Received: 5 February 2021 | Revised: 17 May 2021 | Accepted: 25 May 2021

DOI: 10.1111/gcb.15734

Global Change Biology WILEY

PRIMARY RESEARCH ARTICLE

An integrative synthesis to global amphibian conservation priorities

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Funding information
This study was funded by the College of Biology and the Environment, Nanjing Forestry University.

Abstract

Human activities are driving many species to the brink of extinction, and the current distribution of protected areas only weakly alleviates pressure on threatened species. This discrepancy reflects the presence of protected areas on lands available instead of the ecological, evolutionary, or conservation values of species present. Habitat loss consequently continues to impact threatened species, as illustrated by geographic patterns of biodiversity loss for amphibians. Given the need to better align the boundaries of protected areas with at-risk biodiversity, we assessed the importance of various factors for identifying global and biome-level conservation priority areas, specifically for amphibians. We identified, mapped, and ranked areas of critical conservation importance for all amphibian species on earth using a new integrative tool that scores the urgency of conserving each species and location based on a combination of species characteristics and ecoregion-level human impacts. Our integrative approach is novel in that it accounts for likely threats to Data Deficient species, considers the irreplaceability of unique species that are phylogenetically isolated, and addresses the localized conservation implications of species endemicity and projected future human impacts to an ecoregion. For comparison, we also mapped and ranked amphibian biodiversity using species richness and an Evolutionarily Distinct and Globally Endangered (EDGE) score proxy. Our integrative approach predicted key regions for amphibian conservation that were not apparent when using a simple species richness or EDGE score proxy-based approach. Furthermore, by scaling conservation priority scores relative to biome, we identified several temperate and xeric regions of crucial yet overlooked conservation importance for amphibians. Until global amphibian diversity is thoroughly catalogued, we recommend using our integrative scoring approach to set geographic priorities for amphibian habitat protection, while acknowledging that this approach may be complemented by others (e.g., EDGE scores). Our study provides an avenue for avoiding common pitfalls of more simplistic species richness-based approaches for conservation planning, and can be used to improve the future design of protected areas.

KEYWORDS
amphibian, biomes, conservation priority, importance, integrative variables

1 | INTRODUCTION

Despite garnering widespread attention by scientists and managers alike, species declines have gone largely unmitigated throughout the past few decades. Amphibians can serve as useful models for developing tools that address these declines, as they tend to be more imperiled than other vertebrate taxa and are declining more rapidly (Bishop et al., 2012; Pimm et al., 2014; Stuart et al., 2004; Wake & Vredenburg, 2008). We have now entered a major amphibian extinction crisis (Ceballos et al., 2020), with 48% of all extant species (excluding Data Deficient ones) currently classified as Threatened or Near Threatened (IUCN, 2020). Worse yet, this percentage is likely an underestimate of the true severity of modern amphibian declines, as "noncharismatic" species unknown to the public are sometimes assigned overly optimistic Red List statuses (Bruton, 1995). Additionally, of the >20% of extant amphibians classified as "Data Deficient" or "Not Assessed," many have traits (e.g., narrow environmental niches and absence or limited occurrence within protected areas) predisposing them to human-caused declines (Nori & Loyola, 2015), which are rarely considered in conservation decision-making.

A major factor limiting the successful mitigation of amphibian declines is the lack of spatial overlap between the ranges of threatened amphibian species and boundaries of protected areas that are managed with these species in mind. Roughly one quarter of all amphibian species occur exclusively in unprotected areas, and this number is steadily increasing (Nori et al., 2015). Nonetheless, the ranges of many threatened amphibians, and particularly microendemic species, could be protected from specific threats such as habitat loss via only a modest augmentation to boundaries of existing protected areas (Nori et al., 2016), making future biological preserve design an important yet underappreciated factor for mitigating population declines. The need for improved preserve design is further underscored by the fact that tropical areas with globally exceptional amphibian biodiversities are also often among the least protected globally (Bradshaw et al., 2009; Brooks et al., 2002; Gardner et al., 2009; Laurance et al., 2012; Sloan et al., 2014). As a result, suggestions have been made to use the ranges of at-risk species to better delineate protected areas (Ceballos et al., 2020). However, no attempts have been made, to our knowledge, to identify the specific global areas most in need of protection by quantitatively integrating data on threatened local amphibian diversity and the severity of local anthropogenic disturbances.

In order to effectively identify priority areas for global amphibian conservation, it is important to consider species-level and ecoregion-specific factors. Historically, simplistic species richness maps have often served as the basis for protected area planning (Scott et al., 1993), but this system of designation has been imbued with several problems. For example, simple species richness maps are not weighted by species-specific factors such as the conservation status of each species in an area. As such, species richness maps fail to account for the fact that certain species are more in need of proactive conservation than others (Carmona et al., 2020). In addition, simple species richness-based conservation strategies fail to consider the uniqueness and irreplaceability of a given species' environmental niche and evolutionary history. Finally, simple species richness-based approaches fail to consider that some ecosystems face greater future anthropogenic threats than others and may therefore be more in need of rapid protection. As such, conservation planning based on amphibian species richness alone may fail to highlight the conservation importance of areas fostering a high diversity of species with unique traits, such as life-history strategies (Bolochio et al., 2020). A more rigorous approach is therefore needed to effectively identify geographic priorities for global amphibian conservation.

Weighting individual species using a scoring system indicative of the urgency of their conservation represents a promising alternative to more simplistic species richness-based approaches for identifying regions of high conservation priority for amphibians (Conroy & Noon, 1996; Groves, 2003). For example, the Evolutionarily Distinct and Globally Endangered (EDGE) scoring approach described by Isaac et al. (2012) synthesizes the evolutionary history and conservation status of an amphibian species into a single metric summarizing the urgency of its conservation. However, EDGE scores are currently only available for amphibian species classified as threatened by the IUCN Red List of Threatened Species (IUCN, 2020), and therefore cannot capture the importance of conserving Data Deficient and non-threatened species. Available EDGE data may therefore be suboptimal for global conservation planning, as Data Deficient amphibian species are often likely to be imperiled and occur exclusively in unprotected areas at an above-average rate of 81% compared to other amphibians (Nori & Loyola, 2015). Moreover, the "evolutionary distinctiveness" subscore incorporated into EDGE scores is based on clade divergence time, and therefore does not fully capture the irreplaceability of functionally unique lineages that have recently evolved. Therefore, while EDGE score-based species weighting may improve conceptualizations of the priority of regions for global conservation, alternative approaches that incorporate more complete information about the conservation status and irreplaceability of each amphibian species may sometimes be more valuable for holistic conservation planning, acknowledging the contrast between simple and cost-effective approaches that can be easily adopted. This may be particularly true in regions where inference about geographic conservation priorities is highly sensitive to species weighting methods. However, the relative severity of this problem in different regions is unknown.

To identify global amphibian conservation priority areas effectively, we propose an "integrative approach" that incorporates several factors related to the urgency of each species' conservation, including Data Deficient species, and quantifies the priority of increasing protected areas within a given region. We tested such an approach by assigning each amphibian species an integrative priority score based on the combination of its range size (Loyola et al., 2007), conservation status (IUCN, 2020), and taxonomic irreplaceability (Brooks et al., 2005; Potter, 2018). As several species do not have a definitive IUCN status (i.e., Data Deficient or Not Assessed), our approach uses a combination of biological and environmental factors to predict true status score. By weighting species richness maps based on endemism, taxonomy, and threat-based subscores for each species, our study provides an avenue for avoiding the common pitfalls of more simplistic species richness-based approaches. Further, by weighting outputs according to the level of future anthropogenic threats to a region, our study incorporates additional, complementary habitat where protection is most urgently needed. Finally, by developing a version of our outputs rescaled by biome, our study provides novel methods and results about underrecognized local hotspots for amphibians with unique climate-specific adaptations, which, if protected, may help amphibians adapt and persist through future climatic changes beyond even humans.

2 | MATERIALS AND METHODS

2.1 | Study design

To determine the importance of various factors for identifying global priority areas for amphibian conservation, we quantified and mapped amphibian biodiversity using three approaches, including species richness (Jenkins et al., 2013), an EDGE score proxy based on Isaac et al. (2012), and an integrative synthesis of extinction risk (IUCN, 2020), endemicity, taxonomic irreplaceability, and the conservation status of ecoregions occupied by each species (Olson et al., 2001). We calculated species richness using the same approach as Jenkins et al. (2013), and describe the methods of our other two approaches below.

2.1.1 | Constructing an EDGE score proxy

The EDGE scoring system combines estimates of how evolutionarily distinct (ED) and globally endangered (GE) species are into a single metric, and it is intended as a proxy for assessing the conservation priority level of each threatened species (Isaac et al., 2012). While ED scores have been calculated for nearly all amphibians based on clade divergence times, GE scores and thus complete EDGE scores are currently only available for amphibians classified by the IUCN Red List of Threatened Species as threatened (IUCN, 2020). Therefore, we estimated relative EDGE scores for all amphibian species described prior to 2018 using a modified version of the approach of Isaac et al. (2012; Table 1). We assigned a GE score proxy of 1–5 to each species based on their IUCN Red List status, where 1 = Least Concern, 2 = Near Threatened, 3 = Vulnerable, 4 = Endangered, and 5 = Critically Endangered. Species considered extinct or extinct in the wild by the IUCN were excluded. To estimate GE scores for data deficient and non-assessed amphibian species, we used Boosted Regression Trees (BRTs; Elith et al., 2008) to predict the true threat statuses of non-Data Deficient amphibian species (i.e., excluding species classified as not assessed or Data Deficient) based on the following variables: range size, range perimeter, ratio of range size to range perimeter, taxonomic order, latitude of range centroid, and use or nonuse of aquatic and terrestrial habitats. We gave each of these variables an equal level of consideration in our initial stage of BRT model fitting. Importantly, BRTs produce predictions that are generally robust to predictor variable collinearity (e.g., between influences of continent and biome on amphibian Red List category), and do not assume that the data follow a particular distribution (Elith et al., 2008). We validated our BRTs using cross-validated correlation scores between predicted and actual status score data for all non-Data Deficient amphibian species (Arlot & Celisse, 2010), then used the model to predict the conservation status of Data Deficient and non-assessed species, using the same predictor variables as previously. High out-of-bag predictive power (~90% cross-validated correlation between predicted and known status scores) suggested that our predictor variables were highly informative of de facto species status, while fitting the model to non-Data Deficient species. Therefore, while we acknowledge that Data Deficient species are poorly understood by definition, we view imperfect estimates of these species' de facto statuses as more useful for conservation planning than the alternative of ignoring their likely heterogeneous conservation needs. We excluded species described after 2018 from these analyses due to the generalized absence of data on their ranges. Additionally, we excluded cryptic species complexes containing unresolved numbers of species or unresolved species range boundaries (*n* = 827 taxa). The inclusion of other poorly understood species in our analyses (e.g., Data Deficient species described before 2018) allowed us to analyze over 80% of known amphibian species in total, helping minimize potential biases in our results caused by our necessary omission of newly described and unresolved taxa that were almost certain to have inaccurate range maps.

We combined ED scores from Isaac et al. (2012) with our GE score proxy to calculate relative EDGE scores for all amphibian species that could be included in our analyses (*n* = 6026) so that our estimated EDGE scores mirrored actual EDGE scores. After standardizing ED and GE scores so that their minimum and maximum values equaled 0 and 1, respectively, we added the two together to derive an initial EDGE score proxy for each species (Table 1). To further improve the similarity of our EDGE score estimates with true EDGE scores, we used BRTs (Elith et al., 2008) to predict true EDGE scores (Isaac et al., 2012) from our initial EDGE score proxy, for species that possessed both scores (*n* = 1085). We then used this model to compare true EDGE scores and the proxy calculated here for the entire dataset (*n* = 6026 species), and used these predicted values as our final EDGE score proxy in subsequent analyses. Final EDGE score estimates and true EDGE scores were 95% correlated, indicating that our final relative EDGE scores were a viable proxy for true EDGE scores. We standardized our EDGE score proxy to a 0–1 scale, so that its distribution mirrored that of other variables used in subsequent analyses.

2.1.2 | Calculating integrative conservation priority scores

We used an integrative scoring approach to quantify the urgency of conserving each amphibian species based on multiple relevant

TABLE 1 Descriptions of variables used in each of our analyses. We used several environmental, geographic, and taxonomic variables to predict the de facto status of Data Deficient species, then used these predictions alongside known statuses of all other species and Evolutionary Distinctiveness (ED) scores (Isaac et al., 2012) to generate our EDGE score proxy. The EDGE score proxy was generated by summing these scores for each species, after converting them to a beta distribution with minimum and maximum values of 0 and 1, respectively

Variable	Range of values or categories	Usage
Latitude of range centroid	−48.2 to 60.4	Predicting status of Data Deficient species
Scaled range size	0–1	Predicting status of Data Deficient species
Scaled range perimeter	0–1	Predicting status of Data Deficient species
Ratio of scaled range perimeter to scaled range size	0.2–4453.0	Predicting status of Data Deficient species
Terrestrial habitat use	True or False	Predicting status of Data Deficient species
Aquatic habitat use	True or False	Predicting status of Data Deficient species
Taxonomic family	Families of amphibians assessed by IUCN with non-Data Deficient status scores	Predicting status of Data Deficient species
Taxonomic order	Caecilian, frog, or salamander	Predicting status of Data Deficient species
IUCN status of species not listed as “Data-Deficient,” “Not Assessed,” “Extinct,” or “Extinct in the Wild"	“Least Concern,” “Near Threatened,” “Vulnerable,” “Endangered,” or “Critically Endangered”	Creating numerical IUCN status scores for non-data deficient species
Numerical status scores of amphibians assessed by IUCN with non-data deficient status scores	1–5	Predicting status of Data Deficient species to develop species status scores
Scaled evolutionary distinctiveness (ED) score	0–1	Creating initial EDGE score proxy
Scaled predicted species status	0–1	Creating initial EDGE score proxy
Latitude of range centroid	−48.2 to 60.4	Predicting status of Data Deficient species
Scaled range size	0–1	Predicting status of Data Deficient species
Scaled range perimeter	0–1	Predicting status of Data Deficient species
Ratio of scaled range perimeter to scaled range size	0.2–4453.0	Predicting status of Data Deficient species
Terrestrial habitat use	True or False	Predicting status of Data Deficient species
Aquatic habitat use	True or False	Predicting status of Data Deficient species
Taxonomic family	Families of amphibians assessed by IUCN with non-Data Deficient status scores	Predicting status of Data Deficient species
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IUCN status of species not listed as “Data-Deficient,” “Not Assessed,” “Extinct,” or “Extinct in the Wild"	“Least Concern,” “Near Threatened,” “Vulnerable,” “Endangered,” or “Critically Endangered”	Creating numerical IUCN status scores for non-data deficient species
Numerical status scores of amphibians assessed by IUCN with non-data deficient status scores	1–5	Predicting status of data deficient species to develop species status scores
Scaled evolutionary distinctiveness (ED) score	0–1	Creating initial EDGE score proxy
Scaled predicted species status	0–1	Creating initial EDGE score proxy
Average annual precipitation in pixel (mm)	0–6733.8	Determining the influence of environmental factors on sensitivity of the integrative score to each of its subscores

(Continues)

TABLE 1 (Continued)

Variable	Range of values or categories	Usage
Average elevation in pixel (m)	−85.5 to 5631.1	Determining the influence of environmental factors on sensitivity of the integrative score to each of its subscores
Biome	Names of NRCS biomes occupying the majority of each pixel	Determining the influence of environmental factors on sensitivity of the integrative score to each of its subscores
Continent	Names of continents occupying the majority of each pixel	Determining the influence of environmental factors on sensitivity of the integrative score to each of its subscores
Land cover in map pixel (%)	0–100	Determining the influence of environmental factors on sensitivity of the integrative score to each of its subscores
Land cover within 1000 km of pixel (%)	0–100	Determining the influence of environmental factors on sensitivity of the integrative score to each of its subscores
Distance-based spatial eigenvectors (n = 3)	−0.02 to 0.03 −0.03 to 0.02 −0.03 to 0.03	Accounting for spatial autocorrelation when determining the influence of environmental factors on sensitivity of the integrative score to each of its subscores

factors (Table 1). For each species, we calculated a conservation priority score using a combination of species conservation status, endemicity, taxonomic irreplaceability, and the World Wildlife Fund conservation status of ecoregions occupied by the species (Olson et al., 2001). We used the same IUCN status-based scoring system as for our GE score proxy, with values ranging 1–5, to represent the conservation status of each amphibian species included in our analyses, and defined the endemicity of each species as the natural log of the inverse of their range size in km^2.

We estimated the taxonomic irreplaceability of amphibian species by considering multiple evolutionary hierarchies. Whereas SG is the number of species in a genus, GF is the number of genera in a family, and FO is the number of families in an order, we standardized these three variables such that their minimum and maximum values equaled 0 and 1, respectively. We then used the following equation to estimate the taxonomic irreplaceability of each species: taxonomic irreplaceability = SG + GF + FO. This approach was preferable to treating ED scores as directly equivalent to taxonomic irreplaceability, because as ED scores are calculated solely from clade divergence times (Isaac et al., 2012), they do not adequately capture the true taxonomic irreplaceability of highly distinct, irreplaceable taxa that emerged relatively recently as a result of recent bouts of rapid evolution (Hairston et al., 2005; Landis & Schraiber, 2017).

To generate integrative conservation priority scores for each species, we synthesized subscores for species status, endemicity, and taxonomic irreplaceability into a single metric. As species status is arguably the largest factor dictating the consequences of conserving a species or not, we assigned it the highest weight of any variable when synthesizing subscores. Thus, whereas IS is the integrative score, E is the endemicity (range = 0–1), TI is the taxonomic irreplaceability (range = 0–1), and CS is the conservation status (range = 1–5), we calculated an integrative conservation priority score for each species using the following equation: $IS = (E + TI) \times CS$. However, to acknowledge likely disagreements about how much species status should dictate amphibian conservation priorities, we also tested several supplementary scoring approaches that either excluded species status or placed it on a 0–1 scale ("scaled species status score" hereafter) and added it to—instead of multiplying by—the sum of endemicity and taxonomic irreplaceability subscores (Figure S1a–v).

2.1.3 | Map construction

For each of our three scoring approaches, we quantified and mapped amphibian biodiversity in ArcMap 10.7 (Environmental Systems Research Institute, Inc.) by summing the scores (or number, for species richness) of species present within 50-km wide (~1600 km^2) pixels of a hexagonal grid covering the extent of the global distribution of amphibians (n = 44,094).

To account for likely future changes to the status of amphibian species given anthropogenic disturbance trajectories in each ecoregion, we calculated ecoregion status scores for every amphibian-inhabited ecoregion (n = 763), using the same ecoregions as Olson et al. (2002). We used ecoregion status assessments from Olson et al. (2002), which categorized relative threats to each ecoregion over the next 30 years, to assign each ecoregion a 1–3 ecoregion status score, where "relatively stable or intact" = 1, "vulnerable" = 2, and "critical or endangered" = 3. We incorporated ecoregion status into our integrative scoring approach by multiplying integrative species scores within each pixel by the status score of the ecoregion occupying the majority of the pixel. While our ecoregion status scores provided only coarse estimates of future threats to each ecoregion, they nonetheless constituted the most viable available method for quantifying future ecoregion-level threats, because these threats depend on several complex interactions among future environmental, social, and economic conditions, which were beyond the scope of our analyses but were considered by Olson et al. (2001). However, to acknowledge the coarse and unavoidably subjective nature of ecoregion status scores, we also tested several alternative scoring approaches, many of which excluded this variable (Figure S1a–v).

Since amphibians often possess ecological traits that are unique to their resident biomes (e.g., extreme drought tolerance in deserts), we used each of our three scoring approaches to identify the 10 highest-priority map pixels within each of 12 global biomes (United States Department of Agriculture, 2020). To account for faunal redundancy among pixels sharing a common ecoregion, we considered only the single highest-scoring pixel (or set of pixels, if tied) within each ecoregion when identifying the top 10 highest-priority pixels, applying this rule separately to each of our three scoring approaches. Pixels were considered to fall within an ecoregion when the majority (or if necessary, a plurality) of their area overlapped the ecoregion.

To provide information about the conservation status of top-scoring pixels in each biome, we calculated the proportion of their terrestrial habitat remaining (i.e., not developed or used for agriculture) using global land cover classification maps from the Copernicus Climate Data Store (Thépaut et al., 2018). Additionally, we used each of our three scoring approaches to construct biome-specific conservation priority maps by dividing the scores of each pixel in our global map by the maximum score of other pixels within the same biome. We excluded the “ice/glacier” biome (which harbors no extant amphibians) from these analyses, and combined the “tundra interfrost” and “tundra permafrost” biomes into a single tundra biome when assessing biome-level amphibian conservation priorities. To complement our pixel-level rankings within each biome at a broader spatial scale, we also used each scoring approach to identify the top 10 ecoregions accounting for the largest percentage of biodiversity within their biomes, per unit of the ecoregion's area.

Although we only directly compared three approaches for mapping global amphibian conservation priorities (species richness, EDGE score proxy, and the integrative approach), we recognize that there is no single set of widely accepted approaches for identifying conservation priority regions, and that the three approaches we evaluated are subjective. Therefore, to explore alternative options, we also generated several additional, supplementary maps using alternative combinations of the subscores from our integrative approach to map global amphibian conservation priorities (Figure S1a–v).

2.2 | Statistical analyses

To compare amphibian conservation priority scores derived from each of our three scoring approaches (species richness, EDGE scores, and the integrative approach), we *z*-scored the outputs of each of these approaches across all map pixels ($n = 44{,}094$ total pixels). We calculated the absolute values of pairwise *z*-score disparities for each possible pair of approaches ($n = 3$) at each pixel, and used a Kruskal–Wallis test (Kruskal, 1964) to determine whether mean disparities differed among the pairs collectively, based on the null hypothesis that the three approaches would produce identical *z*-scored outputs, and thus all pairwise score disparities would be equal to each other and to zero. We also used a post hoc one-sample Wilcoxon signed-rank test (Woolson, 2007) to assess how much score disparities among specific pairs of approaches (Species Richness-EDGE proxy, Species Richness-Integrative, and EDGE proxy-Integrative) differed from zero. We acknowledge that adjacent pixels contained overlapping species and thus overlapping score disparities, and that our data for the above analyses were, functionally, the census of conservation scores at all pixels inhabited by amphibians. Thus, we also calculated raw effect sizes for score disparities among pairs of scoring approaches and emphasize these as a key metric for comparing the three approaches.

To assess whether amphibian conservation priorities differed among our three scoring approaches for biodiverse areas specifically, we also used the above method to compare score rankings for the 50 globally highest-ranking pixels from each approach. To reduce taxonomic redundancy among top-scoring pixels, we only considered the single highest-scoring pixel (or multiple, if tied) from each ecoregion and for each scoring approach. However, we allowed species to contribute to scores of top-ranked pixels in multiple separate ecoregions, as the alternative would have required that some pixels with low or modest biodiversity be selected as “top-ranked” to completely avoid taxonomic redundancy in the pixel rankings. Given the importance of top-ranked pixels for amphibian conservation, we also calculated the proportion of their land considered protected by the IUCN (IUCN World Database on Protected Areas, 2020) and the proportion of their terrestrial habitat remaining (Thépaut et al., 2018) to inform their future protection. We are unaware of similar metrics for the aquatic ecosystems used by many amphibians, but these ecosystems are often impacted by terrestrial habitat loss equally or more so than terrestrial ecosystems (Allan & Castillo, 2007).

To determine the relative influence each integrative approach subscore (endemicity, taxonomic irreplaceability, species status, and ecoregion status) had on the total integrative score, we calculated the amount of change in integrative scores that resulted from individually excluding each of its four subscores. Additionally, to determine how environmental factors influenced the sensitivity of pixel scores in the integrative approach to endemicity, taxonomic irreplaceability, species status, and ecoregion status subscores, we calculated the difference in relative scores between the complete integrative model and versions that individually excluded each of its subscores. We assessed how environmental factors influenced the sensitivity of the total integrative score to each of its four subscores with BRTs, each using mean annual temperature, mean annual precipitation, proportion of land (as opposed to water) within a 1000-km radius of each pixel, biome, continent, and geographic location as predictor variables. The response variable in each of these models ($n = 4$ with one model for each subscore) was the disparity between the total integrative score and a reduced version of this score that was calculated with the subscore of interest excluded. We also used this approach to determine how environmental conditions influenced the sensitivity of scores of the 50 top-ranked ecoregions (using total integrative scores) to each of the four integrative subscores.

3 | RESULTS

3.1 | Pixel-level outputs

Species richness, EDGE score proxy, and integrative scoring approaches varied considerably in the pixel-level scores they produced relative to one another, and the Kruskal–Wallis test for all pixel-level scores was highly significant ($p < 2.2 \times 10^{-16}$, $\chi^2 = 817.78$, $df = 2$). Additionally, outputs of subsequent one-sample Wilcoxon signed-rank tests of all pixels were too highly significant to determine the exact values of test statistics ($v > 9.7 \times 10^8$ and $p < 2.2 \times 10^{-16}$ for all tests), though 95% confidence intervals for absolute values of pairwise disparities in z-scored outputs were successfully calculated as 0.106–0.110 (Species Richness-EDGE; median estimate = 0.108), 0.164–0.170 (Species Richness-Integrative; median estimate = 0.167), and 0.165–0.170 (EDGE-Integrative; median estimate = 0.167).

The three scoring approaches also varied significantly in the selection and precise rankings of their 50 highest-ranked pixels ($p = 0.01849$, $\chi^2 = 7.9805$, $df = 2$). Of the three possible pairs of approaches, one-sample Wilcoxon signed-rank tests highlighted that rankings of pixels differed the most for the species richness-integrative ranking comparison (median estimate = 83.0; 95% CI = 59.5–101.0; $v = 3403$; $p = 1.9 \times 10^{-15}$), followed by the species richness-EDGE score proxy comparison (median estimate = 44.0; 95% CI = 36.5–54.5; $v = 3403$; $p = 1.9 \times 10^{-15}$). The EDGE score proxy-integrative pair had the lowest ranking disparities among the three pairs of approaches, though the difference in rankings was still substantial between them (median estimate = 33.5; 95% CI = 25.5–50.0; $v = 3081$; $p = 8.5 \times 10^{-15}$). Supplementary approaches tested also yielded a wide variety of outputs (Figure S1a–v), although the large number of these alternative approaches ($n = 22$) precluded an in-depth analysis of all pairwise differences between them ($n = 231$ possible pairs).

3.2 | Regional variation in approach sensitivity

The sensitivity of relative pixel scores to the scoring approach used varied widely between regions (Figures 1a–c and 2a–c; Figure S2a–c). In particular, the relative scores of the central and eastern Amazon Basin were highly sensitive to the scoring approach used, with the species richness, and to a lesser extent EDGE score proxy, assigning higher relative scores to this region than the integrative approach. This also resulted in lower relative priority scores for non-Amazonian regions using the species richness approach compared to the others, including much of Central America, south-central Chile, Tanzanian and Kenyan highlands, the southern coast of West Africa, the Western Ghats of India, the southeastern United States, the Iberian Peninsula, Southeast Asia, and the eastern coast of Australia. Moreover, relative conservation priority scores of the latter four of these regions were also lower than average for the EDGE scoring proxy approach than in the three scoring approaches overall (Figure 1a–c). The integrative scoring approach, by contrast, produced below-average relative conservation priority scores for most of the Amazon Basin compared to other approaches. These results were accompanied by increased relative conservation priority scores for all of the above regions that were devalued in the species richness approach compared to others.

3.3 | Universally top-ranked priority areas and biomes

Although globally top-scoring pixels varied significantly in their precise rankings among scoring approaches (Data File S1), several were highly ranked for all three approaches. For example, 23 ecoregions had a high-scoring pixel ranked in the top 50 for all three approaches (Data File S1; see also Figure 1a–c), in part because top-ranked pixels were stratified by ecoregion. Moreover, the three approaches overlapped considerably in their top-ranking n pixels ("highest-priority pixels" hereafter), where n is the minimum number of pixels necessary to capture >15% of global amphibian biodiversity ($n = 17$, 18, and 14 for species richness, EDGE score proxy, and integrative scoring approaches, respectively). On average, 42.9% of the highest-priority pixels for any given approach were also of highest priority in the other two approaches, with the seven unanimous highest-priority pixels located in Cameroonian Highlands forests (Cameroon), Costa Rican seasonal moist forests (Costa Rica and Nicaragua), Cross-Sanaga-Bioko coastal forests (Cameroon and Nigeria), Eastern Cordillera real montane forests (Ecuador, Colombia, and Peru), Malagasy lowland forests (Madagascar), Northwestern Andean montane forests (Columbia and Ecuador), and Talamancan montane forests (Costa Rica and Panama). These seven ecoregions all feature a Tropical Humid biome (United States Department of Agriculture, 2020). Most of the highest-priority pixels (range = 57.1–82.4%) occurred in the Neotropics for all three approaches, although the species richness scoring approach tended to score neotropical pixels more favorably than the other two approaches (Figure 2a–c). All pixels that had a score above the 90th percentile for at least one scoring approach also had a 34.1% likelihood of scoring above the 90th percentile for all three approaches ($n = 6660$ pixels; Figure 3).

3.4 | Ecoregion and biome-level outputs

The precise rankings of top-scoring pixels varied considerably among our three scoring approaches when applied to the biome

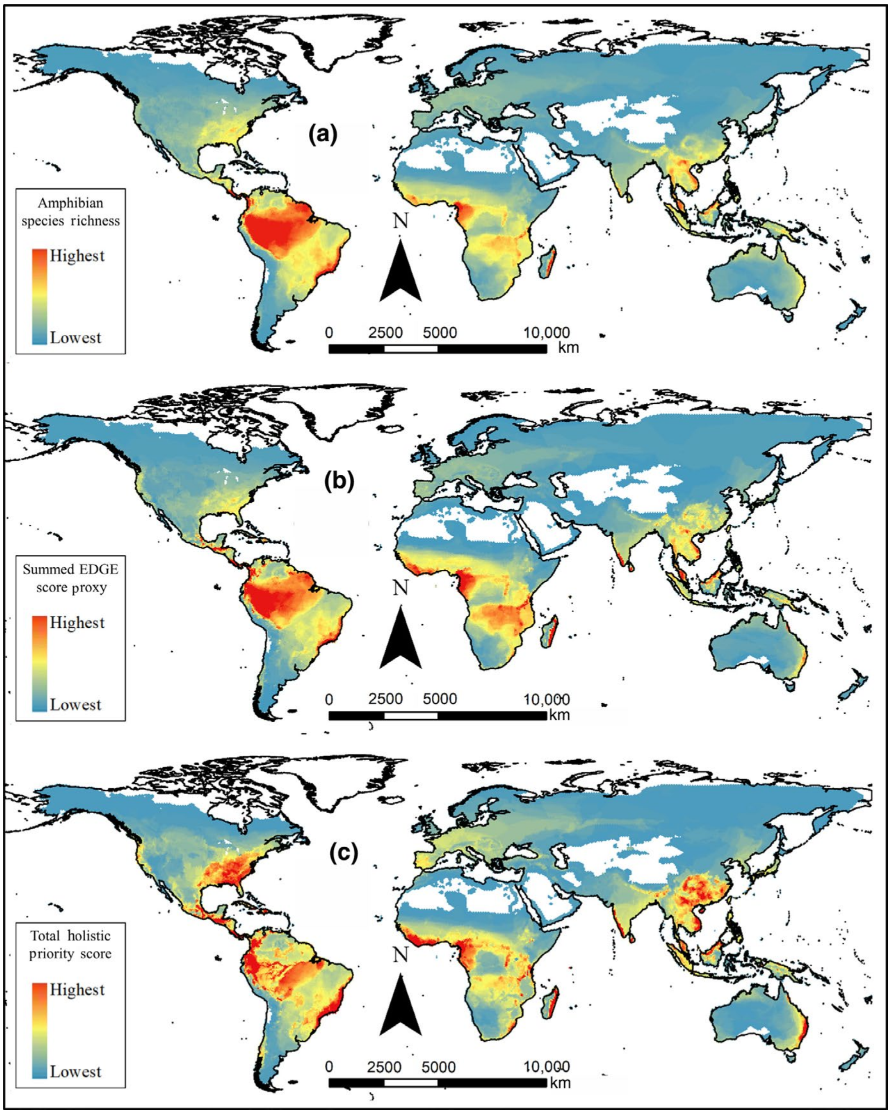


FIGURE 1 Relative conservation priority scores for amphibians using species richness (a), EDGE score proxy (b), and the integrative approach (c). We calculated priority scores for each approach by summing the scores (or number) of species overlapping each grid cell. The spatial distribution of high-scoring pixels differed considerably among the three approaches, with the integrative and EDGE score proxy approaches suggesting higher conservation priorities in the Paleotropics than the species richness approach

level, though the effect of scoring approach was lower for scores scaled to biome level than for unscaled priority scores. Only two of 12 biomes (Boreal Humid and Tropical Arid) had the same top-ranked pixel for all three scoring approaches (Data File S1). In contrast, the top 10 ranking global ecoregions based on the percent of biome-level biodiversity captured per unit of area were almost identical among the three scoring approaches, with nine ecoregions scoring in the top 10 of every approach, including a unanimous top two ecoregions: Enriquillo wetlands (Dominican Republic) and Santa Marta páramo (Colombia; Table S1). High-elevation páramo habitats were a prominent feature of these top 10 rankings, which included four páramo ecoregions for all three approaches.

3.5 | Spatial distribution of top scores at different scales

As with ecoregion-level scores, pixels located in the Neotropics tended to have the highest values (Figure 1a–c). However, biome-adjusted pixel-level scores (i.e., the relative score of each pixel divided by the maximum score of any pixel in the same biome) were distributed roughly evenly across most of the globe (Figure 4a–c). The precise distribution of biome-level hotspots depended moderately on the scoring approach used, with species richness, EDGE score proxy, and integrative approaches producing above-average relative scores in either tropical South America, south-central Africa, or the eastern United States, respectively. The average disparity among *z*-scored outputs of the three approaches was highly correlated with species richness, and was influenced by mean annual precipitation more than any other environmental variables, with the largest score disparities occurring in pixels with annual precipitation ~1500–4000 mm (Figure S3).

3.6 | Contributions of each subscore to the total integrative score

Endemicity, taxonomic irreplaceability, and ecoregion status subscores contributed roughly equally to overall integrative scores on average (Figure 5), but the influences of these subscores varied widely among pixels. Species status had lowest average (but also

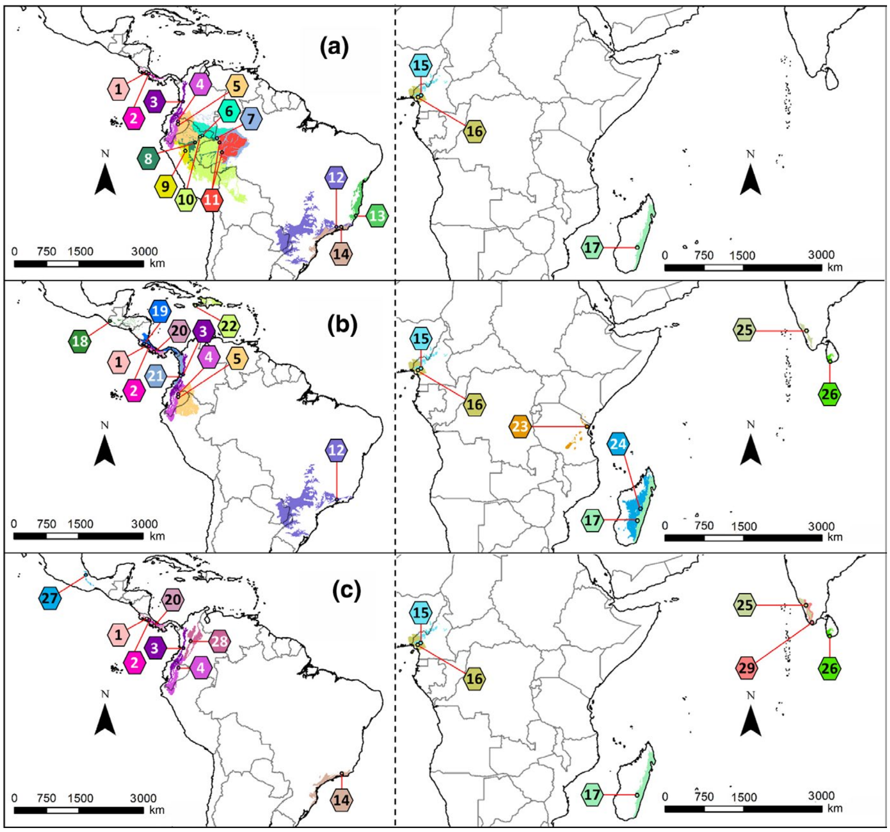


FIGURE 2 Locations and associated ecosystems of the *n* highest-ranking pixels for global amphibian conservation, where *n* is the minimum total number of pixels necessary to capture >15% of global amphibian conservation priorities, based on species richness (a), EDGE score proxy (b), or the integrative scoring approach (c). A red line links each top-scoring pixel to it associated hexagon, with hexagon color mirroring the color of the ecoregion that the pixel occurs in. Ecoregion numbers: 1 = Costa Rican seasonal moist forests, 2 = Talamancan montane forests, 3 = Northwestern Andean montane forests, 4 = Eastern Cordillera real montane forests, 5 = Napo moist forests, 6 = Solimões-Japurá moist forests, 7 = Purus varzeá, 8 = Iquitos varzeá, 9 = Ucayali moist forests, 10 = Southwest Amazon moist forests, 11 = Juruá-Purus moist forests, 12 = Alto Paraná Atlantic forests, 13 = Bahia coastal forests, 14 = Serra do Mar coastal forests, 15 = Cameroonian Highlands forests, 16 = Cross-Sanaga-Bioko coastal forests, 17 = Malagasy lowland forests (Madagascar), 18 = Central American montane forests, 19 = Isthmian-Atlantic moist forests, 20 = Isthmian-Pacific moist forests, 21 = Chocó-Darién moist forests, 22 = Hispaniolan moist forests, 23 = Eastern Arc forests, 24 = Malagasy subhumid forests (Madagascar), 25 = South Western Ghats montane rain forests, 26 = Sri Lanka lowland rain forests, 27 = Oaxacan montane forests, 28 = Magdalena Valley montane forests, and 29 = South Western Ghats moist deciduous forests

the most variable) influence on the integrative scores among the four subscores. Biome and continent were the most influential variables dictating the sensitivity of the total integrative score to each of its four subscores overall (Figure S3). The sensitivity of the total integrative score to its species and ecoregion status subscores depended highly on the mean annual precipitation and was lowest in moist regions. In contrast, the influence of the four integrative subscores on rankings of the top 50-ranked ecoregions in the integrative approach varied widely among subscores and was dictated by a wider variety of environmental factors, including temperature, precipitation, continent, and land cover within 1000 km (Figure S4).

4 | DISCUSSION

Clear differences in the outputs of our three scoring approaches demonstrate that conventional species richness-based approaches do not capture all forms of amphibian biodiversity that may be important for determining geographic conservation priorities, especially in biodiverse regions where these differences were maximized (Figure 1a–c). Considering alternative factors, such as species endemism, taxonomic irreplaceability, and status may therefore yield a more holistic outlook of global biodiversity when required. As such, we recommend our integrative scoring approach be used to quantify geographic conservation priorities in complement with or in place of species richness, depending on precise conservation planning goals and regions (e.g., especially in biodiverse areas). This recommendation is applicable to both global and biome-level scales, as conservation priorities depended highly on scoring approach at both scales.

Biome-level biodiversity scores revealed several typically overlooked regions (e.g., páramos, Northern Indochina subtropical forests, Malagasy spiny thickets (Madagascar), Southern African bushveld, Edwards Plateau savannas, Southeast Tibetan shrublands and meadows, Southwest Iberian Mediterranean sclerophyllous and

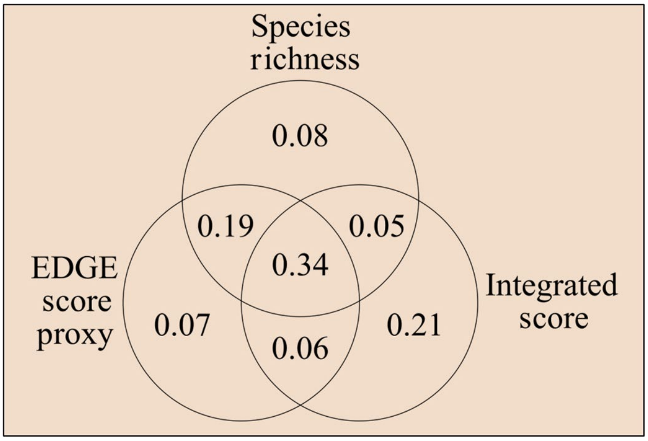


FIGURE 3 Proportional overlaps between pixels scoring in the top 10% for species richness, EDGE proxy, and/or integrative scoring approaches (*n* = 6660/44,094 pixels with a score in the top 10% for at least one metric). High-ranking pixels for the integrative score differed more from the species richness and EDGE score proxy approaches than these latter two approaches differed from each other

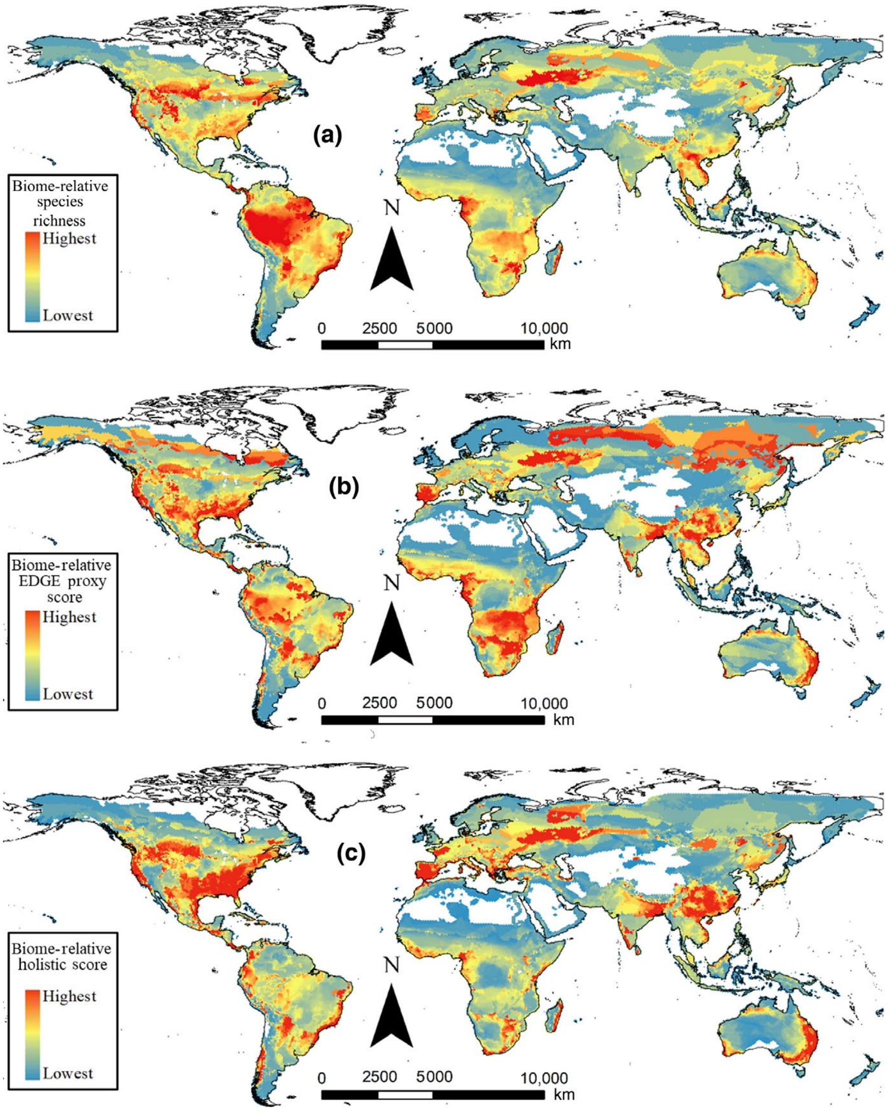
mixed forests, and Victoria Plains tropical savannas) to be of high importance for protecting amphibian lineages that have unique environmental preferences (Data File S1). Many of these overlooked regions are currently under considerable threat (IUCN, 2020). Our finding of high biome-specific amphibian biodiversity within these regions (Figure 4a–c) parallels and builds upon similar results of earlier studies. For example, Bolochio et al. (2020) identified a high, largely imperiled diversity of torrential amphibians in Northern Southeast Asia ("Indochina") subtropical forests, which our results demonstrate are among the highest-priority regions for amphibian conservation within the Temperate Humid biome.

Our findings also provide additional evidence that amphibians within overlooked environment-specific hotspots are often threatened, in agreement with Bolochio et al. (2020) and multiple other previous studies (Bolochio et al., 2020; Noss et al., 2015; Vale et al., 2015). For example, high-altitude páramo ecoregions (*n* = 5) within the Neotropics accounted for four of the 10 highest-ranked global ecoregions based on their percentages of biome-level biodiversity captured per unit of area. Páramo ecoregions harbor roughly half (48%) of all amphibian species documented within tundra environments (~188/388 species), of which an alarming two thirds are currently classified as threatened (IUCN, 2020). Thus, páramos are clearly important target regions for protecting cold-adapted amphibian lineages (e.g., *Atelopus* and *Pristimantis*). As global rather than local threats (e.g., climate change and chytridiomycosis) appear to pose the greatest risks to páramo-adapted amphibians (Gross, 2008; Larsen et al., 2011; Lips, 2016; Scheele et al., 2019), targeted local initiatives alone are unlikely to be sufficient for protecting most of these species. Due to the overall sensitivity of amphibians to land use-related habitat loss (Cushman, 2006), local conservation efforts are nonetheless invaluable for protecting páramo-adapted amphibians if coupled with additional global efforts to curb carbon emissions and disease transmission. Moreover, local conservation initiatives will be invaluable for protecting biome-level amphibian diversity in general, as several high-scoring pixels from multiple biomes have already been destroyed (Data File S1).

Geographic sampling biases represent a limitation of our study, and were highly evident in all three of our biodiversity scoring approaches, though especially for species richness. For example, well-sampled portions of the Amazon Basin and Cameroon each had much higher (known) species richness and consistently received moderately higher EDGE proxy and integrative scores than less sampled adjacent regions (Duellman, 1999) with similar tropical rainforest climates (e.g., the interior Congo Basin and the Colombian and western Brazilian Amazon). Moreover, several regions (mostly in the Congo Basin, South Asia, and Southeast Asia) achieved moderately high biodiversity scores in spite of being poorly sampled (Figure 1a–c), suggesting that the true amphibian biodiversity of these regions could rival that of prominently known amphibian hotspots, yet be largely undescribed. Based on our results and remarks of other authors regarding geographic sampling biases (Duellman, 1999; Troia & McManamay, 2016), we suspect that particularly high undescribed amphibian biodiversity may exist within Guinean rainforests, lowland rainforests in Nicaragua, Indonesian portions of New Guinea and Borneo, western Ethiopia, and several remote areas within the Amazon and Congo Basins, among other regions. Until global amphibian diversity becomes thoroughly catalogued, we recommend using our integrative biodiversity scoring approach in conjunction with others, due to its ability to synthesize multiple important criteria into a single score and its apparent lower sensitivity to sampling bias than species richness. Importantly, our integrative scoring approach also recognizes the irreplaceability of recently evolved genetically unique taxa unlike EDGE scores (Isaac et al., 2012), making its contributions to conservation planning unique and complementary.

Another important factor influencing the designation of priority areas for conservation is the geographic scope of map units to be scored and ranked based on their biodiversity. For example, we caution against treating entire ecoregions as single units for such analyses. The wide variation in ecoregion sizes causes ecoregion-wide biodiversity scores to be confounded by the existence of a species–area relationship (Connor & McCoy, 1979; Rosenzweig, 1995). Treating ecoregions as single units is also of limited utility for localized conservation initiatives that have insufficient political power and funding to protect entire ecoregions. Importantly, dividing the scores of ecoregions by their area (even after standardizing both variables) should not be viewed as a solution to the above problem for identifying geographic conservation priorities, as it instead merely substitutes one problem for another by overinflating the importance of extremely small ecoregions that harbor only a few amphibian species (e.g., small islands). Moreover, using relatively small, equal-sized hexagonal pixels as map units can provide a solution to these challenges, but only if accounting for spatially autocorrelated scores of adjacent pixels—particularly for neighboring pixels that also share a common ecoregion. As such, assessments of ranked geographic conservation priorities should not rely on raw pixel

FIGURE 4 Conservation priority scores for each pixel relative to other pixels within the same biome, for the species richness (a), EDGE score proxy (b), and integrative scoring approach (c). We calculated global-scale priority scores for each approach by summing the scores (or number) of species overlapping each grid cell. We scaled these scores to biome level by dividing the score of each pixel by the score of the highest-scoring pixel within the same biome. Our biome-scale adjustments highlight several key areas for conserving temperate and xeric-adapted amphibians, which are not visually apparent in our global-scale maps. Numerical scores are not provided to avoid confusion, as these scores are on different scales for each approach. However, these data are available in Data File S1



scores alone, as "top-ranked" pixels using this approach will tend to be clustered around only a few geographic regions and thus contain redundant biodiversity, limiting the total biodiversity captured by top-ranked pixels collectively. Thus, we found it most reasonable to rank geographic conservation priorities using a subset of pixels for each scoring approach that consisted of the single top-scoring pixel within each ecoregion.

With some notable exceptions (e.g., in páramos, African moorlands, Andean punas, and other ecoregions facing severe impacts from anthropogenic climate change and/or disease transmission), habitat loss and degradation represent the greatest overall threats to amphibians (Collins & Storfer, 2003; Cushman, 2006; Ford et al., 2020), including in several top-scoring pixels. In fact, for a few areas and for several imperiled microendemic species, there may be so little viable habitat remaining that certain resident amphibian species will soon be or are already functionally extinct (Frankham, 1995; Hanski & Ovaskainen, 2002; With & King, 1999).

Our study is among the first to test different approaches for quantifying geographic priorities for amphibian conservation (Bolochio et al., 2020; Isaac et al., 2012), and in doing so highlights the limitations of relying solely on species richness and nonbiome-specific approaches to identify areas of high conservation importance. Given the accelerating pace of global amphibian declines (Blaustein et al., 2011; Grant et al., 2016; Wiens, 2016) and an alarming lack of protected areas within many apparent amphibian hotspots that are unidentifiable using known species richness alone, we recommend that complementary approaches be used for conservation planning. For example, holistic biodiversity scoring approaches like our integrative approach may provide more detailed conservation planning guidance to managers and policymakers than species richness alone, particularly when proactive management is needed to forestall unseen extinctions of Threatened and Data Deficient species. This point is especially important for relatively unsampled regions outside of the Neotropics, which received higher and likely more reasonable scores using the integrative and EDGE proxy scoring approaches than with species richness. However, while our integrative scoring approach produced estimates of global amphibian diversity that were less reflective of sampling biases than those derived from species richness, the efficiency of all scoring approaches was limited by major gaps in amphibian sampling. To improve the

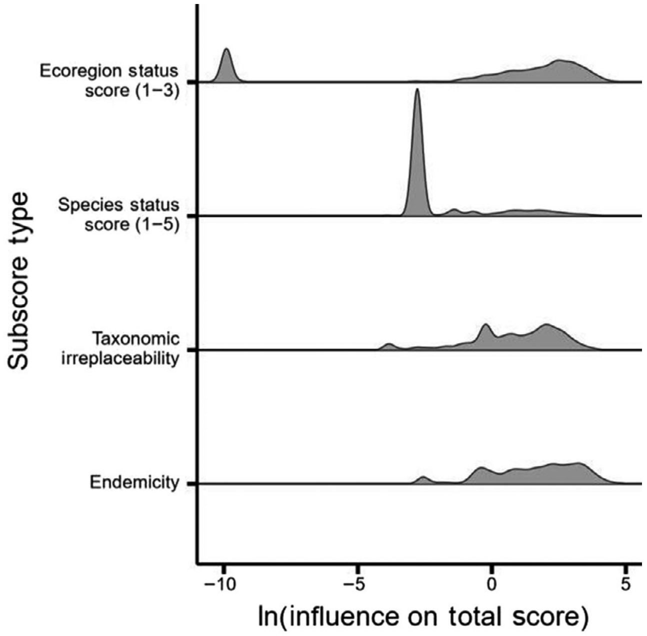


FIGURE 5 Density ridgeline plots of the pixel-level influences of integrative subscores on the total integrative score (*n* = 44,094 pixels). Horizontal lines within boxes represent mean values, upper and lower bounds of boxes represent interquartile ranges, points represent outliers, and vertical lines above and below boxplots represent the ranges of values outside of the interquartile range that were not also considered outliers

accuracy of these approaches and improve the documentation of global amphibian biodiversity, future studies should therefore consider combining integrative amphibian biodiversity scores with analyses of global sampling bias to determine which regions are likely to foster the highest diversity of undescribed and at-risk amphibian fauna, and should be targeted for biodiscovery. We also acknowledge that our integrative scoring approach assumes that patterns of de facto species threat levels are similar for Data Deficient and non-Data Deficient species, and we encourage future studies to test this assumption in order to further refine the approach.

While controversial, some have argued for shifting conservation efforts away from areas with functionally extinct species and redirecting them toward regions where amphibians have a more reasonable chance of long-term persistence (Gerber, 2016). As no amount of human-caused extinction is obviously desirable, however, we recommend that this "conservation triage" approach only be undertaken when all other viable options have been exhausted (Wiedenfeld et al., 2021). This "need" could quickly be rendered obsolete if social and economic barriers to the funding of amphibian conservation were removed. In other words, humanity unquestionably already possesses sufficient resources to pursue the protection all amphibian species, if desired. Thus, being forced to choose between which species to protect or let perish is undeniably an artificially created problem (Czech, 2000; Czech et al., 2000; Parr et al., 2009). To reduce the number of future amphibian extinctions, we therefore endorse the perspective that scientists should view conservation biology not merely as an applied academic discipline, but as a multifaceted task that will ultimately require dismantling social and economic barriers to environmental protection in general (Czech, 2000; Ford et al., 2020). For example, conservation scientists should take proactive steps toward establishing relationships with local wildlife managers, and should be institutionally supported in doing so. In addition, conservation scientists should ensure that researchers and personnel under their responsibility consistently foster inclusion and empower decision-making by applied conservationists—particularly members of marginalized groups (e.g., indigenous communities), who can offer novel perspectives toward conservation planning. However, for integrated conservation models to be implemented in conservation practices in a widespread and standardized manner, governmental branches in charge of conservation should maintain and deploy an updated conservation assessment and prioritization protocol. This type of consistent and regular updating of conservation techniques is currently missing from most governments, and an overarching regulation requiring the inclusion of these practices would greatly improve the effectiveness of future efforts to conserve imperiled species.

CONFLICT OF INTEREST

The authors declare no competing interests.

AUTHOR CONTRIBUTION

Both the authors were involved in developing the experimental design. Sky Button conducted all data analyses and wrote an initial draft of the paper. Amaël Borzée edited the manuscript drafts.

DATA AVAILABILITY STATEMENT

All data needed to evaluate the conclusions of this paper can either be downloaded here: Data File S1: https://data.mendeley.com/datasets/2d74krbdyt/1 (Mendeley Data, V1, https://doi.org/10.17632/2d74krbdyt.1), or be derived from the datasets on iucnredlist.org, edgeofexistence.org, worldwildlife.org, wordclim.org, and cds.climate.copernicus.eu using the methods described herein, or can be downloaded directly from these sources.

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REFERENCES

Allan, J. D., & Castillo, M. M. (2007). *Stream ecology: Structure and function of running waters*. Springer Science & Business Media.

Arlot, S., & Celisse, A. (2010). A survey of cross-validation procedures for model selection. *Statistics Surveys*, *4*, 40–79. https://doi.org/10.1214/09-SS054

Bishop, P., Angulo, A., Lewis, J., Moore, R., Rabb, G., & Moreno, J. G. (2012). The amphibian extinction crisis – What will it take to put the action into the Amphibian Conservation Action Plan? *SAPIENS*, *5*(2), 97–111.

Blaustein, A. R., Han, B. A., Relyea, R. A., Johnson, P. T., Buck, J. C., Gervasi, S. S., & Kats, L. B. (2011). The complexity of amphibian population declines: Understanding the role of cofactors in driving amphibian losses. *Annals of the New York Academy of Sciences*, *1223*(1), 108–119. https://doi.org/10.1111/j.1749-6632.2010.05909.x

Bolochio, B. E., Lescano, J. N., Cordier, J. M., Loyola, R., & Nori, J. (2020). A functional perspective for global amphibian conservation. *Bolochio*, *245*, 108572. https://doi.org/10.1016/j.biocon.2020.108572

Bradshaw, C. J., Sodhi, N. S., & Brook, B. W. (2009). Tropical turmoil: A biodiversity tragedy in progress. *Frontiers in Ecology and the Environment*, *7*(2), 79–87. https://doi.org/10.1890/070193

Brooks, T. M., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A. B., Rylands, A. B., Konstant, W. R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G., & Hilton-Taylor, C. (2002). Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology*, *16*(4), 909–923. https://doi.org/10.1046/j.1523-1739.2002.00530.x

Brooks, T. M., Pilgrim, J. D., Rodrigues, A. S., & da Fonseca, G. A. (2005). Conservation status and geographic distribution of avian evolutionary history. In *Phylogeny and Conservation*, 267–294. https://doi.org/10.1017/CBO9780511614927.012

Bruton, M. N. (1995). Have fishes had their chips? The dilemma of threatened fishes. *Environmental Biology of Fishes*, *43*(1), 1–27. https://doi.org/10.1007/BF00001812

Carmona, C. P., Tamme, R., Pärtel, M., de Bello, F., Brosse, S., Capdevila, P., Gonzalez-M, R., Gonzalez-Suarez, M., Salguero-Gomez, R., Vasquez-Valderrama, M., & Toussaint, A. (2020). Mapping extinction risk in the global functional spectra across the tree of life. *bioRxiv*. https://doi.org/10.1101/2020.06.29.179143

Ceballos, G., Ehrlich, P. R., & Raven, P. H. (2020). Vertebrates on the brink as indicators of biological annihilation and the sixth mass extinction. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(24), 13596–13602. https://doi.org/10.1073/pnas.1922686117

Collins, J. P., & Storfer, A. (2003). Global amphibian declines: Sorting the hypotheses. *Diversity and Distributions*, *9*(2), 89–98. https://doi.org/10.1046/j.1472-4642.2003.00012.x

Connor, E. F., & McCoy, E. D. (1979). The statistics and biology of the species-area relationship. *The American Naturalist*, *113*(6), 791–833. https://doi.org/10.1086/283438

Conroy, M. J., & Noon, B. R. (1996). Mapping of species richness for conservation of biological diversity: Conceptual and methodological issues. *Ecological Applications*, *6*(3), 763–773. https://doi.org/10.2307/2269481

Cushman, S. A. (2006). Effects of habitat loss and fragmentation on amphibians: A review and prospectus. *Biological Conservation*, *128*(2), 231–240. https://doi.org/10.1016/j.biocon.2005.09.031

Czech, B. (2000). Economic growth as the limiting factor for wildlife conservation. *Wildlife Science Bulletin*, *28*(1), 4–15.

Czech, B., Krausman, P. R., & Devers, P. K. (2000). Economic associations among causes of species endangerment in the United States: Associations among causes of species endangerment in the United States reflect the integration of economic sectors, supporting the theory and evidence that economic growth proceeds at the competitive exclusion of nonhuman species in the aggregate. *BioScience*, *50*(7), 593–601. https://doi.org/10.1641/0006-3568(2000)050[0593:EAACOS]2.0.CO;2

Duellman, W. E. (1999). *Patterns of distribution of amphibians: A global perspective*. JHU Press.

Elith, J., Leathwick, J. R., & Hastie, T. (2008). A working guide to boosted regression trees. *Journal of Animal Ecology*, *77*(4), 802–813. https://doi.org/10.1111/j.1365-2656.2008.01390.x

Ford, J., Hunt, D. A., Haines, G. E., Lewis, M., Lewis, Y., & Green, D. M. (2020). Adrift on a sea of troubles: Can amphibians survive in a human-dominated world? *Herpetologica*, *76*(2), 251–256. https://doi.org/10.1655/0018-0831-76.2.251

Frankham, R. (1995). Inbreeding and extinction: A threshold effect. *Conservation Biology*, *9*(4), 792–799. https://doi.org/10.1046/j.1523-1739.1995.09040792.x

Gardner, T. A., Barlow, J., Chazdon, R., Ewers, R. M., Harvey, C. A., Peres, C. A., & Sodhi, N. S. (2009). Prospects for tropical forest biodiversity in a human-modified world. *Ecology Letters*, *12*(6), 561–582. https://doi.org/10.1111/j.1461-0248.2009.01294.x

Gerber, L. R. (2016). Conservation triage or injurious neglect in endangered species recovery. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(13), 3563–3566. https://doi.org/10.1073/pnas.1525085113

Grant, E. H. C., Miller, D. A. W., Schmidt, B. R., Adams, M. J., Amburgey, S. M., Chambert, T., Cruickshank, S. S., Fisher, R. N., Green, D. M., Hossack, B. R., Johnson, P. T. J., Joseph, M. B., Rittenhouse, T. A. G., Ryan, M. E., Waddle, J. H., Walls, S. C., Bailey, L. L., Fellers, G. M., Gorman, T. A., … Muths, E. (2016). Quantitative evidence for the effects of multiple drivers on continental-scale amphibian declines. *Scientific Reports*, *6*, 25625. https://doi.org/10.1038/srep25625

Gross, J. (2008). Population decline in six species of anuran amphibians in Paramo Mucubaji, Merida State, Venezuela/Declive en poblaciones de seis especies de anfibios Anuros del Paramo de Mucubaji, Estado Merida, Venezuela. *Herpetotropicos: Tropical Amphibians and Reptiles*, *5*(1), 9–21.

Groves, C. (2003). *Drafting a conservation blueprint: A practitioner's guide to planning for biodiversity*. Island Press.

Hairston Jr., N. G., Ellner, S. P., Geber, M. A., Yoshida, T., & Fox, J. A. (2005). Rapid evolution and the convergence of ecological and evolutionary time. *Ecology Letters*, *8*(10), 1114–1127. https://doi.org/10.1111/j.1461-0248.2005.00812.x

Hanski, I., & Ovaskainen, O. (2002). Extinction debt at extinction threshold. *Conservation Biology*, *16*(3), 666–673. https://doi.org/10.1046/j.1523-1739.2002.00342.x

Isaac, N. J., Redding, D. W., Meredith, H. M., & Safi, K. (2012). Phylogenetically-informed priorities for amphibian conservation. *PLoS One*, *7*(8), e43912. https://doi.org/10.1371/journal.pone.0043912

IUCN. (2020). *The IUCN red list of threatened species*. International Union for Conservation of Nature.

Jenkins, C. N., Pimm, S. L., & Joppa, L. N. (2013). Global patterns of terrestrial vertebrate diversity and conservation. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(28), E2602–E2610. https://doi.org/10.1073/pnas.1302251110

Kruskal, J. B. (1964). Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika*, *29*(1), 1–27. https://doi.org/10.1007/BF02289565

Landis, M. J., & Schraiber, J. G. (2017). Pulsed evolution shaped modern vertebrate body sizes. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(50), 13224–13229. https://doi.org/10.1073/pnas.1710920114

Larsen, T. H., Brehm, G., Navarrete, H., Franco, P., Gomez, H., Mena, J. L., Morales, V., Argollo, J., Blacutt, L., & Canhos, V. (2011). *Range shifts and extinctions driven by climate change in the tropical Andes: Synthesis and directions*. Inter-American Institute for Global Change Research (IAI) and Scientific Committee on Problems of the Environment (SCOPE).

Laurance, W. F., Useche, D. C., Rendeiro, J., Kalka, M., Bradshaw, C. J., Sloan, S. P., Laurance, S. G., Campbell, M., Abernethy, K., Alvarez, P., & Arroyo-Rodriguez, V. (2012). Averting biodiversity collapse in tropical forest protected areas. *Nature*, *489*(7415), 290–294. https://doi.org/10.1038/nature11318

Lips, K. R. (2016). Overview of chytrid emergence and impacts on amphibians. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1709), 20150465. https://doi.org/10.1098/rstb.2015.0465

Loyola, R. D., Kubota, U., & Lewinsohn, T. M. (2007). Endemic vertebrates are the most effective surrogates for identifying conservation priorities among Brazilian ecoregions. *Diversity and Distributions*, *13*(4), 389–396. https://doi.org/10.1111/j.1472-4642.2007.00345.x

Nori, J., Lemes, P., Urbina-Cardona, N., Baldo, D., Lescano, J., & Loyola, R. (2015). Amphibian conservation, land-use changes and protected areas: A global overview. *Biological Conservation*, *191*, 367–374. https://doi.org/10.1016/j.biocon.2015.07.028

Nori, J., & Loyola, R. (2015). On the worrying fate of data deficient amphibians. *PLoS One*, *10*(5), e0125055. https://doi.org/10.1371/journal.pone.0125055

Nori, J., Torres, R., Lescano, J. N., Cordier, J. M., Periago, M. E., & Baldo, D. (2016). Protected areas and spatial conservation priorities for endemic vertebrates of the Gran Chaco, one of the most threatened ecoregions of the world. *Diversity and Distributions*, *22*(12), 1212–1219. https://doi.org/10.1111/ddi.12497

Noss, R. F., Platt, W. J., Sorrie, B. A., Weakley, A. S., Means, D. B., Costanza, J., & Peet, R. K. (2015). How global biodiversity hotspots may go unrecognized: Lessons from the North American Coastal Plain. *Diversity and Distributions*, *21*(2), 236–244. https://doi.org/10.1111/ddi.12278

Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., D'amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P., & Kassem, K. R. (2001). Terrestrial ecoregions of the world: A new map of life on Earth: A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *BioScience*, *51*(11), 933–938. https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

Parr, M. J., Bennun, L., Boucher, T., Brooks, T., Chutas, C. A., Dinerstein, E., Drummond, G. M., Eken, G., Fenwick, G., Foster, M., Martínez-Gómez, J. E., Mittermeier, R., & Molur, S. (2009). Why we should aim for zero extinction. *Trends in Ecology & Evolution*, *24*(4), 181. https://doi.org/10.1016/j.tree.2009.01.001

Pimm, S. L., Jenkins, C. N., Abell, R., Brooks, T. M., Gittleman, J. L., Joppa, L. N., Raven, P. H., Roberts, C. M., & Sexton, J. O. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, *344*(6187), 1246752. https://doi.org/10.1126/science.1246752

Potter, K. M. (2018). Do United States protected areas effectively conserve forest tree rarity and evolutionary distinctiveness? *Biological Conservation*, *224*, 34–46. https://doi.org/10.1016/j.biocon.2018.05.007

Rosenzweig, M. L. (1995). *Species diversity in space and time*. Cambridge University Press.

Scheele, B. C., Pasmans, F., Skerratt, L. F., Berger, L., Martel, A., Beukema, W., Acevedo, A. A., Burrowes, P. A., Carvalho, T., Catenazzi, A., & De la Riva, I. (2019). Amphibian fungal panzootic causes catastrophic and ongoing loss of biodiversity. *Scheele*, *363*(6434), 1459–1463. https://doi.org/10.1126/science.aav0379

Scott, J. M., Davis, F., Csuti, B., Noss, R., Butterfield, B., Groves, C., Anderson, H., Caicco, S., D'Erchia, F., Edwards Jr., T. C., & Ulliman, J. (1993). Gap analysis: A geographic approach to protection of biological diversity. *Wildlife Monographs*, *123*, 3–41.

Sloan, S., Jenkins, C. N., Joppa, L. N., Gaveau, D. L., & Laurance, W. F. (2014). Remaining natural vegetation in the global biodiversity hotspots. *Biological Conservation*, *177*, 12–24. https://doi.org/10.1016/j.biocon.2014.05.027

Stuart, S. N., Chanson, J. S., Cox, N. A., Young, B. E., Rodrigues, A. S., Fischman, D. L., & Waller, R. W. (2004). Status and trends of amphibian declines and extinctions worldwide. *Science*, *306*(5702), 1783–1786.

Thépaut, J.-N., Dee, D., Engelen, R., & Pinty, B. (2018). *The Copernicus Programme and its climate change service*. Paper presented at the IGARSS 2018–2018 IEEE International Geoscience and Remote Sensing Symposium.

Troia, M. J., & McManamay, R. A. (2016). Filling in the GAPS: Evaluating completeness and coverage of open-access biodiversity databases in the United States. *Ecology and Evolution*, *6*(14), 4654–4669. https://doi.org/10.1002/ece3.2225

United States Department of Agriculture. (2020). Natural Resources Conservation Service. https://www.nrcs.usda.gov/

Vale, C. G., Pimm, S. L., & Brito, J. C. (2015). Overlooked mountain rock pools in deserts are critical local hotspots of biodiversity. *PLoS One*, *10*(2), e0118367. https://doi.org/10.1371/journal.pone.0118367

Wake, D. B., & Vredenburg, V. T. (2008). Are we in the midst of the sixth mass extinction? A view from the world of amphibians. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(Supplement 1), 11466–11473. https://doi.org/10.1073/pnas.0801921105

Wiedenfeld, D. A., Alberts, A. C., Angulo, A., Bennett, E. L., Byers, O., Contreras-MacBeath, T., Drummond, G., da Fonseca, G. A. B., Gascon, C., Harrison, I., Heard, N., Hochkirch, A., Konstant, W., Langhammer, P. F., Langrand, O., Launay, F., Lebbin, D. J., Lieberman, S., Long, B., ... Zhang, L. I. (2021). Conservation resource allocation, small population resiliency, and the fallacy of conservation triage. *Conservation Biology*. https://doi.org/10.1111/cobi.13696

Wiens, J. J. (2016). Climate-related local extinctions are already widespread among plant and animal species. *PLoS Biology*, *14*(12), e2001104. https://doi.org/10.1371/journal.pbio.2001104

With, K. A., & King, A. W. (1999). Extinction thresholds for species in fractal landscapes. *Conservation Biology*, *13*(2), 314–326. https://doi.org/10.1046/j.1523-1739.1999.013002314.x

Woolson, R. (2007). Wilcoxon signed-rank test. In *Wiley encyclopedia of clinical trials* (pp. 4739–4740). Wiley encyclopedia of clinical trials.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Button, S., & Borzée, A. (2021). An integrative synthesis to global amphibian conservation priorities. *Global Change Biology*, 00, 1–14. https://doi.org/10.1111/gcb.15734