

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

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Abstract

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

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).

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

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

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

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

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

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

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

Species-level priorities for gecko conservation

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

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

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

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

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

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

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

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

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

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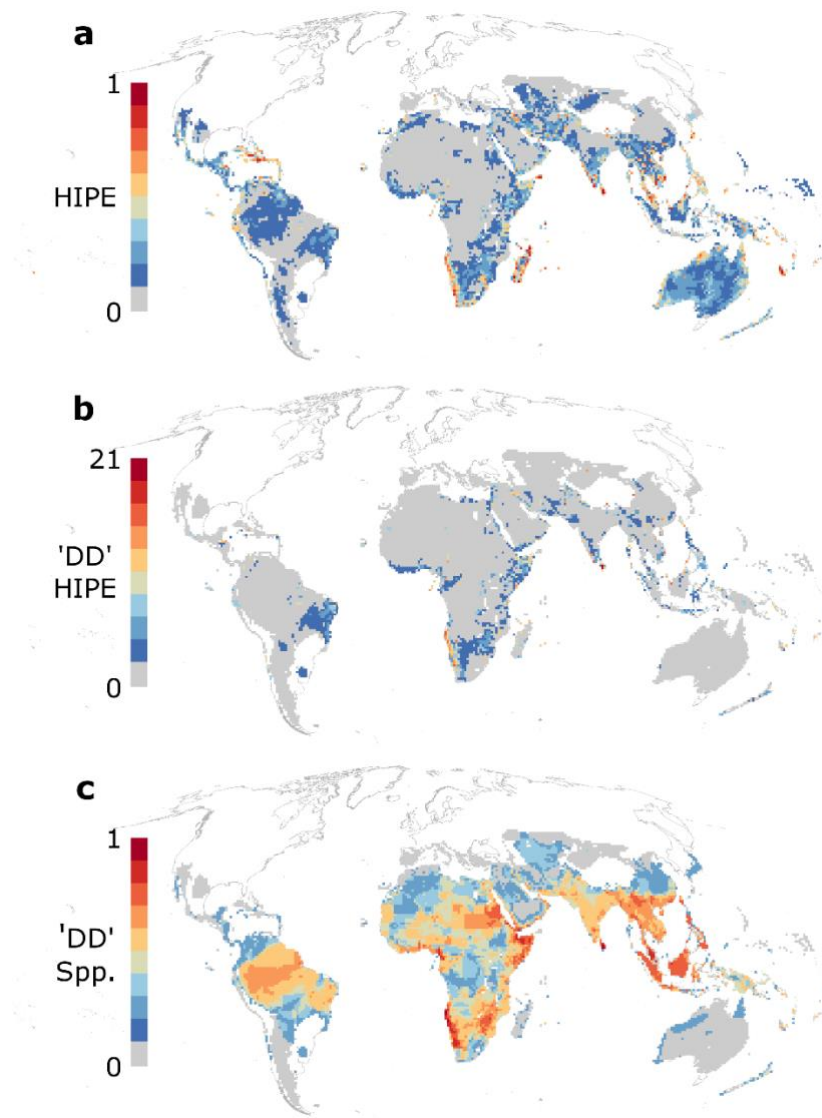
Results

Spatial patterns of irreplaceable gecko diversity

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

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

Global patterns of unassessed or Data Deficient gecko species richness are weakly correlated with 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, $p < 0.0001$; Figure 1b). Regions with particularly high levels of irreplaceable gecko diversity (i.e. high HIPE values) and also relatively low levels of extinction risk knowledge (i.e. high levels of unassessed/Data Deficient species) are Sri Lanka and the western coast of southern Africa (Figure 1c). High levels of extinction risk knowledge across the Caribbean and Madagascar capture large 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).

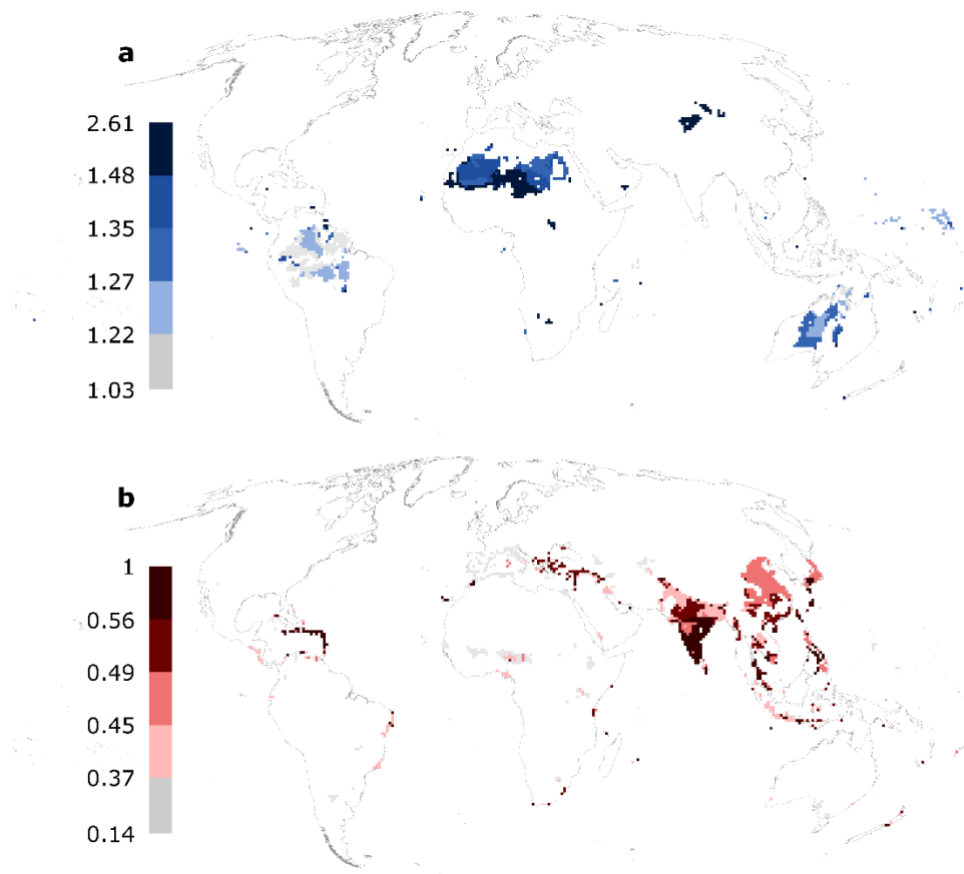


Figure 2: The ratio of grid cell values under Human-Impacted Phylogenetic Endemism (HIPE) compared to standard PE. a) regions of ‘no’ human pressure ($HF = 0$) are highlighted, where values close to 1 represent grid cells with Phylogenetic Diversity that is highly endemic to no pressure regions ($HF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

Species-level priorities for gecko conservation

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

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

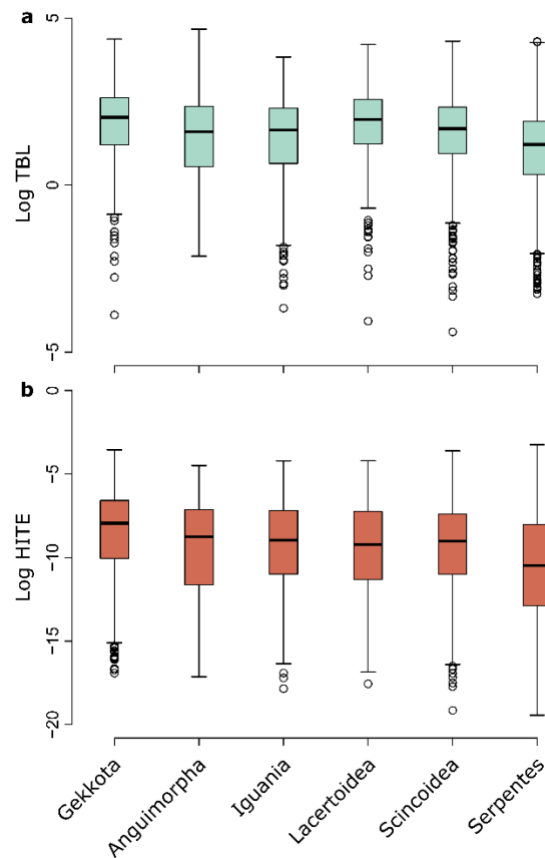


Figure 3: Species-level measures of Phylogenetic Diversity for six major lepidosaur groups. The distribution of a) terminal branch lengths (TBL), a measure of the unique contribution of a species to global Phylogenetic Diversity, and b) Human-Impacted Terminal Endemism scores, which weights the terminal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

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

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

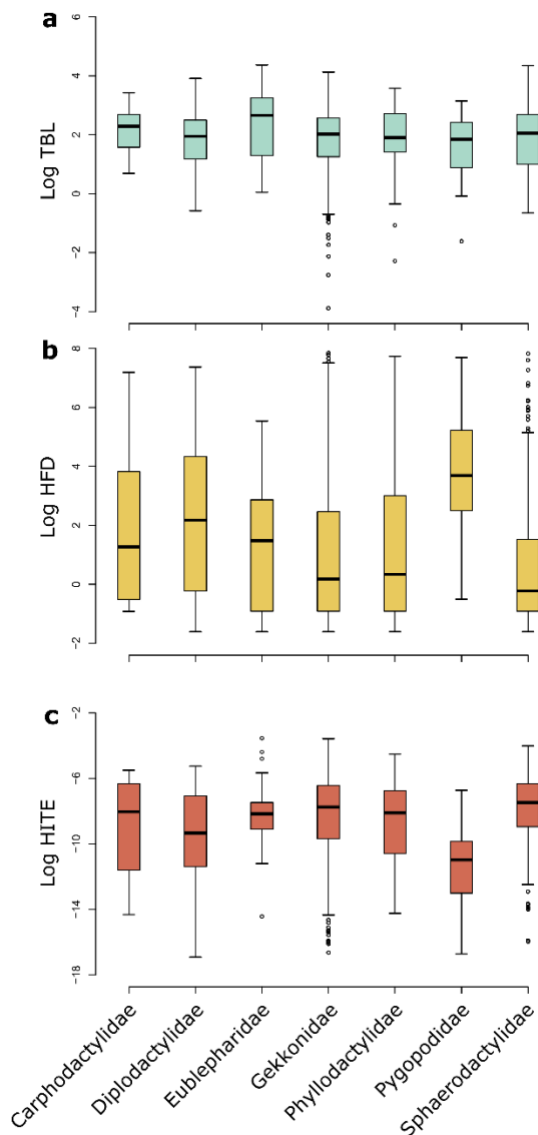


Figure 4: Species-level measures of Phylogenetic Diversity and Human Footprint for the seven gecko families. The distribution of a) terminal branch lengths (TBL); b) HF-weighted distribution (HFD) scores, with lower values indicating a species is range restricted and occurs in regions of high human pressure; and c) Human-Impacted Terminal Endemism (HITE) scores across the seven gecko families.

Gecko terminal branch lengths do not increase with increased extinction risk ($p = 0.02$, $p = 0.51$; Figure 5a), however gecko HITE does increase with increased extinction risk ($p = 0.18$, $p < 0.0001$). Gecko species Not Evaluated by the IUCN Red List have comparable HITE scores to Near Threatened geckos, and Data Deficient (DD) geckos have comparable HITE scores to Endangered geckos (adjusted p -value = 0.51), with only Critically Endangered geckos having significantly greater HITE scores (adjusted p -value = 0.0001; Figure 5b).

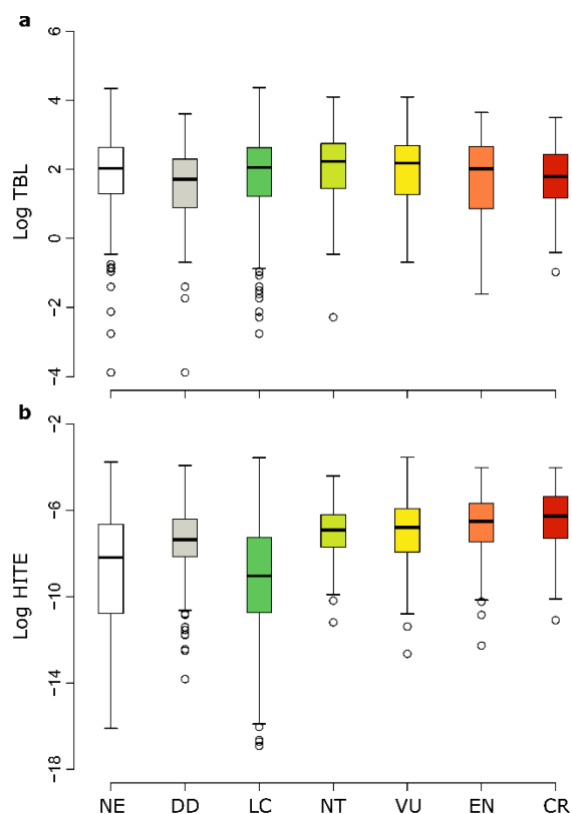


Figure 5: Species-level measures of Phylogenetic Diversity for geckos across IUCN Red List categories.

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

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

When limited to geckos listed in threatened IUCN Red List categories (VU, EN, CR), HITE rankings are significantly positively correlated with EDGE rankings ($\rho = 0.18$, $p = 0.01$). A large majority (19/20) of the highest-ranking threatened HITE geckos are also priority EDGE gecko species. The top 20 highest-ranking HITE geckos which are unassessed or listed as DD by the IUCN Red List comprise 13 gekkonid, four sphaerodactylid, two phyllodactylid and one eublepharid species (Table 1). The highest ranking unassessed gecko is *Lepidodactylus yami*, known only from its type locality on Lanyu Island, Taiwan (Meiri et al., 2018).

Table 1: Top 20 gecko species, when ranked by their Human-Impacted Terminal Endemism (HITE) score, which are either unassessed (NE) or listed as Data Deficient (DD) by the IUCN Red List. TBL = terminal branch length, a measure of the unique contribution of a species to global Phylogenetic 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</i>	DD	0.2	15.90	0.85
	<i>oskrobapreinorum</i>				
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).

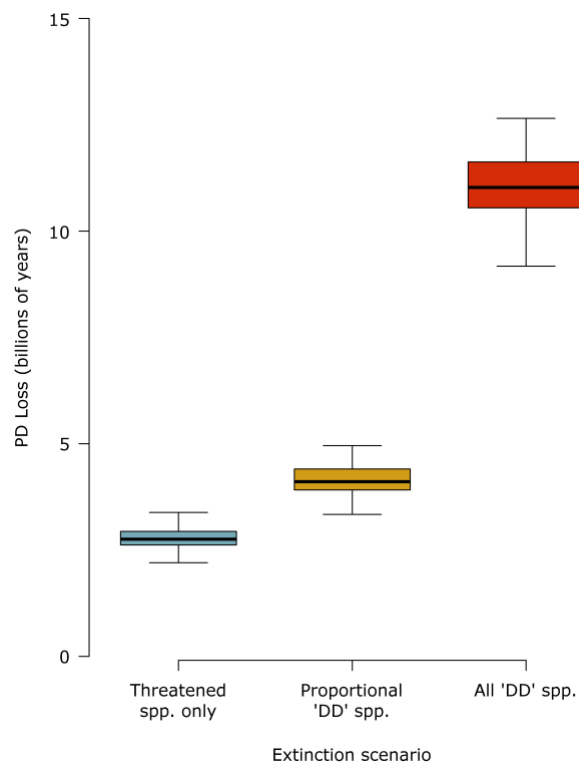


Figure 6: Loss of gecko PD under three extinction scenarios. The extent of PD lost, in billions of years, if we were to lose gecko species under three scenarios: the 'Baseline', where all threatened species (VU, EN, CR categories on IUCN Red List) become extinct; the 'Moderate' scenario, where all threatened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

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-

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

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

Conclusions

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

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