Small is big: A new conservation paradigm for amphibians

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Abstract

Many countries have responded to the current global biodiversity crisis by committing to protect 30% of the Earth by 2030, a goal known as “30 x 30”. However, an excessive emphasis on megafauna to the exclusion of other species weakens our current protected area (PA) network. This limited perspective overvalues large, connected PAs, while disregarding the potential impacts of small PAs in preserving biodiversity. Using public databases of 31,828 terrestrial vertebrate species we demonstrate that range sizes for the most vulnerable class of vertebrates, the amphibians, are smaller than those of reptiles, birds, and mammals and suggest that small PAs are overlooked as conservation tools for this group. We found that, though each of many endangered amphibians could have their entire distribution protected by a single microreserve (< 10 km^2), the current PA network fails at adequately protecting most threatened amphibian species. Furthermore, we show that many current microreserves have amphibian species richnesses rivaling those of the largest PAs (10,000–100,00 km^2), and that PA networks accumulate new amphibian species more rapidly through the addition of smaller rather than larger PAs. Unfortunately, the global rate of new PA establishment has slowed since 2010, so we illustrate global regions where the addition of microreserves could be most beneficial to amphibian conservation. We conclude that incorporating the needs of overlooked taxa into PA design will require us to complement networks of large, connected PAs with many strategically-placed, biodiversity-motivated microreserves.

Main Text

Introduction

As the world unites behind efforts to mitigate the effects of the sixth mass extinction (1) by protecting 30% of the earth's surface by the year 2030 (2), we are at a pivotal moment to critically evaluate land-based conservation planning. Key questions include where to locate new protected areas (PAs), as well as how to balance the size versus the number of new PAs.

More than 15% of earth's terrestrial surface is already protected (3), but the existing PA network is inadequate in representing biodiversity– particularly threatened and endemic biodiversity (4–6). These deficiencies have multiple causes. The motivations for creating the earliest PAs were to protect scenic landscapes and wildlife, safeguard natural resources, and provide recreational opportunities, rather than to sustain biodiversity (7). As the PA network has grown to include biodiversity-motivated PAs, it fails to maximize biodiversity conservation due to taxonomic bias. Historically, megafauna and/or mammalian and avian biodiversity have been used for spatial prioritization, to the neglect of other taxa (8, 9). For example, the existing PA network serves amphibians particularly poorly (10), such that they are the most underrepresented class of terrestrial vertebrates (6, 11). In some regions, the PA network does not represent amphibian diversity better than if PAs had been placed by chance (5); in others, it is entirely contrary to patterns of amphibian endemism (12).

Similar to other taxa overlooked by PA planners, like insects or freshwater mollusks, amphibians are undergoing global declines and extinctions, with habitat loss serving as a major driver (1, 13–16). As the pace of habitat conversion is accelerating (17), therefore, protected Area (PA) designation will be critically important to the persistence of many amphibian species. Amphibians have existed on earth for over 300 million years, yet in just the last decades there have been an alarming number of extinctions. Nearly 168 species are believed to have gone extinct and over 43% of species have populations that are declining (16, 18). The rate of current declines set amphibians on track for extinction rates that exceed those estimated for previous mass extinction events (19). To help slow or prevent a planetary mass extinction, maximizing the biodiversity value of the expanding PA network (an additional 22 million km^2) requires explicit consideration of traditionally neglected taxa such as the amphibians.

Classical studies in ecological theory predict that biodiversity value increases with PA size (20, 21), but we propose that this principle is not sufficient to conserve threatened taxa like amphibians. Amphibian conservation can be effective at small spatial scales (22), likely because amphibians generally appear to have small ranges and high beta diversity (23, 24).
For this reason, however, amphibians are likely to be excluded when their needs are not actively considered in PA design (25). Currently, there is little information regarding how we might use amphibians' small ranges to their advantage—by prioritizing strategically-placed, microreserves to enhance the value of the PA network for amphibians (26). Here, we provide an up-to-date assessment of amphibian coverage provided by the global PA network using new range information we generated for nearly all amphibians (7,094 of 8,498 recognized species) (27), examine temporal trends in PA establishment relative to the PA network's coverage of amphibians and particularly threatened amphibians, and consider how to most efficiently improve this coverage through microreserve creation.

Results

We assembled species-specific geographic range area maps from 31,828 species, including all of the major terrestrial vertebrate groups (7,094 amphibians, 8,397 non-avian reptiles, 5,850 mammals, and 10,487 birds). Amphibians had a smaller median range size than other vertebrates considered together (Figure 1A; $p<0.001$), as well as a smaller median range size than non-avian reptiles, mammals, and birds in pairwise comparisons ($p<0.001$). When we compared range sizes of threatened species across all taxa (as determined by the IUCN Red List), amphibians had significantly smaller median range compared to all other vertebrate groups (Figure 1B; $p<0.001$), and amphibian ranges were significantly smaller than bird and mammal ranges in pairwise analyses ($p<0.001$). Finally, within class Amphibia, threatened species had a smaller median range size than non-threatened species (Wilcoxon rank sum test; $p<0.001$).

Although 97.3% (241,000 of 247,785) of PAs with a terrestrial component overlap with the range of at least one of the 7,094 amphibians with range maps, 15.7% of amphibian species (1,115 species) are left unprotected by the existing network (Figure 2). There is a higher proportion of threatened and extinct species (T&E species) among amphibians unprotected by the current PA network (35.8%; 400 species) compared to species protected by the current network (29.6%; 1,771 species). Likewise, data deficient species (DD species) and species that have not yet been assessed are overrepresented among unprotected species (57.5%; n=641 species), compared to only 20.8% among protected species (1,244 species).

We found a positive relationship between current PA size and amphibian species richness, but that relationship is weak. For example, as PA size increases on a log scale, amphibian richness increases by only a few species (estimate of the slope is 0.41, $p<0.05$, $r2=0.07$). Most microreserves (1–10 km^2) are currently located in areas of low amphibian richness, but microreserves are also able to capture areas of high richness and endemism (Figure 3A: a, b, & c). We found that the cumulative amphibian diversity protected by iterative resampling of the existing world PA database increased faster when smaller PA size categories were sampled (Figure 3B). Thus, amphibian species diversity included in the PA network is maximized through the addition of many microreserves rather than through an equivalent geographic area contributed by only a few large PAs (Figure 3B; largest reserves 10,000–100,000 km^2).

The rate of new PA establishment for all PAs and for microreserves increased almost monotonically in the PA database until the early 2000s (Figure 4A), corresponding with a steady increase in the cumulative number of amphibian species covered by the global PA network (Figure 4A). However, since the early 2000s the rate of PA establishment has dropped, echoed by a decline in the rate of new microreserves established. Despite this recent decline in new PAs, the cumulative number of protected amphibian species protected by the network continues to increase (Figure 4A). Over time, increasing numbers of new PAs have been established in zones of high amphibian vulnerability (Figure 4B). Meanwhile, amphibian-rich microreserves that were established 90 or more years ago may still maintain a 0% proportion of threatened amphibian species (Figure 4B: a, b, & c)

Across different geographic regions, the size of PAs, total amphibian species richness, and the proportional representation of threatened species among protected and unprotected amphibians varied greatly. Europe had the smallest median PA size (Figure 5, 0.27 km^2) but also the lowest number of amphibians that do not overlap PAs (0%). Madagascar had the largest median PA size (270.40 km^2) and only four species that do not overlap PAs (1.2%). The region with the highest proportion of unprotected species was Melanesia, Micronesia, and Polynesia (41.4%; 123 species), while South America and Asia had the highest number of unprotected species (349 and 246 species, respectively). Central America, Mexico, and the Caribbean had the highest number of threatened amphibian species whose ranges do not overlap PA areas (107 species), as well as the largest differential between the proportion of threatened species that are protected versus unprotected (27.5% more threatened species among unprotected than protected species).

PA establishment occurs at the scale of the country, and the most amphibian-rich country is Brazil (944), followed by Colombia (810), Peru (566), and Ecuador (520; Figure S1A). The country with the highest number of threatened amphibians is Colombia (233), followed by Mexico (227), Ecuador (184), and Madagascar (134; Figure S1B). The country with the highest number of unprotected amphibian species is China (156), followed by Papua New Guinea (122), India (111), and Mexico (99; Figure S1C). Colombia, Peru, Ecuador, China, and Mexico are all within the top-ten countries in terms of their number of amphibian species, threatened species, and unprotected amphibian species.

Discussion

As the sixth mass extinction unfolds, protected area (PA) design will become increasingly valuable in efforts to conserve the Earth’s biodiversity (28). Current biodiversity-motivated PAs were not designed holistically regarding vertebrate taxa but were focused mostly on charismatic megafauna. Discovery of new species, especially in taxonomic groups like amphibians, continues to rapidly grow. For example, in 1980 there were 4,318 named amphibians, and today there are well over 8,400 species. Although the number of PAs also has increased rapidly throughout the world (Fig. 4A; 24,993 in 1980; 189,720 in 2020), the number of unprotected amphibian species increased from 913 in 2004 to 1,115 today (29).

Our results corroborate earlier studies in finding that threatened amphibians are inadequately represented by the global PA network (6, 11, 25, 29). We find that unprotected species have a 6.2% higher chance of being threatened with extinction than protected species (Figure 2). However, land-based conservation efforts have become more targeted over time (Figure 4B), such that since 2004 the number of unprotected, threatened amphibian species has decreased from 411 to 399 and the proportion of threatened amphibians that are unprotected has decreased from 26.6% to 18.4% (Figure 2)(6).

Our study finds that data deficient (DD) amphibians are highly underrepresented by the WDPA network (Figure 2). DD amphibians are significantly more likely to fall into threatened IUCN categories (VU, EN, CR) than amphibians that have already been listed in non-DD categories by the IUCN (30, 31). In fact, machine learning-derived probabilities predict that 85% of DD amphibians are likely to be imperiled(32). Therefore, our estimate that 35.8% of unprotected amphibians are threatened with extinction is an underestimation and should be considered the lower-bound estimate of the actual value. For the purposes of conservation planning, it may be appropriate to assume DD amphibians are threatened until more information is gathered; although species that have already been designated as threatened can still be prioritized.

Microreserves: low-hanging fruit for targeted amphibian conservation

One of the major ways in which current land-based conservation efforts show taxonomic bias is in the assumption that PAs cannot be small if they are to be meaningful. Amphibians are implicitly neglected by this assumption, as potentially are many other taxa (e.g. insects, mollusks) (14, 15). We find that microreserves can host high amphibian species richnesses comparable to the largest PAs in the world (Figure 3A), and that we can increase amphibian representation in the WDPA network faster through the addition of microreserves than through the addition of larger-sized PAs (Figure 3B). Although the conservation value of microreserves has already been recognized for plants (33), we suggest that a greater recognition of their conservation value may help reverse a worrying trend: the steep decline in the rate of new PA establishment within the WDPA network since 2000 (Figure 4A).

We highlight countries (Figure S1) and larger global regions (Figure 5) where the addition of microreserves could yield the greatest conservation benefit. However, the areas of the world richest in amphibian endemism, data deficient amphibians, and newly described amphibians (e.g. Southeast Asia, South America) also tend to be regions prioritizing the creation of expansive PAs to the detriment of strategic microreserve creation (Figure 5). Regions of the world characterized by the greatest disparity between the proportion of threatened amphibian species existing within versus entirely outside of their PAs also tend to have larger median PA sizes (Central America, Mexico, and the Caribbean; and South America; Figure 5). Thus, complementing the existing PA network with targeted microreserves to capture threatened amphibian species could be particularly transformative to the amphibian conservation landscape of these regions. For example, Mexico could benefit greatly from the addition of biodiversity-targeted microreserves because we identify many amphibian species currently not overlapping with PAs there, many of which are threatened. Also, as is particularly true at lower latitudes, Mexico has many microendemic amphibian species that are intrinsically well-suited to be protected by microreserves (See S1 and S2).

Admittedly, our estimates of where to establish microreserves for the greatest biodiversity gains is limited by current shortcomings in the World Database of Protected Areas (WDPA). Private PAs, which tend to be smaller and of disproportionate biological importance relative to government-managed PAs, are under-reported in the WDPA (34), with only 20% of records in the WDPA currently listed as non-governmental. To this point, amphibian-rich Peru emerges in our analyses as being a country with some of the highest amphibian species diversity in its microreserves (Figure 3A; field sites indicated), likely because Peru has reported more privately protected PAs within the WDPA than any other country in the world (35)(28,795 km^2). Better reporting of private PAs in the WDPA would facilitate better global gap analyses for the conservation of amphibians and other taxa with small range size.

Effective microreserves must be strategically designed

Microreserves must be placed strategically if they are to provide added value for amphibian conservation. We demonstrate that a microreserve of <10 km^2 could cover all or most of the distributional range of many amphibian species (e.g., microendemics, Figure 1A), and this is particularly true of threatened amphibians (Figure 1B). Species with small ranges are frequently characterized by low local abundances (36), putting them at a higher risk of global extinction (37) and making their small ranges particularly valuable areas to include in the PA network. In other cases, due to the extent of land conversion, tiny patches may be all that remains of once broader distributions (38, 39).

Beyond microendemic amphibians, microreserves could be used to increase the PA network's coverage of point localities for data deficient or newly described species of amphibians, many of which are known from a single locality. The establishment of microreserves might also play a significant role in protecting important source populations for amphibian species that exist in metapopulations or in protecting critical and endangered habitat types that may be so small they are ignored by traditional PA planning (40). Microreserves could also be deployed to protect strings of habitat patches along climate migration corridors (41). Using microreserves in these ways implies a transformation of current, accepted concepts in PAs design. Microreserves currently appear in the literature almost exclusively for PA creation in urban-adjacent zones (33, 42, 43). We propose to strategically deploy microreserves directly for biodiversity conservation, rather than for recreation or other means. Ideally, we can conceive of microreserve establishment as building capillary networks that complement existing PAs, promoting connectivity and supporting the long-term functioning of larger PAs (44).

To improve biodiversity conservation of species with small ranges, our results can be integrated into several important initiatives that provide information needed to support strategic microreserve design. For instance, the Alliance for Zero Extinction maintains a database of discrete sites serving as the last refuge of Endangered of Critically Endangered species (45). The EDGE framework allows conservation planners to integrate considerations of phylogenetic distinctness (46), and a spatial prioritization approach that additionally incorporates endemism and anthropogenic pressures on a site has also been proposed (47). In the U.S.A., the Priority Amphibian and Reptile Conservation Areas project (48) is conducting regional assessments to identify critical sites for herpetofaunal conservation based on species rarity, species richness, and landscape integrity.

Conclusion

The ongoing sixth mass extinction of global biodiversity highlights the need for urgent conservation action. As humanity unites in ambitious land-based conservation goals for the near future, it is a pivotal moment to revisit our assumptions about how PAs are designed and located. The default assumption that larger PAs are better will result in worse conservation outcomes for amphibians and likely many other taxa. Based on our analyses, we propose the strategic deployment of microreserves globally. This action could add significant amphibian conservation value to the PA network. Establishing biodiversity-motivated microreserves across the world could help protect thousands of threatened and endemic species, source populations that can shore up larger metapopulations, point localities of data deficient and newly described species, small but critical habitats, and strings of habitat along climate migration corridors.

Materials and Methods

All data analysis and visualization was performed in Quantum GIS v3.2, ESRI ArcGIS v10.8, and in R v4.1.1 using libraries stringr v1.4.0, dplyr v1.0.7, plyr v1.8.6, tidyr v1.1.3, lessR v4.1.4, forcats v0.5.1, data.table v1.14.2, hexbin v1.28.2, ggridges v0.5.3, ggplot2 v3.3.5, raster v3.4., scales v1.1.1, and cowplot v1.1.1. Tables and scripts to generate our analysis are available at https://github.com/AmphibiaWeb/amphibian-pas.

Data acquisition

We used amphibian range maps from AmphibiaWeb (available for 7,094 species, or over 83% of named amphibian species)(27). For mammals and reptiles, we used ranges from the IUCN (8,397 reptiles and 5,850 mammals)(49); for birds, we used ranges for 10,487 species from BirdLife International that excluded species they consider sensitive (50). We joined all range polygons for each bird species, which were originally separated into resident, breeding season, non-breeding season, passage, and seasonal occurrence uncertain components. We acquired species' conservation status from the IUCN Red List of Threatened Species (49). For amphibians, we included provisional statuses (27).

We used the 240,999 PA polygons in terrestrial biomes from the World Database of Protected Areas database (3). The Russian Federation, Estonia, Saint Helena, Ascension, Tristan da Cunha, and China withhold all or part of their PA spatial data from public release (3). Polygons of PAs that overlapped with each other were merged. We removed two polygons by searching for records that included the text “not protected”, “degazetted,” “proposed,” “recommended,” “in preparation,” or “unset”.

Vertebrate terrestrial range sizes

We estimated species distribution sizes from GIS polygon vectors. We compared ranges between amphibians and all other taxa, as well as pairwise between each two taxa, using Wilcoxon rank sum tests with continuity correction. We performed the same test for threatened or extinct members of these taxa (VU, EN, CR, EW, EX; as described in IUCN), as well as between all versus only threatened amphibians (Figure 1). We visualized differences between all species of each taxa with a smoothed density histogram (Figure 1) and between threatened species using box and whisker plots.

Overlap of PAs and amphibian ranges

To determine which amphibian species overlapped with a PA, we used QGIS 3.20 and reprojected the PA and amphibian range shapefiles in EPSG: 3857. We took the intersection to generate lists of amphibians overlapping with each PA, with no minimum area threshold enforced. We calculated overlap statistics for both species that are threatened and not threatened, generating lists of species that are protected and unprotected. We used hexbins to describe how PA size relates to its amphibian species richness. We used linear regression to define the relationship between PA area and amphibian species richness, integrating the continental location of a PA as a covariate in the model given significant spatial heterogeneity in amphibian species richness across global regions (richness ~ log(area) + continent) to generate a heatmap for the bins (Figure 2, 3)

To understand the impact of PA size on accumulated amphibian diversity, we categorized PAs into size classes: 0–10 km^2, 10–100 km^2, 100–1,000 km^2, 1,000–10,000 km^2, and 10,000–100,000 km^2. We resampled PAs from a given size class with replacement until the cumulative area sampled reached the size of the total WDPA database (27,939,673 km^2). As each new PA was added, the cumulative number of unique amphibian species represented in the growing set was recorded. For each PA size class, this protocol was repeated 1000 times, and the mean number of cumulative species at each successive sampling stage was calculated. These mean values were used to create growth curves for each PA size class, with the x-axis scaled to represent equal area added and the y-axis representing the total number of amphibian species. We plotted the growth portion of these curves to compare the marginal benefit of adding PAs of different sizes to network coverage of amphibian diversity (Figure 3).

To understand how PA age might impact its conservation value, we used a hexbin heatmap to illustrate the relationship between the year of establishment and the proportion of threatened amphibian species of each PA. We visualized the history of counts of PAs established since 1860, both overall and for microreserves only (Figure 4), and added a line representing the cumulative amphibian species coverage of the WDPA over time.

Overlap of PA polygons, amphibian ranges, and geographic regions

To understand regional differences of PA size, and how well amphibian richness and threatened amphibian richness are represented in the WDPA network, we used the following biogeographic regions significant to amphibian richness and endemism: Africa (excluding Madagascar); Asia (excluding SE Asia); Australia and New Zealand; Canada and the U.S.A.; Central America, Mexico, and the Caribbean; Europe; Madagascar; Melanesia, Micronesia, and Polynesia; and Southeast Asia (Brunei, East Timor, Indonesia, Malaysia, Philippines). For each region, we plotted a smoothed frequency histogram of PA size and graphed the total species in that region with respect to its conservation status of protected and unprotected amphibian species (Figure 5).

To highlight countries of high conservation interest, we generated lists that ranked the top countries based on total, threatened, and unprotected amphibian species richness. We selected Mexico as a case study to highlight how PA network and amphibian diversity interact at a country-level (Figure S2).

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Figures and Tables

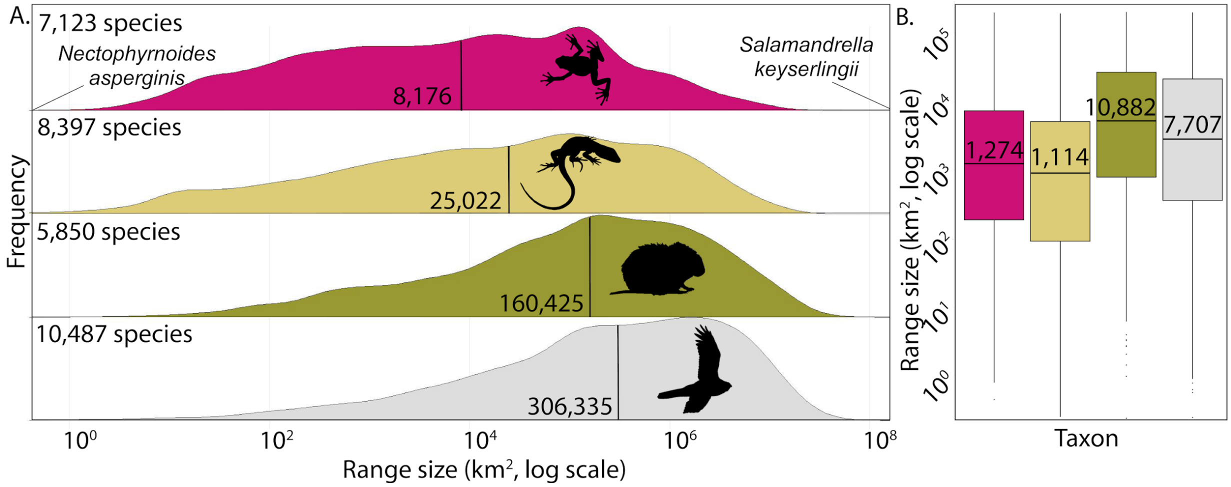

***Figure 1**. **Comparison of range sizes for terrestrial vertebrate classes.** (A.) Smoothed density histogram for terrestrial vertebrate range sizes: amphibians, birds, reptiles, and mammals. Only the terrestrial range area of each species is considered. The median range size of each taxon is marked with a vertical black line. For amphibians, the Kihansi spray toad (*Nectophrynoides asperginis*, *0.104 km^2) has the smallest range and the Siberian newt (*Salamandrella keyserlingii*, *14,700,000 km^2) has the largest range. (B.) Range size (in km^2, log scale) of threatened and extinct species in each taxon.*

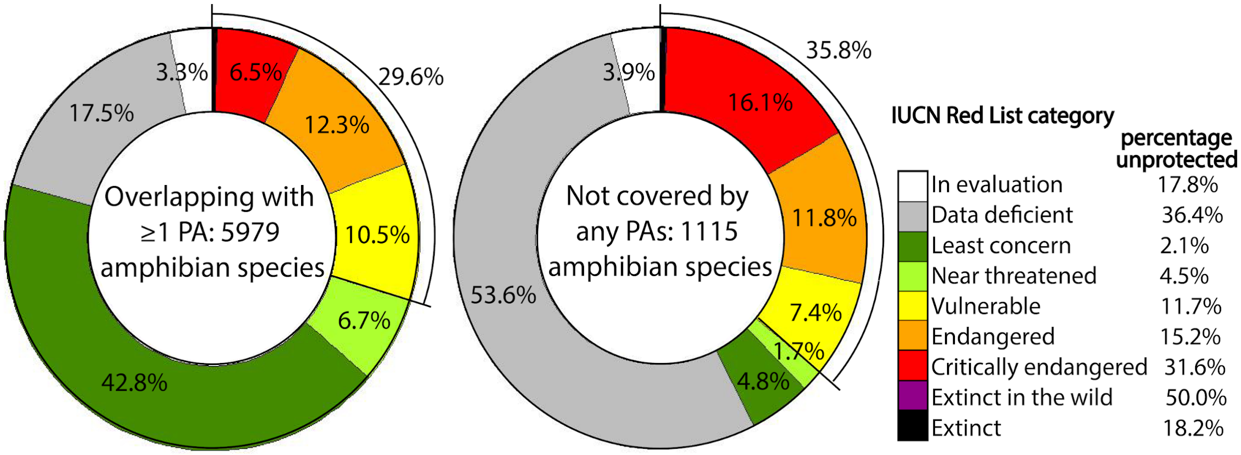

Figure 2. Conservation status of amphibians protected and not protected by the current PA network.

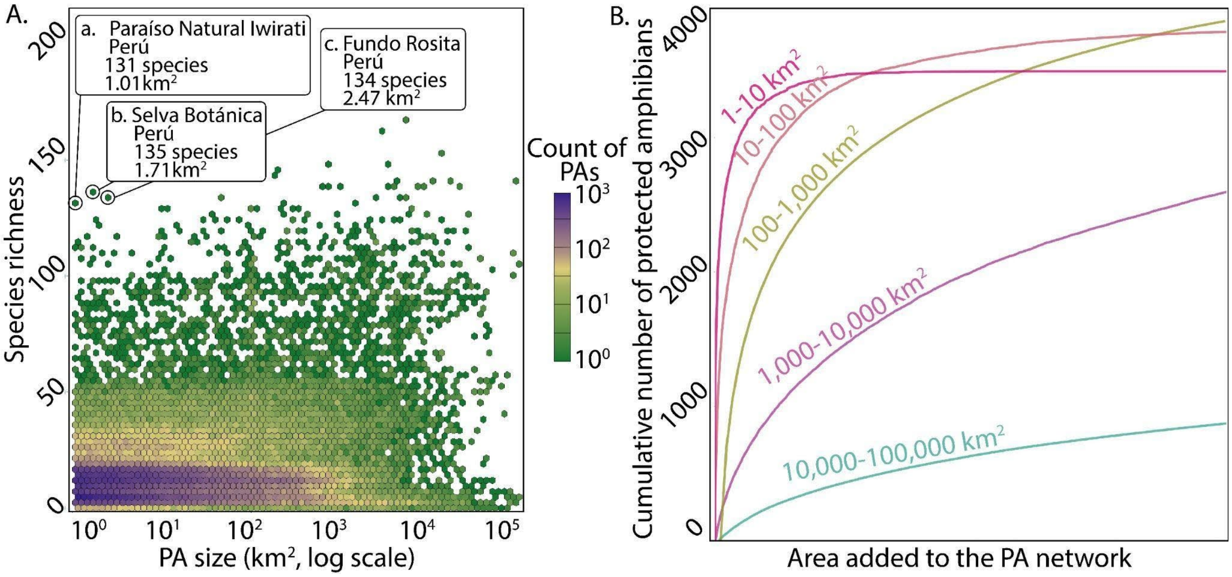

Figure 3. Relationship between amphibian species richness and PA size, and amphibian species accumulation across five different PA size categories. *(A.) How PA size relates to the amphibian species richness it contains. Microreserves with the highest species richness are identified. (B.) Cumulative proportion of protected amphibian species as you sample PAs of each size category (0–10 km^2, n=208,496; 10–100 km^2, n=27,762; 100–1,000 km^2, n=11,975; 1,000–10,000 km^2, n=3,045; and 10,000–100,000 km^2, n=430) drawn from the WDPA database. The x-axis is scaled such that it represents equivalent area protected, regardless of the PA size category considered. The cumulative number of amphibian species with range data available was 7,094.*

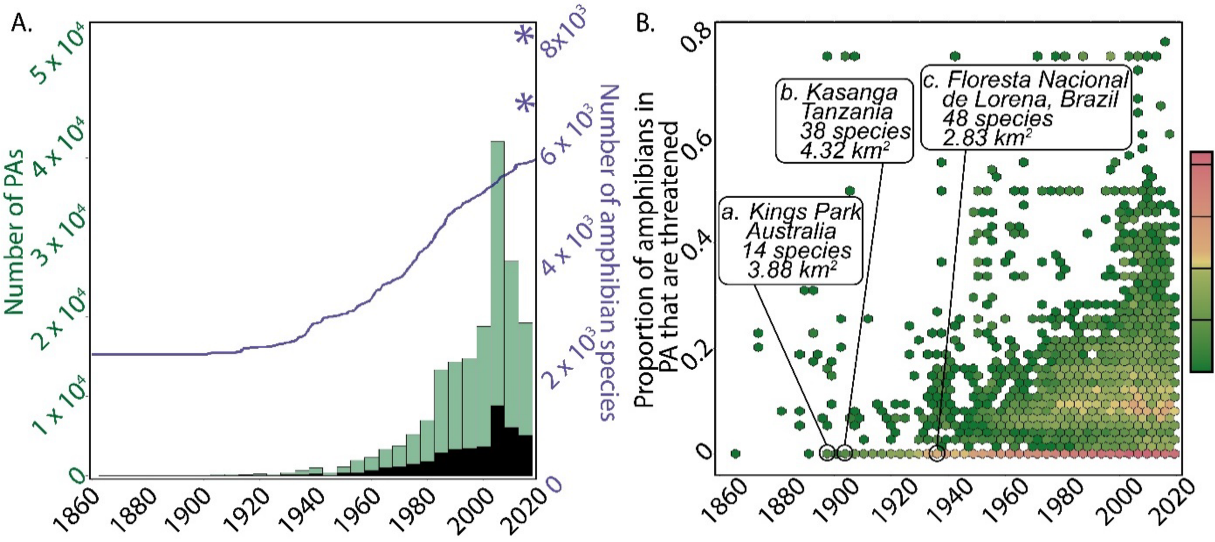

Figure 4. Trends in PA placement over time. *(A) Counts of PAs established over time (left axis) and how that relates to the cumulative number of protected amphibian species (right axis). The green bar plot shows counts of PAs established over time, binned by 5-year units, and the black bar plot shows the same thing for microreserves only (area <10 km^2). The purple line shows the cumulative count of protected amphibians. The lower star represents the total number of amphibians in this study with spatial data (n=7,094), and the higher star represents total amphibian species described (n=8,489). (B) The proportion of amphibian species in a microreserve that are threatened today relative to the year that microreserve was established. Old microreserves from three continents with a low (zero or near-zero) proportion of IUCN-threatened species are annotated. Old microreserves from three continents with high species richness but no threatened species are identified.*

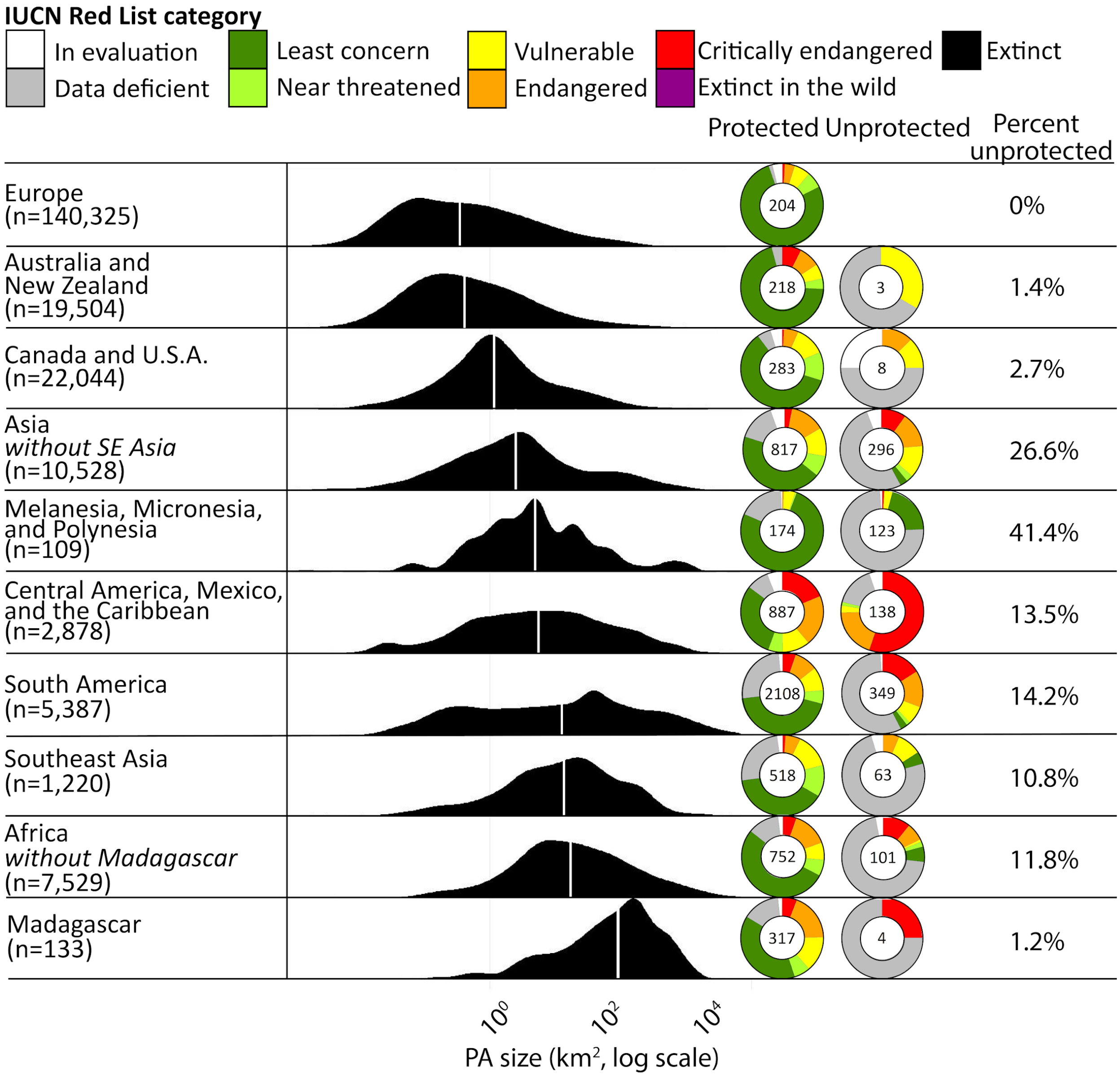

Figure 5: *Protected area size and threat status distribution by global regions. From left to right, each global region shows a smoothed frequency histogram of PA sizes, a pie chart of the conservation status of protected amphibians, a pie chart for conservation status of unprotected amphibians, and the proportion of unprotected species. The number of unprotected and protected species are shown on each pie chart. Regions are ordered by PA median size.*

Supporting Information

To illustrate the intersection of protected areas (PA), threatened amphibian species according to IUCN categories, and unprotected species with no portion of their range in a PA at meaningful scales, we generated lists by country and use Mexico as a case study. Amphibian alpha-richness and threatened species richness was calculated with the range polygons used in this analysis and converted to a raster based on counts of overlapping polygons (implemented in R, raster v3.4).

Mexico has 1,171 protected areas currently registered in the World Database of Protected Areas (WDPA). 418 amphibian species occur within this country's borders, and 294 of those species are endemic to Mexico. In our analysis, Mexico is seventh of countries with the highest amphibian richness (Figure S1.A). 56% (232 species) of Mexico's amphibian diversity is threatened with extinction (Figure S2.B). Ninety-nine, or over 23%, of Mexican amphibian species currently show no overlap with the existing protected area network (Figure S2.C). Adding only 7.15% (140,414 km2) of Mexico's terrestrial area (1,962,939 km2) would provide coverage to all currently unprotected species, bringing Mexico's total terrestrial PA coverage to over 32% allowing Mexico to reach its 30x30 goal.

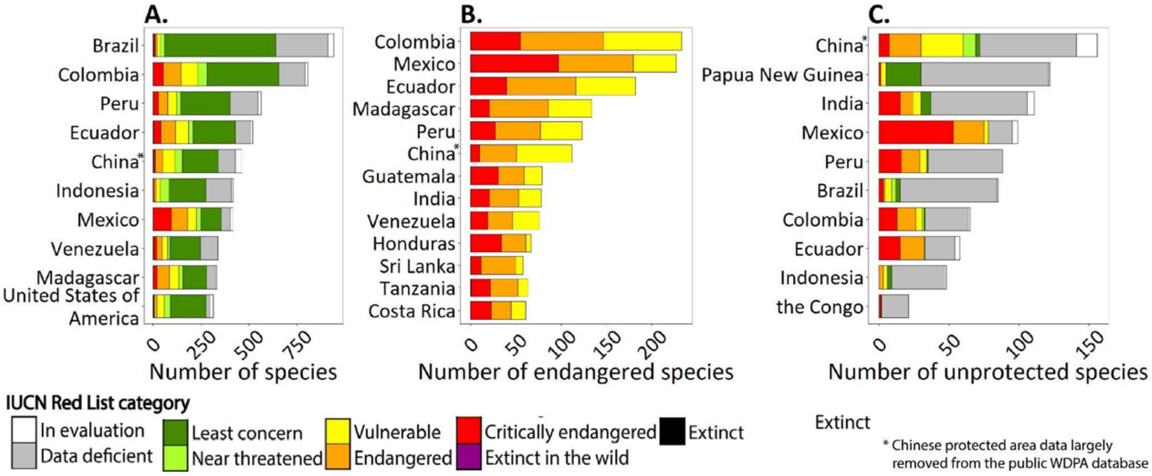

Figure S1. Country profile plots. (A) Top ten global countries in terms of total amphibian species richness, using all IUCN categories. (B) Top ten global countries in terms of threatened (VU, EN, CR, EW, EX) amphibian species, highlighting only IUCN threatened categories. (C) Top ten countries in terms of amphibian species richness entirely unprotected by the current protected area network, showing all IUCN categories.

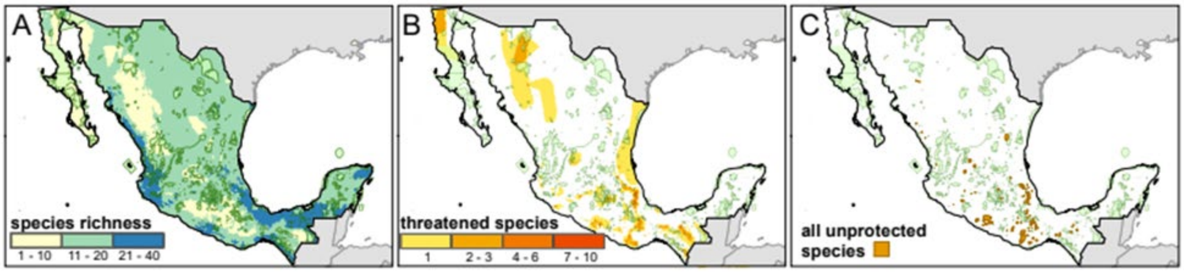

Figure S2. Mexico: a case study. (A) Amphibian alpha-richness relative to protected area placement (green outlined polygons). (B) Threatened amphibian species richness relative to protected areas (green outlined polygons). (C) The ranges of amphibian species with no overlap with the existing PA network (orange filled polygons) relative to protected area placement (green outlined polygons).