2016. IUCN Red List of Threatened Species. Version 2016-3 [WWW Document]. URL
485 www.iucnredlist.org

486 Jetz, W., Thomas, G.H., Joy, J.B., Redding, D.W., Hartmann, K., Mooers, A.O., 2014. Global Distribution
487 and Conservation of Evolutionary Distinctness in Birds. *Curr. Biol.* 24, 919–930.
488 <https://doi.org/10.1016/j.cub.2014.03.011>

489 Mace, G.M., Gittleman, J.L., Purvis, A., 2003. Preserving the tree of life. *Science* (80-.). 300, 1707–
490 1709. <https://doi.org/10.1126/science.1085510>

491 Mccarthy, D.P., Donald, P.F., Scharlemann, J.P.W., Graeme, M., Balmford, A., Green, J.M.H., Bennun,
492 L.A., Burgess, D., Fishpool, L.D.C., Garnett, S.T., David, L., Maloney, R.F., Morling, P., Schaefer,
493 H.M., Wiedenfeld, D.A., Butchart, S.H.M., International, B., Court, W., Rspb, U.K., Lodge, T.,
494 2012. Financial Costs of Meeting Global Biodiversity Conservation Targets: Current Spending and
495 Unmet Needs. *Science* (80-.). 338, 946–949.

496 Meiri, S., Bauer, A.M., Allison, A., Castro-Herrera, F., Chirio, L., Colli, G., Das, I., Doan, T.M., Glaw, F.,
497 Grismer, L.L., Hoogmoed, M., Kraus, F., LeBreton, M., Meirte, D., Nagy, Z.T., Nogueira, C. de C.,
498 Oliver, P., Pauwels, O.S.G., Pincheira-Donoso, D., Shea, G., Sindaco, R., Tallowin, O.J.S., Torres-
499 Carvajal, O., Trape, J.-F., Uetz, P., Wagner, P., Wang, Y., Ziegler, T., Roll, U., 2018. Extinct,
500 obscure or imaginary: The lizard species with the smallest ranges. *Divers. Distrib.* 24, 262–273.
501 <https://doi.org/10.1111/ddi.12678>

502 Meiri, S., Chapple, D.G., 2016. Biases in the current knowledge of threat status in lizards, and bridging
503 the “assessment gap.” *Biol. Conserv.* 204, 6–15. <https://doi.org/10.1016/j.biocon.2016.03.009>

504 Nunes, L.A., Turvey, S.T., Rosindell, J., 2015. The price of conserving avian phylogenetic diversity: a
505 global prioritization approach. *Philos Trans R Soc L. B Biol Sci* 370, 20140004.
506 <https://doi.org/10.1098/rstb.2014.0004>

507 Osorio, F., Vallejos, R., 2018. SpatialPack: Package for analysis of spatial data (R package version 0.3,
508 2018).

509 Owen, N.R., Gumbs, R., Gray, C.L., Faith, D.P., 2019. Global conservation of phylogenetic diversity

510 captures more than just functional diversity. *Nat. Commun.* 10, 859.
511 <https://doi.org/10.1038/s41467-019-08600-8>

512 Pollock, L.J., Thuiller, W., Jetz, W., 2017. Large conservation gains possible for global biodiversity
513 facets. *Nat. Publ. Gr.* 546, 141–144. <https://doi.org/10.1038/nature22368>

514 Roll, U., Feldman, A., Novosolov, M., Allison, A., Bauer, A.M., Bernard, R., Böhm, M., Castro-Herrera,
515 F., Chirio, L., Collen, B., Colli, G.R., Dabool, L., Das, I., Doan, T.M., Grismer, L.L., Hoogmoed, M.,
516 Itescu, Y., Kraus, F., LeBreton, M., Lewin, A., Martins, M., Maza, E., Meirte, D., Nagy, Z.T., de C.
517 Nogueira, C., Pauwels, O.S.G., Pincheira-Donoso, D., Powney, G.D., Sindaco, R., Tallwin, O.J.S.,
518 Torres-Carvajal, O., Trape, J.-F., Vidan, E., Uetz, P., Wagner, P., Wang, Y., Orme, C.D.L., Grenyer,
519 R., Meiri, S., 2017. The global distribution of tetrapods reveals a need for targeted reptile
520 conservation. *Nat. Ecol. Evol.* 1, 1677–1682. <https://doi.org/10.1038/s41559-017-0332-2>

521 Rosauer, D., Laffan, S.W., Crisp, M.D., Donnellan, S.C., Cook, L.G., 2009. Phylogenetic endemism: A
522 new approach for identifying geographical concentrations of evolutionary history. *Mol. Ecol.* 18,
523 4061–4072. <https://doi.org/10.1111/j.1365-294X.2009.04311.x>

524 Rosauer, D.F., Jetz, W., 2015. Phylogenetic endemism in terrestrial mammals. *Glob. Ecol. Biogeogr.*
525 24, 168–179. <https://doi.org/10.1111/geb.12237>

526 Rosauer, D.F., Pollock, L.J., Linke, S., Jetz, W., 2017. Phylogenetically informed spatial planning is
527 required to conserve the mammalian tree of life. *Proc. R. Soc. B Biol. Sci.* 284, 20170627.
528 <https://doi.org/10.1098/rspb.2017.0627>

529 Safi, K., Armour-Marshall, K., Baillie, J.E.M., Isaac, N.J.B., 2013. Global Patterns of Evolutionary Distinct
530 and Globally Endangered Amphibians and Mammals. *PLoS One* 8.
531 <https://doi.org/10.1371/journal.pone.0063582>

532 Sanderson, E.W., Jaiteh, M., Levy, M. a., Redford, K.H., Wannebo, A. V., Woolmer, G., 2002. The
533 Human Footprint and the Last of the Wild. *Bioscience* 52, 891–904.

534 [https://doi.org/10.1641/0006-3568\(2002\)052\[0891:THFATL\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2002)052[0891:THFATL]2.0.CO;2)

535 Tapley, B., Michaels, C.J., Gumbs, R., Böhm, M., Luedtke, J., Pearce-Kelly, P., Rowley, J.J.L., 2018. The
536 disparity between species description and conservation assessment: A case study in taxa with
537 high rates of species discovery. *Biol. Conserv.* 220, 209–214.
538 <https://doi.org/https://doi.org/10.1016/j.biocon.2018.01.022>

539 Tonini, J.F.R., Beard, K.H., Ferreira, R.B., Jetz, W., Pyron, R.A., 2016. Fully-sampled phylogenies of
540 squamates reveal evolutionary patterns in threat status. *Biol. Conserv.* 204, 23–31.
541 <https://doi.org/10.1016/j.biocon.2016.03.039>

542 Uetz, P., Freed, P., Hosek, J., 2016. The Reptile Database [WWW Document]. URL [http://www.reptile-](http://www.reptile-database.org)
543 [database.org](http://www.reptile-database.org) (accessed 4.15.16).

544 Venter, O., Sanderson, E.W., Magrath, A., Allan, J.R., Beher, J., Jones, K.R., Possingham, H.P., Laurance,
545 W.F., Wood, P., Fekete, B.M., Levy, M.A., Watson, J.E.M., 2016. Sixteen years of change in the
546 global terrestrial human footprint and implications for biodiversity conservation. *Nat. Commun.*
547 7, 12558.

548 Veron, S., Penone, C., Clergeau, P., Costa, G.C., Oliveira, B.F., S??o-Pedro, V.A., Pavoine, S., 2016.
549 Integrating data-deficient species in analyses of evolutionary history loss. *Ecol. Evol.*
550 <https://doi.org/10.1002/ece3.2390>

551 Weitzman, M.L., 1998. The Noah’s Ark Problem. *Econometrica* 66, 1279–1298.
552 <https://doi.org/10.3982/ECTA9075>

553 Zheng, Y., Wiens, J.J., 2016. Combining phylogenomic and supermatrix approaches, and a time-
554 calibrated phylogeny for squamate reptiles (lizards and snakes) based on 52 genes and 4162
555 species. *Mol. Phylogenet. Evol.* 94, 537–547. <https://doi.org/10.1016/j.ympev.2015.10.009>

556