

The global distribution of tetrapods reveals a need for targeted reptile conservation

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The distributions of amphibians, birds and mammals have underpinned global and local conservation priorities, and have been fundamental to our understanding of the determinants of global biodiversity. In contrast, the global distributions of reptiles, representing a third of terrestrial vertebrate diversity, have been unavailable. This prevented the incorporation of reptiles into conservation planning and biased our understanding of the underlying processes governing global vertebrate biodiversity. Here, we present and analyse the global distribution of 10,064 reptile species (99% of extant terrestrial species). We show that richness patterns of the other three tetrapod classes are good spatial surrogates for species richness of all reptiles combined and of snakes, but characterize diversity patterns of lizards and turtles poorly. Hotspots of total and endemic lizard richness overlap very little with those of other taxa. Moreover, existing protected areas, sites of biodiversity significance and global conservation schemes represent birds and mammals better than reptiles. We show that additional conservation actions are needed to effectively protect reptiles, particularly lizards and turtles. Adding reptile knowledge to a global complementarity conservation priority scheme identifies many locations that consequently become important. Notably, investing resources in some of the world's arid, grassland and savannah habitats might be necessary to represent all terrestrial vertebrates efficiently.

Our knowledge of the distributions of a broad variety of organisms has improved greatly in the past decade^{1–3}, in turn aiding our efforts to conserve biodiversity^{4–6} and significantly enhance our grasp of broad-scale evolutionary and ecological processes^{7–12}. Nevertheless, despite comprising one third of terrestrial vertebrate species, knowledge of reptile distributions remained poor and unsystematic. This represented a major gap in our understanding of the global structure of biodiversity and our ability to conserve nature. Historically, broad-scale efforts towards the protection of land vertebrates (and thus also of reptiles) have been based predominantly on data from plants, birds, mammals and to a lesser degree amphibians^{13–15}. Here we present complete species-level global distributions of nearly all reptiles: 10,064 known, extant, terrestrial species for which we could identify precise distribution information. These distributions cover the Sauria (lizards, 6,110 species), Serpentes (snakes, 3,414 species), Testudines (turtles, 322 species), Amphisbaenia ('worm lizards', 193 species), Crocodylia (crocodiles, 24 species) and Rhynchocephalia (the tuatara, 1 species).

This dataset completes the global distribution mapping of all described, extant, terrestrial vertebrates (Fig. 1a), providing information that has been missing from much of the global conservation planning and prioritization schemes constructed over the past twenty years⁴. We use our reptile distribution data to: (a) examine the congruence in general, hotspot and endemism richness patterns across all tetrapod classes and among reptile groups; (b) explore how current conservation networks and priorities represent reptiles; and

(c) suggest regions in need of additional conservation attention to target full terrestrial vertebrate representation and highlight current surrogacy gaps, using a formal conservation prioritization technique.

Results and discussion

Species richness of reptiles compared to other tetrapods. The global pattern of reptile species richness (Fig. 1b) is largely congruent with that of all other terrestrial vertebrates combined ($r=0.824$, e.d.f. = 31.2, $p \ll 0.0001$; Fig. 2a, Supplementary Fig. 1, Supplementary Table 1). However, the major reptile groups (Figs. 1c–e, 2b,c Supplementary Fig. 1, Supplementary Table 1) show differing degrees of congruence with the other tetrapod taxa. The richness distribution of snakes (Fig. 1d) is very similar to that of other tetrapods (Fig. 2c) in showing pan-tropical dominance ($r=0.873$, e.d.f. = 30.2, $p \ll 0.0001$). Lizard richness is much less similar to non-reptilian tetrapod richness ($r=0.501$, e.d.f. = 38.3, $p \ll 0.001$, Fig. 2b). It is high in both tropical and arid regions, and notably in Australia (Fig. 1c, Supplementary Fig. 1). Turtle richness is also less congruent with diversity patterns of the other tetrapods ($r=0.673$, e.d.f. = 55.2, $p \ll 0.001$), and peaks in the southeastern USA, the Ganges Delta, and Southeast Asia (Fig. 1e).

Snakes dominate reptile richness patterns due to their much larger range sizes compared with lizards, even though lizards are about twice as speciose (median range size for 3,414 snake species: 62,646 km²; for 6,415 lizard species: 11,502 km²; Supplementary Fig. 2). Therefore snakes disproportionately influence global reptile richness patterns^{16,17} (Supplementary Table 1, Supplementary Fig. 1).

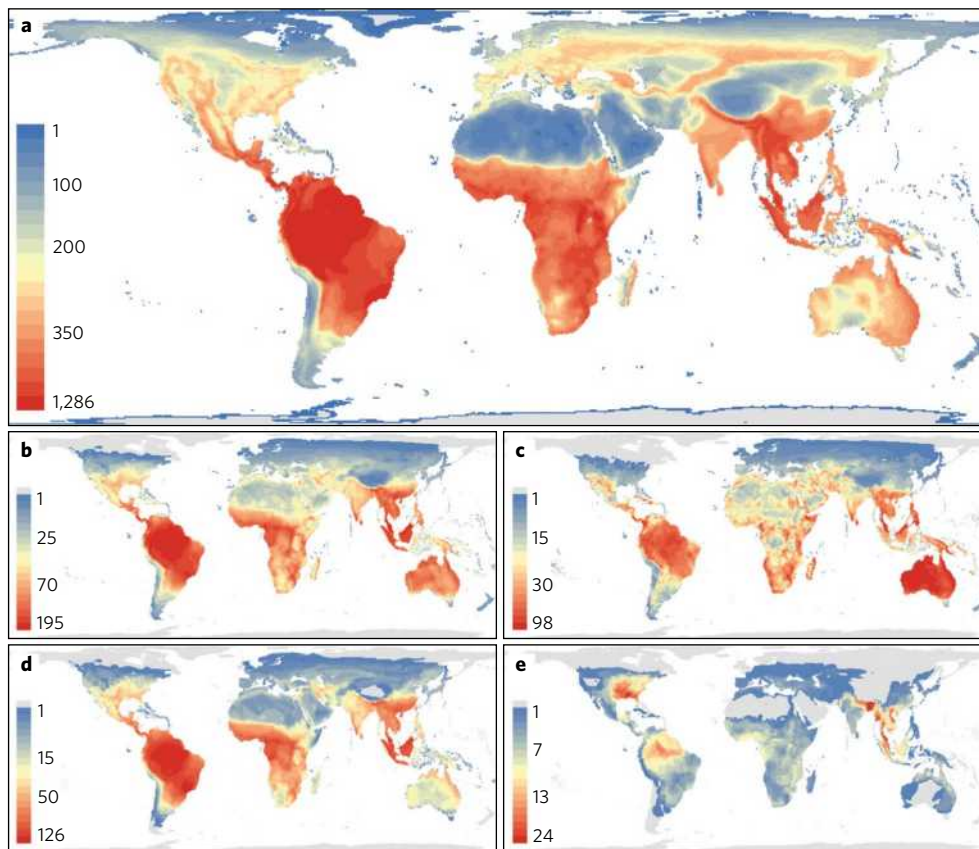


Fig. 1 | Species richness maps of terrestrial tetrapods. **a**, Richness of all tetrapods (reptiles, amphibians, birds and mammals). **b–e**, Species richness of reptile groups: all reptiles (**b**), lizards (**c**), snakes (**d**) and turtles (**e**). Grey areas denote terrestrial regions devoid of species in a particular group. Blue colours denote regions with few species and red ones denote regions with many species (note that the scale differs between panels). All maps in an equal area, Behrmann projection at a 48.25×48.25 km grid-cell resolution, scale bar values represent species richness.

Hotspots of richness and range-restricted species. As with overall richness patterns, hotspots of richness (the richest 2.5%, 5%, 7.5% and 10% of grid-cells) for all reptiles combined, and of snakes, are largely congruent with those of other tetrapod classes. However they are incongruent with hotspots of lizard or turtle richness (Fig. 3; Supplementary Fig. 3).

Congruence in the richness of range-restricted species (those species with the smallest 25% or 10% ranges in each group) between tetrapod groups is lower than the congruence across all species¹ (Supplementary Table 1). Endemic lizard and turtle distributions are least congruent with the endemics in other tetrapod classes (Supplementary Table 1). Global hotspots of relative endemism (or range-size-weighted richness, see Methods) for reptiles differ from those of non-reptilian tetrapods (Supplementary Fig. 4). Island faunas in places such as Socotra, New Caledonia and the Antilles are highlighted for reptiles, while hotspots of endemism for non-reptilian tetrapods are more often continental.

The utility of protected areas and current priority schemes in capturing reptile richness. Reptiles, like amphibians, are poorly represented in the global network of protected areas (Supplementary Table 2; Supplementary Figs. 5,6). Only 3.5% of reptile and 3.4% of amphibian species ranges are contained in protected areas (median species range overlap per class, with IUCN categories I–IV), compared with 6.5% for birds and 6% for mammals. Within reptile groups, strict protected areas (IUCN category I) overlap less with lizard ranges than with other reptile groups but there are no important differences between taxa for the more permissive protected area types (Supplementary

Table 2; Supplementary Fig. 5). Amphibians have the highest proportion of species whose ranges lie completely outside protected areas, when compared to the other tetrapod groups. Lizards, also fare poorly and have the highest proportion of species outside protected areas when compared with the other reptile groups (Supplementary Fig. 6a). Turtles have the lowest proportion of species with at least 10% of their range covered by protected areas (Supplementary Fig. 6b). We suggest that these low overlaps may have been caused by the inability to consider reptile diversity for direct protection, probably arising from ignorance of their distributions.

We explored the coverage of all tetrapods in three global prioritization schemes^{13,14,18} and a global designation of sites for biodiversity significance¹⁵ that have recently used distribution data to highlight regions for targeted conservation. These four global prioritizations/designations cover 6.8–37.4% of the Earth's land surface with 34–11,815 unique sites. Terrestrial vertebrate groups have 68–98% of their species with at least some range covered by these schemes (Supplementary Fig. 6c). However, reptiles and amphibians are sampled least well by these global schemes, and within reptiles lizards have the lowest representation (Supplementary Fig. 6c).

Fortunately, reptiles seem better situated in terms of conservation costs compared with other tetrapods. The median conservation opportunity cost¹⁹ (using the loss of agricultural revenue as a proxy for land-cost) for reptiles is lower than that for other tetrapods ($F_{3, 31850} = 17.4$, $p < 0.001$; Supplementary Fig. 7). Within reptiles, the opportunity cost is lowest for lizards, and highest for turtles and crocodiles, which could reflect their greater dependence on more valuable freshwater habitats ($F_{3, 10060} = 88.4$, $p < 0.001$; Supplementary Fig. 7b).

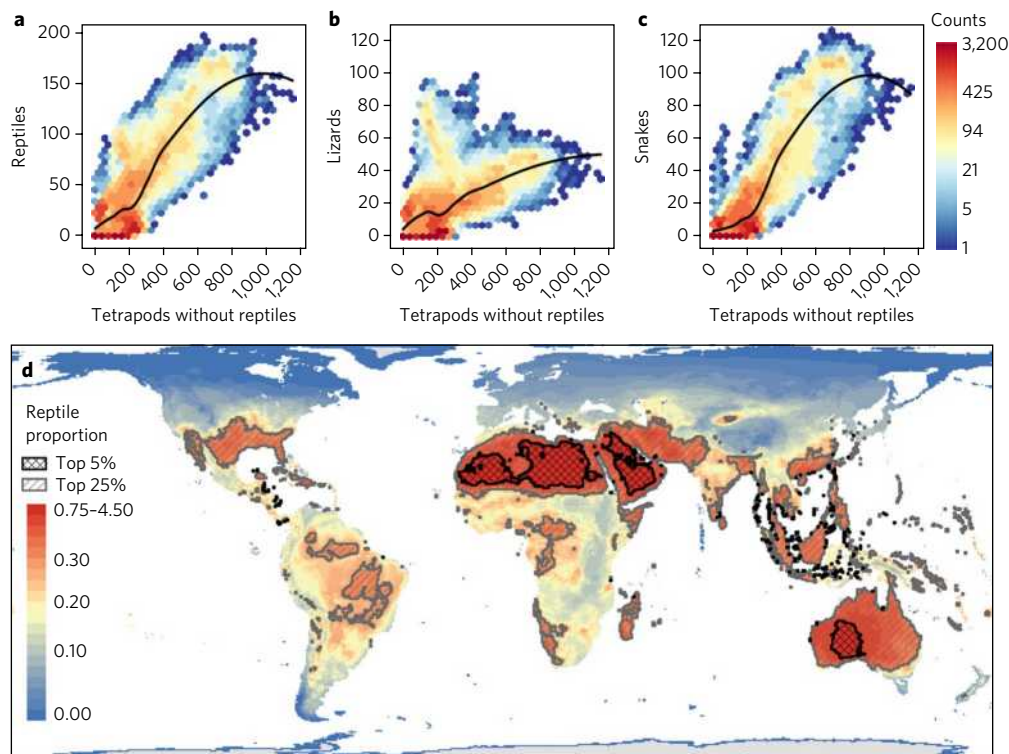


Fig. 2 | Comparing reptile richness to other tetrapods. **a–c**, Hexagon scatter plots comparing species richness values per grid-cell with binning (black line indicates a LOESS fit, $\alpha=0.6$) of tetrapods without reptiles to all reptiles (**a**), lizards (**b**) and snakes (**c**). **d**, Map of the ratio of reptile richness to non-reptilian tetrapod richness per grid-cell (note the wide range of values for the top category). Hatched regions designate areas where this proportion is the top 5% (black) and 25% (grey).

Conservation priorities for all tetrapods, incorporating reptile distributions. Our results suggest that reptiles, and particularly lizards and turtles, need to be better incorporated into conservation schemes. We used relative endemism within a complementarity analysis²⁰ to identify broad areas within which international and local conservation action should reduce reptile extinction risk (Fig. 4, Supplementary Fig. 8), and repeated this analysis to also incorporate conservation opportunity costs¹⁹ (Supplementary Fig. 8d,e). Many previously identified priority regions^{13,14}, have been retained with the addition of reptile distributions. These include northern and western Australia; central southern USA and the gulf coast of Mexico; the Brazilian Cerrado; Southeast Asia and many islands.

Nevertheless, our analyses also reveal many new priority regions, not currently perceived as biodiversity conservation priorities for tetrapods. These priority areas are predominantly arid and semi-arid habitats (see also Supplementary Fig. 8f for mean rank change per biome, for prioritization with and without reptiles). They include parts of northern Africa through the Arabian peninsula and the Levant; around Lake Chad; in inland arid southern Africa; central Asian arid highlands and steppes; central Australia; the Brazilian Caatinga, and the southern Andes. These regions have been previously unrecognized as priorities because their non-reptile vertebrate biotas could be more efficiently represented in other locations. Our analyses show that those locations were poor spatial surrogates for reptile distributions and that conservation efforts in our suggested locations may afford better protection for reptiles while maintaining efficient representation of other vertebrates. We note that many of these locations have low conservation opportunity costs so may be especially attractive for conservation. However, the location of these areas is not primarily driven by conservation opportunity costs. When these costs are incorporated into the analyses, very similar regions are highlighted for special attention due to the inclusion of reptile distributions (Supplementary Fig. 8d,e).

Summation. The complete map of tetrapod species richness presented here reveals important and unique properties of reptile diversity, particularly of lizards and turtles (Figs. 1–3). At a regional scale, reptiles have previously been shown to be unusually diverse in arid and semi-arid habitats^{21–23}. Here we reveal that this pattern is global, and also show reptile prominence in island faunas (Fig. 2d, Supplementary Fig. 4). Furthermore, we show that the unique diversity patterns of reptiles have important implications for their conservation. Targeted reptile conservation lags behind that of other tetrapod classes, probably through ignorance^{24–26}. The distributions provided here could make a vital contribution to bridging this gap. Concentrations of rare species in unexpected locations (Fig. 4) require explicit consideration when planning conservation actions. Highlighting such locations for new taxa could be especially beneficial for resource-constrained planning, especially where land costs are low. The lower global congruence with recognized diversity patterns for reptiles should also serve as a warning sign, contrary to some recent suggestions²⁷, for our ability to use distributions of well-studied groups in order to predict diversity patterns of poorly known taxa. The distinctive distribution of reptiles, and especially of lizards, suggests that it is driven by different ecological and evolutionary processes to those in other vertebrate taxa^{23,28}. The complete distributions of terrestrial tetrapods we now possess could greatly enhance our ability to study, understand and protect nature.

Methods

Data collection and assembly was carried out by members of the Global Assessment of Reptile Distributions (GARD) group, which includes all the authors of this paper. Regional specialist group members supervised the integration of geographic data for all species from field guides and books covering the terrestrial reptilian fauna of various regions, as well as revised

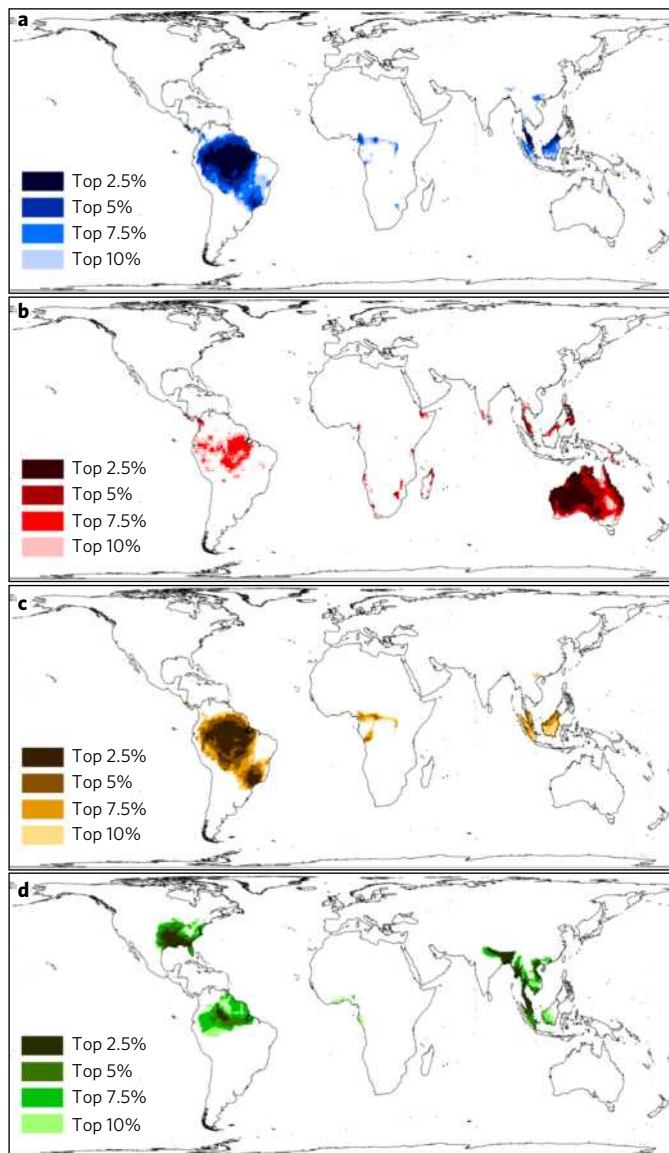


Fig. 3 | Species richness hotspots of reptiles and reptile groups. a–d, In each panel the lightest colour denotes the 10% of 48.25×48.25 km grid-cells with the highest numbers of species, and as the colours get darker they represent the top 7.5%, 5% and richest 2.5% cells. Panels show all reptiles (a), lizards (b), snakes (c) and turtles (d).

museum specimen databases, online meta-databases (including the IUCN, GBIF and Vertnet), our own observations and the primary literature. We followed the taxonomy of the March 2015 edition of the Reptile Database²⁹. Source maps were split or joined on that basis. We used the newest sources available to us. Polygonal maps—representing species extent of occurrence—were preferred over other map types. One of the reasons for this preference was that the distributional representations for the other tetrapod classes to which reptiles were compared were of a similar nature. Point locality data were modelled to create polygons representing the extent of occurrence using hull geometries (see Supplementary Information). Gaps in reptile distribution knowledge for particular locations or taxa were filled using de novo polygon and gridded maps created by GARD members specializing in the fauna of particular regions and taxa. These maps and all data obtained from online databases and the primary literature were then internally vetted, in a manner analogous to the IUCN Specialist Group process. Further details on data collection and curation, modelling of point localities and a full list of data sources per species are available in the supplement. Overall we analysed distribution maps for 10,064 extant species, which represent 99% of the species found in the Reptile Database of March 2015. For all analytical purposes we contrasted snakes with the paraphyletic lizards (here defined as lepidosaurs exclusive of snakes).

Polygonal representations of the extent of species' occurrences, such as we assembled and use in our analyses, are fundamentally important to contemporary conservation planning³⁰. The IUCN's assessment of the extinction risk of individual species requires (and produces) such data, and both they and many other organizations and researchers have used such data in aggregate and at regional-to-global scales for several decades³¹. Like any representation of species distributions, polygonal range maps can include errors both of omission and commission. Both kinds of inaccuracy can lead to erroneous conclusions by unwary users and this has led to some controversy over the use of polygonal range maps. Of course, all biogeographic representations—specimen localities, SDM outputs, atlas data, polygonal maps and explorers' narratives—lie along this omission–commission spectrum, and can equally be misused or found useless³². For global prioritization, we follow a comprehensive recent study³³ demonstrating the effectiveness of polygonal range maps in highlighting priority areas, despite errors at the level of individual species. We do, however, recognize that specimen data, if collected, curated and made available (at a suitable scale) remain a gold standard for some uses³⁴.

Our grid-cell analyses were conducted in a Behrmann equal area projection of 48.25 km^2 grid-cells ($\sim 0.5^\circ$ at 30° N/S). All analyses were repeated at a grid size of 96.5 km^2 ($\sim 1^\circ$ at 30° N/S) and results were qualitatively unchanged. GIS and statistical analyses were carried out in R and PostGIS.

Range-size-weighted richness (rswr) was calculated, for each cell, using the following formula: $\text{rswr}_i = \sum_j q_{ij}$ where q_{ij} is the fraction of the distribution of the species j in the cell i .

We used 'zonation'²⁰ to produce a ranked prioritization amongst cells, assuming equal weight to all species and assuming an equal cost for all cells. Cell value was the maximum proportion of any species range represented in it. Cell priority was calculated by iteratively removing the least valuable cell and updating cell values²⁰. We analysed all tetrapod species combined and tetrapods without reptiles separately, to reveal the change in rank importance induced by adding reptile distributions (See Supplementary Fig. 8). We repeated our prioritization using per-cell agricultural opportunity costs¹⁹, and found via rank correlation that our priority regions are fairly insensitive to the use of land costs (Fig. 4, Supplementary Fig. 8).

Data availability. The reptile distribution data used in this study are available from Dryad (<https://doi.org/10.5061/dryad.83s7k>).

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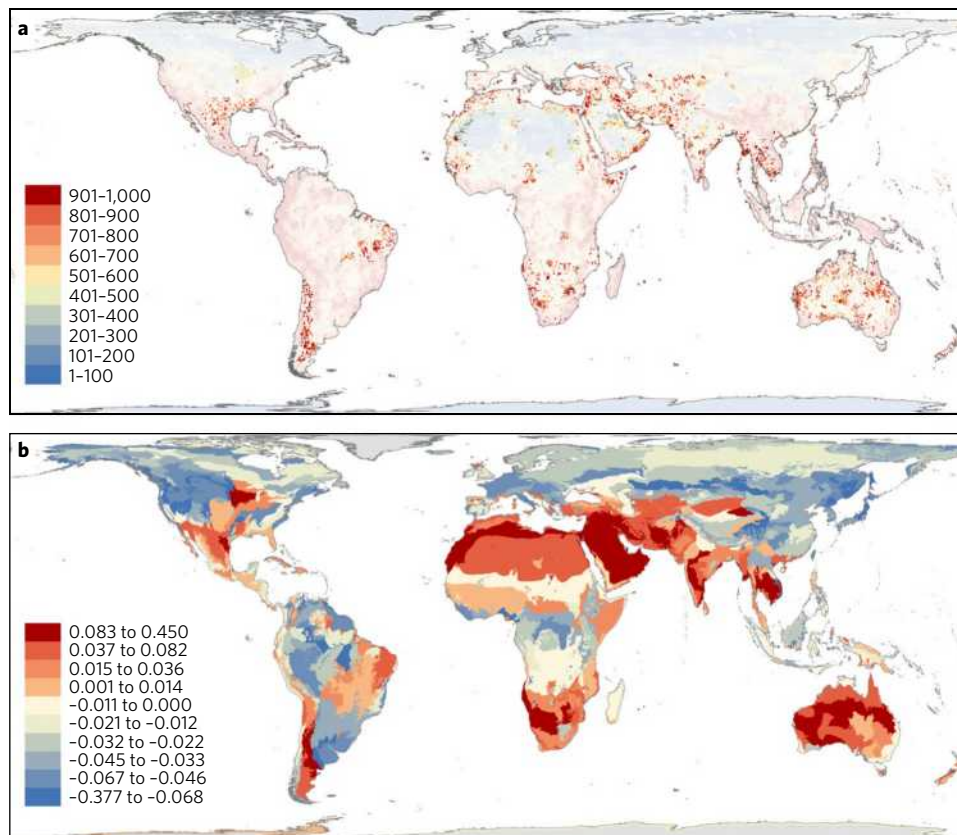


Fig. 4 | Key areas for tetrapod conservation, highlighting regions that rise in importance for conservation due to inclusion of reptiles. Cells were ranked in a formal prioritization scheme²⁰, based on complementarity when ranking cells in an iterative manner. Cells were ranked twice: (1) with all tetrapods and (2) with all tetrapods excluding reptiles. **a**, Patterns per 0.5 degree grid-cell where colours represent the priority ranks for the scheme that included all tetrapods (blue = low, red = high). The cells that are highlighted with the bold foreground colours are those that pinpoint those regions that gain in conservation importance due to the inclusion of the reptile data. These cells were selected following two rules: (1) they were in the top 10% of increase in rank, when subtracting the ranks of the analysis with reptiles from the ranks of the analysis without them; and (2) were part of statistically significant spatial clusters of rank changes (using local Moran's I^{*}). **b**, The mean change in rank between prioritizations with and without reptiles (using the above method) per ecoregion (red, ecoregions that become more important due to the inclusion of reptile information; blue, ecoregions becoming less important).

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Author contributions

A.M.B., R.G., S.M., U.R. conceived the study. R.G., C.D.L.O., U.R. designed the analyses. U.R. conducted the analyses. A.F., S.M., M.N., U.R. complied, designed and curated the dataset. R.G., S.M., U.R. wrote the paper. A.A., A.M.B., M.B., R.B., B.C., F.C.H., L.C., G.R.C., L.D., I.D., T.M.D., A.F., L.L.G., M.H., Y.I., F.K., A.L., M.L., E.M., D.M., M.M., S.M., C.C.N., M.N., Z.T.N., G.P., O.S.G.P., D.P.D., U.R., R.S., O.J.S.T., O.T.C., J.F.T., E.V., P.U., P.W., Y.W. provided, collated and verified underlying data. All authors read and commented on the manuscript.

Competing interests

The authors declare no competing financial interests.

Additional information

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