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RESEARCH ARTICLE

# Climate change threatens amphibians and species representation within protected areas in tropical wetlands

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## Abstract

1. Protected areas (PAs) are crucial for biodiversity conservation, yet climate change threatens their long-term effectiveness by displacing species distributions. Among the most climate-threatened organisms are the amphibians, highly dependent on water and wetlands.
2. The world's largest continuous tropical wetland, the Pantanal and surroundings, is situated in the Upper Paraguay River Basin (UPRB) in South America. Of the 74 amphibian species found there, 4% are threatened. Less than 5% of the basin is within PAs. Recurrent droughts and increasing human pressures further endanger the region's semiaquatic fauna if adequate protection measures are not implemented.
3. Using Ensemble of Small Models, we mapped habitat suitability of amphibian species and projected amphibian richness and composition across the UPRB. We applied null models to evaluate the representation of amphibian ranges within the current PA network under both current and future climate scenarios. To prioritize areas for PA network expansion under climate change scenarios, we used a systematic conservation planning algorithm.
4. By 2100, over 80% of amphibian species from the study area are projected to lose suitable habitat, with 99% of amphibian assemblages facing climate-driven species loss. Although the existing PA network had limited species representation, protecting on average less than 5% of amphibian ranges. However, 13.7% of PAs are expected to shelter more amphibian species than expected by chance under future climate conditions. Highlands, particularly in the northern and southeastern boundaries of the UPRB, are identified priority areas for PA network expansion due to their high projected changes in amphibian biodiversity.
5. *Synthesis and applications*. Our findings reveal the extensive impacts of climate change on a major semiaquatic group in the world's largest tropical wetland.

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Although the current PA network in the Pantanal and surroundings safeguards fewer amphibians than expected, its limited coverage provides opportunities for systematic, data-driven expansion to achieve the Post-2020 Global Biodiversity Framework's 30 by 30 target. Expanding PAs is urgent, but addressing drivers of environmental degradation, including unsustainable practices in agriculture and livestock farming, is equally critical for conserving this biodiverse ecosystem.

**KEYWORDS**
conservation biogeography, environmental change, Pantanal, species distribution, systematic conservation planning

## 1 | INTRODUCTION

The world is experiencing a biodiversity crisis with species going extinct at unprecedented rates, making it crucial to implement effective conservation strategies (Ladle & Whittaker, 2011; Pimm et al., 2014). One of the cornerstones of biodiversity conservation is the establishment of Protected Areas—PAs—that can provide safe habitats and help mitigate the impacts of anthropogenic activities (Gallardo et al., 2017; Margules & Pressey, 2000; Xin et al., 2023). However, many existing PAs were established without a sufficient understanding of local and regional biodiversity (Hannah et al., 2007). As a result, these areas, originally created as nature reserves and wildlife refuges, may not be optimal for protecting the overall biodiversity (Ladle & Whittaker, 2011). Since PAs are fixed geographic units, adapting them to new environmental conditions is challenging (Nori et al., 2015). Climate change, in particular, has shifted species distributions (Guisan et al., 2013) and altered species composition within biological assemblages (Ladle & Whittaker, 2011). Anticipating changes in species representation within PAs is important for the designing PAs that can effectively protect biodiversity in the long-term (Araújo et al., 2011).

Because climate change is impacting biodiversity, researchers need to understand how PAs can continue to support species as they potentially shift their ranges. This might involve expanding the PA network to mitigate climate change impacts (Nori et al., 2015; Oliveira, Soares-Filho, et al., 2017). Around 16% of the Earth's land surface is protected (UNEP-WCMC and IUCN, 2023), which is nearly half of the goal set by the Convention on Biological Diversity to achieve 30% coverage by 2030. To assess the effectiveness of these PAs and decide where to expand, it is crucial to use species distribution data at a spatial scale relevant to conservation planning. For instance, species occurrence data obtained at fine spatial resolution is useful to identify where different species live, but it often lacks coverage for rare species and can be biased by limited sampling (Meyer, 2016). To overcome such sparse spatial nature of occurrence data, it is common to use species distribution models to predict species distributions given their environmental preferences (Guisan et al., 2013). By reprojecting these fine-scale models to future climate scenarios, we can predict changes in species richness and assemblage composition (Moura, Nascimento, et al., 2023; Moura, Silva, et al., 2023). This information helps guide conservation planning and support decision makers in creating long-term strategies to safeguard biodiversity (Hannah et al., 2007; Zhang et al., 2017).

Among the animal groups most threatened by climate change stand out the amphibians, which are also impacted by habitat change, invasive species, and diseases (Luedtke et al., 2023). Over 41% of amphibian species are at risk, with many of them poorly represented or completely missing from the global network of PAs (Nori et al., 2015; Pimm et al., 2014). Since most amphibians depend on aquatic environments (Oliveira, São-Pedro, et al., 2017), protecting wetlands and other freshwater habitats is crucial for their survival. One of the largest wetland regions of the world is found in central South America, the Upper Paraguay River Basin (UPRB), which includes the Pantanal floodplain and portions of neighbouring ecoregions like the Cerrado, Humid and Dry Chaco, and Chiquitano Dry Forest (Dinerstein et al., 2017; Junk & Wantzen, 2004). However, the UPRB is increasingly under threat due to soybean plantation expansion, deforestation in river headwaters and severe forest fires, such as the 2020 Pantanal wildfire that burned 3.8 million hectares and killed over 17 million vertebrate animals, including many poorly studied species (Berlinck et al., 2022; Tomas et al., 2021). Despite the confluence of multiple species lineages within the UPRB, less than 4% of this region is protected, leaving many unique species and lineages vulnerable and underrepresented in the existing PA network (Oliveira, Soares-Filho, et al., 2017).

This study aims to evaluate amphibian richness and composition in the UPRB and assess how well the current PA network safeguards these species under current and future climate conditions. We employ different methods to analyse the projected impacts of climate change at a fine spatial scale, focusing on responses at the level of both species- and assemblages. Our study is built around three main aspects: (1) High vulnerability of endemic species: due to the narrower physiological tolerance of microendemic amphibians (Li et al., 2013), we anticipate a relatively greater loss of suitable habitats for these narrow-ranging species under future climate conditions. (2) Limited representation of amphibian ranges within existing PAs: because most PAs were established without prior research on local biodiversity, we expect a low intersection with geographic range of amphibian species. (3) Focus on highlands for future protection: mountainous regions are often identified as climate refuges for biodiversity (Araújo et al., 2011; Lemes et al., 2014). We anticipate that highlands will emerge as priority areas for the expansion of the existing protected area network. By addressing these hypotheses, we aim to identify priority areas that are crucial for long-term amphibian conservation.

## 2 | MATERIALS AND METHODS

### 2.1 | Species data

We compiled occurrence records for the amphibian species that occur in the Upper Paraguay River Basin (UPRB) from two sources: (i) a data paper (Neves et al., 2020) containing curated records for 77 species, totalling 1536 accurate or nearby records in the UPRB; and (ii) the GBIF platform (GBIF.org, 2019) for records covering the entire distribution in South America of the 74 species from the first source, yielding 2688 records. The data paper used here represents an extensive work of occurrence records based on verified preserved specimens deposited in collections from Brazil, Bolivia and Paraguay, alongside fieldwork records derived from ongoing research developed by some of us. GBIF records underwent manual review to retain only points with a spatial precision of at least 5 km. We excluded GBIF records outside the known distribution of the species and located over water (Graham et al., 2008). To reduce the potential effect of sampling bias and spatial autocorrelation in the occurrence dataset, we applied a spatial thinning procedure to remove duplicate records and those located within 5 km of each other, resulting in 4224 occurrence records. Computations were performed in R 4.2.1 (R Core Team, 2022) using the packages *rgbif* (Chamberlain et al., 2018) and *ecospat* (Broennimann et al., 2024).

### 2.2 | Environmental data

Dispersal ability influences an organism's ability to move and explore new environments, while topographic factors can act as barriers to species movement, particularly when combined with climatic gradients (Janzen, 1967). Because amphibians are ectotherms with limited dispersal ability (Weil et al., 2023), they are highly sensitive to these factors. Thus, we modelled species habitat suitability using climatic and topographic-related variables. We included three topographic variables downloaded at 30 arc-sec of spatial resolution, namely: profile curvature, topographic position index and slope (Amatulli et al., 2018). Climatic data were sourced from the WorldClim v2.1 dataset at 30 arc-sec of spatial resolution (Fick & Hijmans, 2017), and included 19 bioclimatic variables based on monthly precipitation and temperature averages from 1970 to 2000 (current time) and projections for 2081 to 2100 (future time). We used a UPGMA clustering analysis on bioclimatic layers to identify clusters with at least 75% similarity (Dormann et al., 2013), retaining one predictor from each cluster based on biological relevance: Annual Mean Temperature, Isothermality, Temperature Seasonality, Annual Precipitation and Precipitation Seasonality.

Future climate projections vary according to different Shared Socioeconomic Pathways (SSPs), which outline scenarios for greenhouse gas emissions and human development. In line with the 6th Assessment Report of the Intergovernmental Panel on Climate Change (IPCC, 2022), we selected two SSPs: the SSP245, reflecting a medium challenges, business-as-usual scenario; and the SSP585, a high-emission scenario representing severe challenges to mitigation and adaptation. For both pathways, we considered future projections for 2081–2100 (hereafter referred to as 2100). Given the uncertainty inherent in selecting general circulation models (GCM), we used three GCMs to capture variability in simulated temperature and precipitation conditions (Firpo et al., 2022), namely: CMCC-ESM2, IPSL-CM6A-LR and MRI-ESM2. We assumed minimal changes between current and future topography conditions and thus used the same topographic data for both.

### 2.3 | Species distribution models

To represent species absences in South America (our background area), we randomly generated pseudo-absences while maintaining a 1:1 ratio of presences to absences (Barbet-Massin et al., 2012). Given the rarity and narrow geographic range of most amphibian species in the UPRB, we applied the Ensemble of Small Models approach (ESM; Breiner et al., 2015). ESM involves constructing numerous sub-models with a limited number of predictors, often using all pairwise combinations of available predictors (Breiner et al., 2015, 2018). We computed sub-models using three algorithms: Artificial Neural Network (ANN; Manel et al., 1999), Generalized Linear Models (GLM; McCullagh & Nelder, 1989), and Classification and Regression Tree (CTA; Breiman et al., 1984). For each species, algorithm, and for the ensemble across algorithms, we obtained the ESM by computing the weighted average of habitat suitability of sub-models using their respective Somers' $D$ [$D = 2 \times (\text{AUC} - 0.5)$] as weights (Breiner et al., 2018).

Models were calibrated using a bootstrapping validation approach, with 75% of randomly selected samples for training and 25% for testing (Araújo et al., 2005). To assess model performance, we compared the similarity between observed and predicted presences using the Sørensen similarity index (Sørensen, 1948), which does not depend on species prevalence (Leroy et al., 2018). To calculate the Sørensen index, it is essential to convert the species habitat suitability into a binary format based on a threshold value. For each algorithm during the baseline period, we selected the species habitat suitability value that maximized the Sørensen index. We also calculated complementary metrics of model performance, including the Boyce index (Boyce, ranging from −1 to 1; Boyce et al., 2002) and the area under the curve (AUC, ranging from 0 to 1; Fielding & Bell, 1997), to facilitate comparisons across literature. The bootstrapping validation procedure was repeated 100 times for each species and algorithm, with the average habitat suitability and the model performance metrics extracted across these iterations. We obtained an ensemble of future projections for each species by averaging outputs across GCMs. To derive an aggregated metric of model uncertainty, we averaged the variance of habitat suitability (squared standard deviations; SD) for species in each cell and then computed the square root to obtain the average SD of habitat suitability across all species (Moura, Silva, et al., 2023). Computations were performed in R 4.2.1 using the *ecospat* (Broennimann et al., 2024), *terra* (Hijmans, 2024), *ncdf4* (Pierce, 2023) and *biomod2* (Thuiller et al., 2023) packages.

## 2.4 | Species turnover under climate change

To measure species gain, loss and turnover across our study area, we first needed to convert the ensemble projections of species habitat suitability into binary maps. We determined the optimal binarization threshold for each species using the minimal predicted area method (MPA; Engler et al., 2004). This method identifies a compact area that includes a specified percentage of known species occurrences. We set the threshold to capture 90% of all observed species presences. To minimize issues with unlimited dispersal within the time frame of projected climate change, we used the presence records of each species to create a 500km buffer, defining species-specific accessible areas. Each species' binary map was then restricted to its respective accessible area. Since we are interested in the UPRB, we masked the binary maps using the UPRB boundary and overlaid them onto a 5×5km grid system to create a presence-absence matrix for the current time and each future SSP scenario. We calculated species richness in each grid cell by summing the present species. Species turnover per cell between current and future periods was quantified using the Jaccard dissimilarity index (hereafter, turnover): (G+L)/(L+S+G), where 'G' is species projected for the future only (species gain), 'L' is species occurring only in the current time (species loss), and 'S' is species shared between current and future times (Ferro et al., 2014). The components 'G' and 'L' were mapped to illustrate projected species gain and loss for each future SSP scenario. We use QGis software (QGIS Development Team, 2024) to map the results.

## 2.5 | Species representation within protected areas

We gathered data on 73 Protected Areas (PAs) in the UPRB, categorized as I–IV by the International Union for Conservation of Nature (IUCN) or registered as Indigenous Land, highlighting their importance for biodiversity conservation. The dataset on PAs was downloaded from the World Database on Protected Areas (WDPA; UNEP-WCMC and IUCN, 2023). In our study area, grid cells were marked as 'protected' if they overlapped, even partially, with a PA. To evaluate if species richness in existing PAs differed from random chance, we used a null model to randomize the locations of PAs within the UPRB while preserving their size, shape and orientation. This procedure was repeated 1000 times for each PA to generate a null expectation of species richness values (Lemes et al., 2014). We compared observed species richness in PAs to the 95% inner values of the corresponding null distribution to identify areas where protection efficiency was higher (observed richness >=97.5% quantile) or lower (observed richness <=2.5% quantile) than expected. Applying the same null model approach to projected colonization ('G') and extinction ('L') surfaces, we identified PAs where species gain and loss differed from expectations. The null model analyses were conducted in R using the shift function in the *terra* package (Hijmans, 2024).

## 2.6 | Spatial prioritization of the Upper Paraguay River Basin

To determine the percentage of amphibian species covered by existing PAs and identify complementary conservation areas in the UPRB, we applied a hierarchical priority ranking analysis in Zonation version 5.2.1 (Moilanen et al., 2014). Zonation creates a priority ranking by progressively removing grid cells that contribute the least to the overall conservation value, while accounting for total and remaining distribution of spatial features (herein the raster files representing the species binary maps). Since our goal was to identify priority areas for expanding the PA network, we used the cells covered by the existing 73 PAs as the starting point (i.e. as a hierarchic mask layer) of our prioritization exercise. Priority ranks for each spatial unit (cell) were calculated using the additive benefit function (ABF), which tracks the performance of spatial features along individual species-area curves while reducing the aggregated extinction risk (Moilanen et al., 2014). To optimize the representation of threatened species within the high priority cells, we used IUCN threat statuses as species weights (LC=1, NT=2, VU=3, EN=4, CR=5). Other Zonation parameters were kept as default (Moilanen et al., 2014).

## 3 | RESULTS

Species distribution models (SDM) for the 77 amphibian species in the Upper Paraguay River Basin (UPRB) showed good predictive performance (average Sørensen = 0.6955 ± 0.145; AUC = 0.9695 ± 0.027; Boyce = 0.9917 ± 0.01; Table S1). Three species peripherally distributed in the UPRB region (*Boana boans*, *Lithodytes lineatus* and *Leptodactylus latinasus*) had no suitable areas projected in the UPRB and were excluded from further analyses. Among the remaining 74 species, 62 species (83.78%) and 65 (87.84%) are projected to lose suitable areas under the SSP245 and SSP585 futures scenarios, respectively (Figure 1, Table S2). Notably, 13 (16.22%) and 20 (27.03%) species are projected to lose all suitable areas. All amphibian species showed less than one-fifth of their current projected distribution within Protected Areas (PAs), with *Ameerega* sp., *Boana fasciata*, *Melanophryniscus klappenbachi* and *Rhaebo guttatus* entirely absent from PAs (Figure 1, Table S2). Projections for 2100 showed

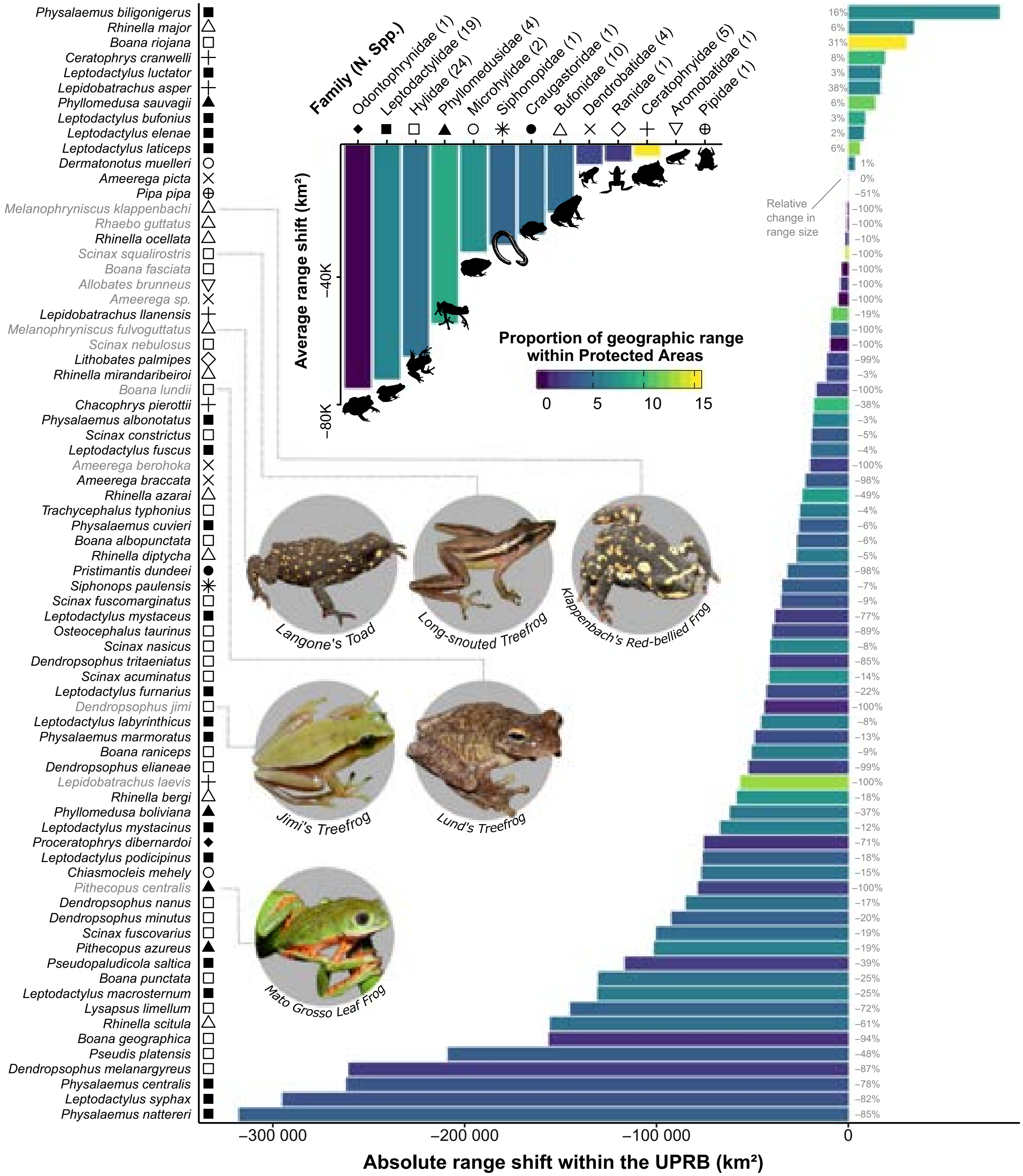

FIGURE 1 Projected range shifts and representation in Protected Areas (PAs) for amphibians in the Upper Paraguay River Basin (UPRB). Bar size denotes the absolute range shift in km$^2$, and bar colour indicates the proportion of each species' geographic range within PAs (considering only the range intersecting with the UPRB). The percentage values on the right side of each bar represent the proportional range shift. Grey labels indicate taxa without projected suitable habitats for 2100 under the SSP245 scenario. Symbols on the left panel correspond to taxonomic families, as shown in the top-left inset plot.

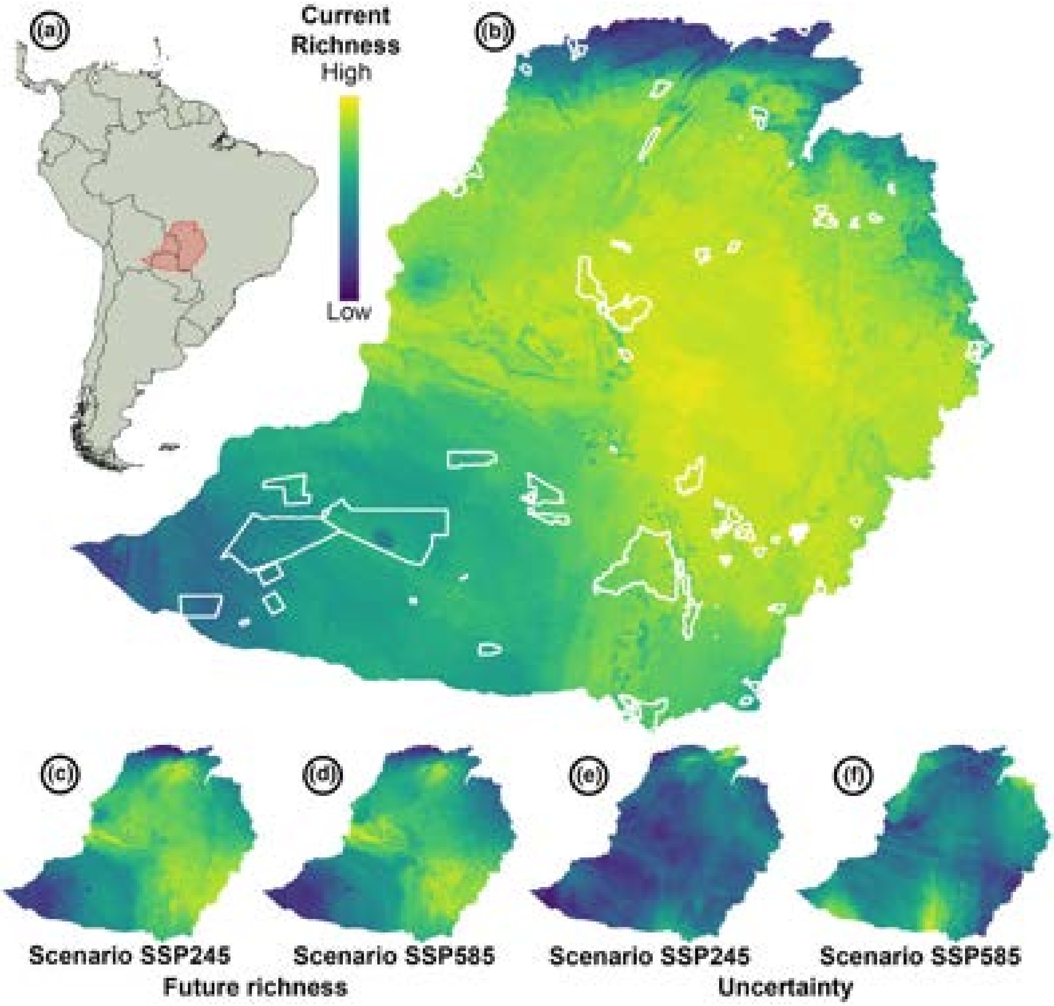

FIGURE 2 Projected patterns of amphibian richness for the Upper Paraguay River Basin (UPRB). (a) Position of the UPRB in South America. (b) Current species richness, with the Protected Areas (PAs) overlaid in white lines (range = 2–44). Future species richness in the (c) SSP245 (range = 3–41) and (d) SSP585 (range = 3–37) scenarios. Aggregated model uncertainty across generalized circulation models for the (e) SSP245 and (f) SSP585 scenarios.

that *Boana riojana* will have the highest percentage of the protected range, with 13.42% and 12.88% of its distribution within PAs for SSP245 and SSP585, respectively (Figure 1, Table S2).

Current projections show that species richness per cell in the UPRB ranged from 2 to 44 species (Figure 2b). High species richness was evident in the Pantanal floodplain in the center, the Chiquitano Dry Forest in the west and the plateaus of the Cerrado in the southeast. In contrast, the far northern and western regions of the UPRB exhibited lower richness. Future projections in both scenarios indicate increased amphibian richness mainly in the lowlands of Bolivia, the Chapada dos Guimarães region in the north, and the southeast of the UPRB, while lower richness is expected in the extreme north and west (Figure 2b,c). Regions with high species richness showed lower uncertainty (variability in projections) across GCMs in both SSPs scenarios. Although the northern region exhibited low richness, it also showed moderate to high values, especially under the SSP585 scenario (Figure 2d,e).

By 2100, species composition is expected to change by an average of 24.6% per cell in the SSP245 scenario and 37.0% per cell in the SSP585 scenario, with higher turnover rates anticipated in northern regions (Figure 3a,d). Projected local extinctions are expected to affect 99.87% of UPRB area under the SSP245 scenario (Figure 3b) and 99.99% under the SSP585 scenario (Figure 3e), with the most pronounced species loss located in the northeast and northwest of the UPRB. Additionally, 85.64% of cells are expected to gain species in the SSP245 scenario (Figure 3c), and 85.49% are expected to do so in the SSP585 scenario (Figure 3f). Overall, future projections point to an average loss of 7.12 species per cell under the SSP245 (range = 0–20) and 11.39 under the SSP585 (range = 0–25). Projected species colonization averaged 0.90 species per cell in SSP245 (range = 0–13) and 0.87 in SSP585 (range = 0–12) scenario.

## 3.1 | Species richness representation within protected areas

Most Protected Areas (PAs) in the UPRB currently show amphibian richness consistent with what would be expected by chance, based

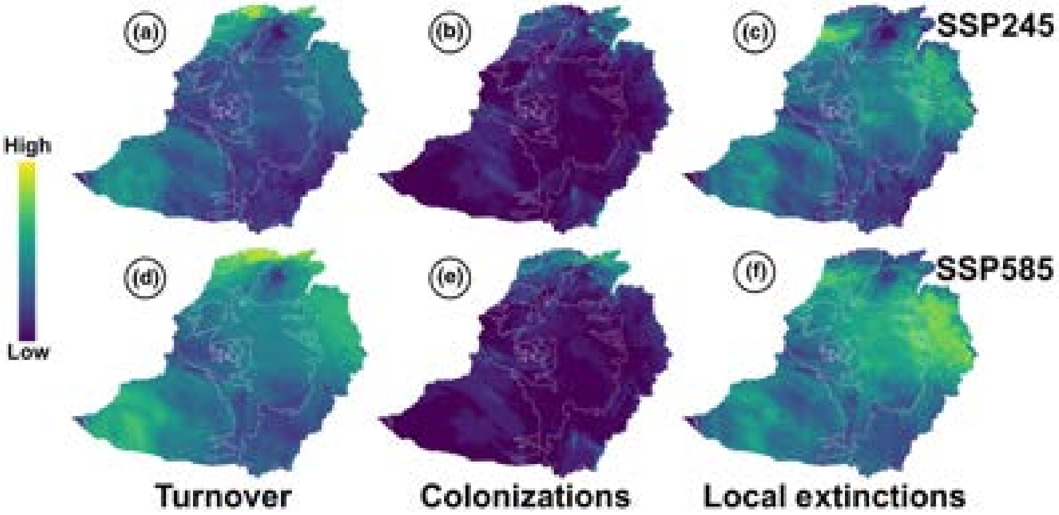

FIGURE 3 Projected changes in amphibian species composition for the Upper Paraguay River Basin by the year 2100. White lines are ecoregions by Dinerstein et al. (2017). Maps are show for both SSPs scenarios, SSP245 (top panels): (a) species turnover (range = 0–84.2), (b) species colonization (0–13), (c) local extinctions (0–20); and SSP585 (bottom panels): (d) Species turnover (0–85.7), (e) Species colonization (0–12), (f) Local extinctions (0–25).

on their size, location, and orientation (Figure 4). Based on SDM outputs for the current period, no PAs exhibited higher than expected amphibian richness, although 8.2% (*n* = 6) showed significantly lower species richness. Future projections indicate a higher-than-expected species gain in 6.8% (*n* = 5) of the PAs under the SSP245 and 4.1% (*n* = 3) under the SSP585, with no PA facing lower-than-expected species gain. Similar numbers were found with respect to future species loss, with most PAs exhibiting values within those expected by chance. However, 2.7% (*n* = 2, under SSP245) and 4.1% (*n* = 3, under SSP585) of PAs were projected to lose more species than expected. In summary, 13.7% of PAs in the UPRB exhibit the potential to harbour more species or, conversely, to lose fewer species than expected by chance in at least one future scenario.

### 3.2 | Spatial prioritization of the Upper Paraguay River Basin

Only 5.85% of the UPRB is covered by protected areas (PAs). These PAs harbour on average 4.88% of current amphibian ranges (range = 0%–15.1%). By 2100, these PAs are projected to safeguard 4.75% of amphibian ranges (range = 0%–13.4%) under the SSP245 scenario and 4.67% (range = 0%–12.8%) under the SSP585 scenario. Following the prioritization rank for expanding the PA network could protected, on average, 28.7% of amphibian ranges (range = 5.3%–30.7%) with 15% of UPRB under protection. If PA coverage reaches the 30% target set by the Convention on Biological Diversity, 47.2% of current amphibian ranges (range = 10.3%–50.4%) would be protected. By 2100, 30% PA coverage could safeguard 51.8% of amphibian ranges (range = 25.9%–55.7%) under SSP245, and 53.4% (range = 26.6%–56.7%) under SSP585. The apparent increase in the percentage of amphibian ranges protected is attributed to the loss of narrow-range species, which currently occur predominantly outside PAs. Moreover, among the top-30% priority cells selected based on current amphibian ranges, only 59.4% overlap with the top-30% cells under SSP245, and 54.9% overlap under SSP585, indicating a spatial mismatch between current and future prioritizations (Figure S1).

The current spatial prioritization procedure identified cells with high conservation values in the Pantanal plateaus (>500 m elevation), including regions in the Cerrado, Dry Chaco and northern Chiquitano Dry Forest. The key areas highlighted include regions in the northern UPRB locally known as Chapada dos Guimarães, Serra das Araras, and the Parecis plateaus, as well as Serra da Bodoquena in the center-south of the UPRB. These regions showed high conservation priority in the current time and are expected to remain important in both future scenarios. The regions of Dry Chaco in the south of the UPRB and Cerrado in the northwest and northeast increase their importance for conservation in the future in the SSP245 and SSP585 scenarios (Figure 5).

## 4 | DISCUSSION

Anticipated climate changes are projected to significantly impact the Upper Paraguay River Basin (UPRB), leading to shifts in species distribution. Our study reveals that reduction in the geographic ranges of amphibian species in the UPRB will outpace any expansions. Notably, there is high species turnover across the UPRB in all future scenarios, both within and outside existing Protected Areas (PAs). Some regions may experience complete shifts in species composition. This turnover contributes to the current low effectiveness of PAs in safeguarding amphibian species, reflecting the broader issue of PA efficiency (Lemes et al., 2014; Oliveira, Soares-Filho, et al., 2017). Despite the low coverage of Pas—currently covering only 5.85% of the UPRB area, well below the 30% target set by the Convention on Biological Diversity for 2030—there is optimism for

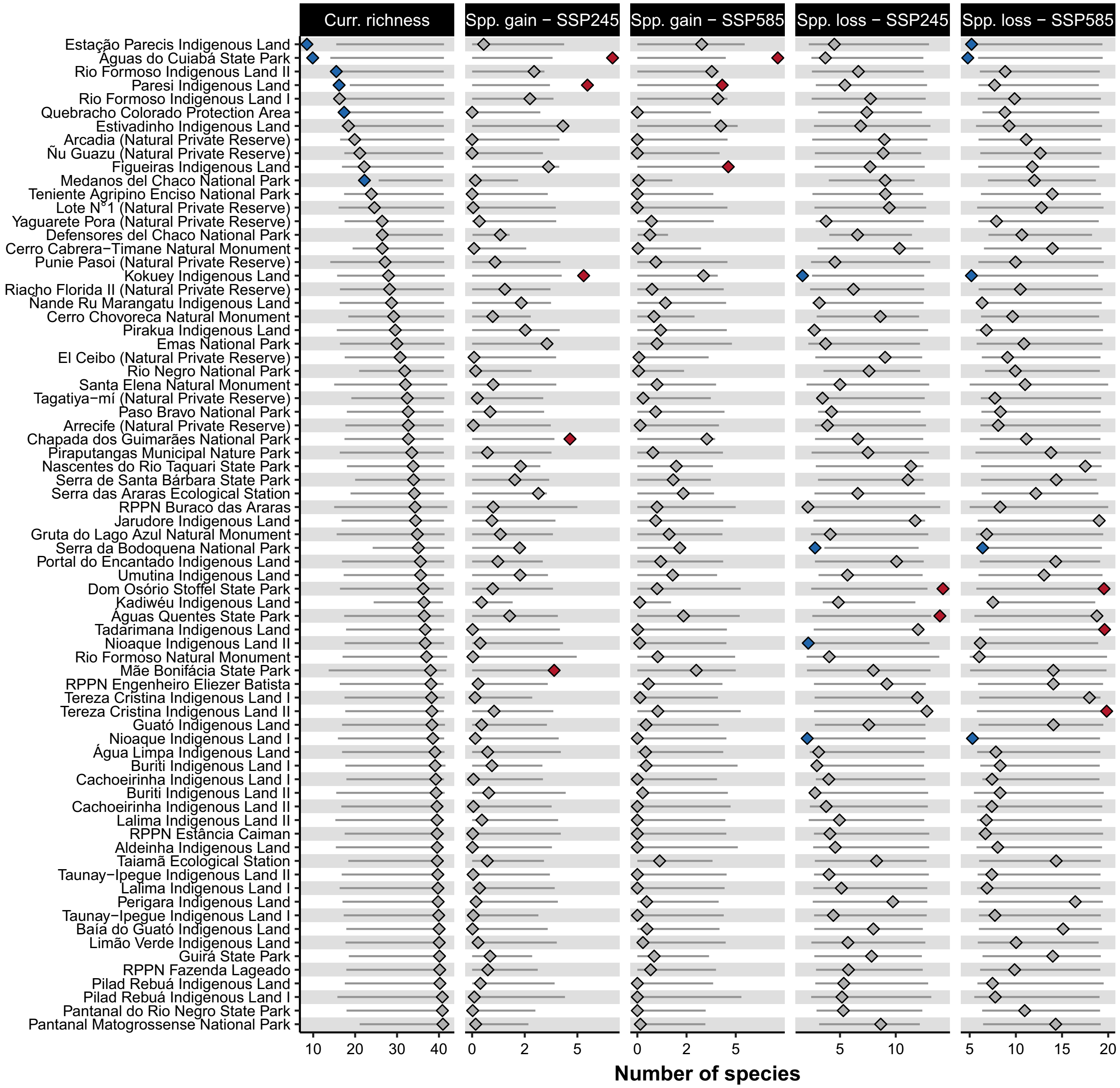

**FIGURE 4** Amphibian richness species representation within Protected Areas in the Upper Paraguay River Basin. Symbols show the observed value of current species richness, future gain or loss of species within each Protected Area (PA) under the SSP245 and SSP585 scenarios. Grey horizontal lines denote the 95% inner values of the null distribution computed for each metric and PA. Values lower or higher than expected by chance are highlighted in blue or red symbols, respectively.

better protection against future climate change. Presently, less than 5% of amphibian geographic ranges are protected within these PAs.

Many amphibian species in the UPRB are expected to lose suitable habitats, especially those whose geographic range reaches transitional zones between ecoregions in the periphery of UPRB. Examples include Amazon-associated species in the northwest UPRB (e.g. *Boana fasciata*, *Rhaebo guttatus* and *Scinax nebulosus*), Cerrado-associated species in the north and east (e.g. *Allobates brunneus*, *Ameerega berohoka*, *A. braccata*, *Boana lundii*, *Dendropsophus jimi*, and *Pithecopus centralis*) and Chaco-associated species in the south/southwest UPRB (e.g. *Lepidobatrachus laevis*, *Melanophryniscus fulvoguttatus* and *M. klappenbachi*). Nearly one-fifth of UPRB species have less than 1% of their geographic range within PAs, rendering them virtually unprotected. Indeed, the vulnerability of amphibians to climate change increases the risk of extinction (Luedtke et al., 2023), with projected local extinctions extirpating from 17% to 27% of species under the moderate (SSP245) and pessimistic climate scenarios (SSP585).

High amphibian species turnover is evident across the UPRB in all models and scenarios, likely due to the convergence of multiple

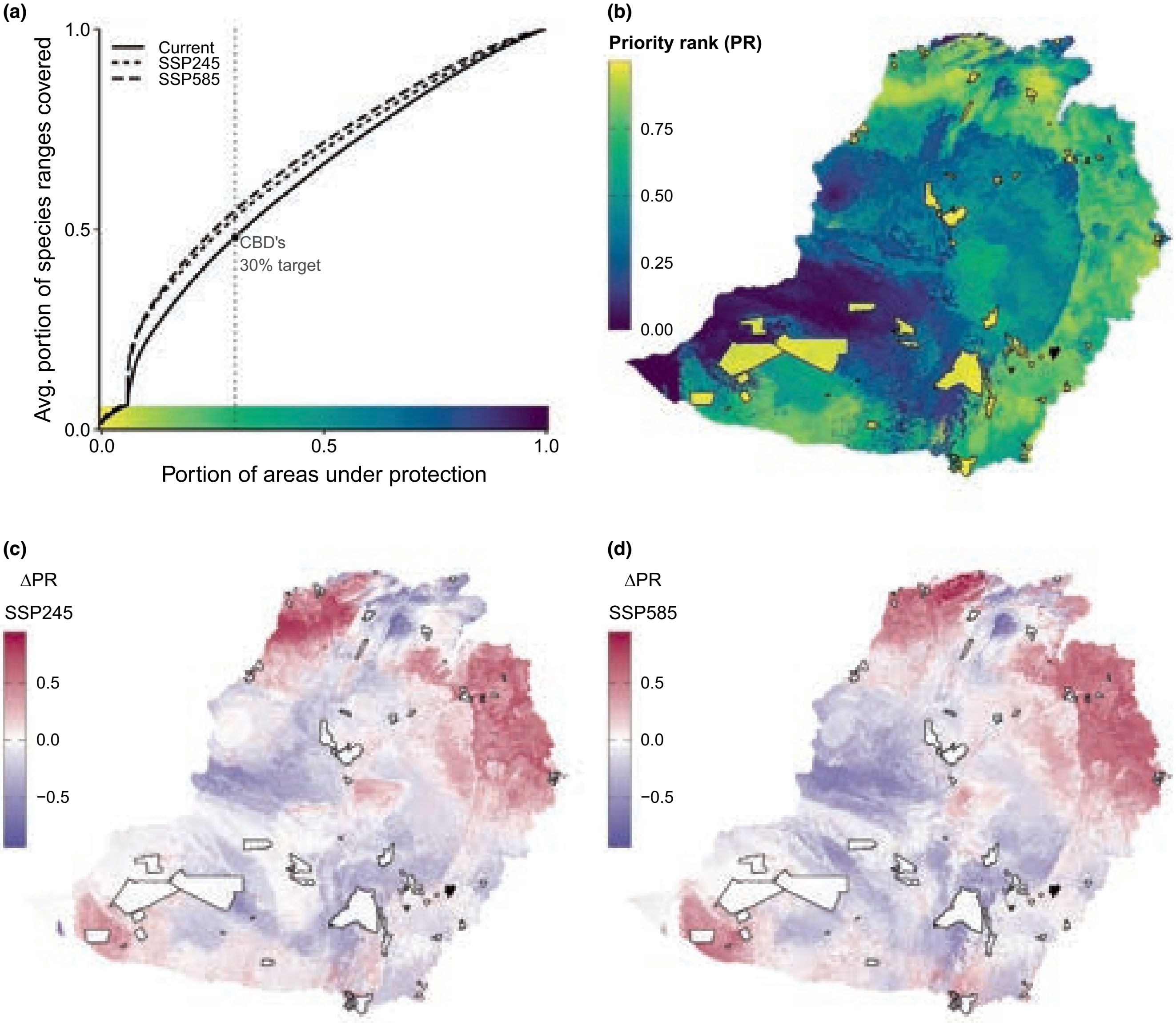

FIGURE 5 Prioritization rank analysis for amphibian conservation in the Upper Paraguay River Basin. (a) Average performance curves for amphibian species under current and two future climate scenarios (SSP245 and SSP585). (b) Priority rank (PR) areas for expanding the Protected Area (PA) network based on current amphibian species ranges. Note that the prioritization algorithm first considered cells within the existing PAs, then expanded the rank to include other regions within the UPRB. (c and d) Change in priority rank between current and future projections ($\Delta PR = PR_{current} - PR_{future}$), with reddish areas showing higher PR values in the future and bluish areas indicating the opposite.

transition zones that host many peripheral species, making them susceptible to fluctuations in their distribution (Lemes et al., 2014). These transition zones may experience changes in species richness, as environmental barriers near ecoregional borders can hinder species migration (Chevalier et al., 2021; Scherrer et al., 2021). In contrast, amphibian assemblages in the highlands of the UPRB are expected to show low species turnover between current and future periods. These mountainous regions, often seen as climatic refuges, have a history of increased colonization events (Klorvuttimontara et al., 2011; Lemes et al., 2014), which aligns with the limited compositional change expected there.

Despite many highlands remaining unprotected (e.g. Serranía de Santiago in Bolivia, portions of Serra de Maracaju, Itiquira plateau), our findings consistently identify them as high conservation priorities (Figure 5). For instance, the northern UPRB includes important highlands such as the São Vicente mountain range, Chapada dos Guimarães, Serra das Araras, and the Parecis plateaus, which harbour species closely tied to the UPRB, like *Pristimantis dundeei*, *Ameerega braccata* and *Pithecopus centralis* (Giaretta et al., 2018; Magalhães et al., 2018). These species could face severe threats by 2100 due to the loss of suitable areas under the SSP585 scenario. High conservation priority is also found among southern highlands, such as the Serra da Bodoquena plateau and transitional regions along the Pantanal, Cerrado, and Humid Chaco. Although some PAs exist in these areas (e.g. Chapada dos Guimarães National Park, Serra da Bodoquena National Park, Serra das Araras Ecological Station), expanding the PA network to increase connectivity is highly recommended to improve conservation effictiveness in line with the CBD's targets. Additionally, a small portion of the Humid Chaco in Brazil is recognized for high conservation priority, hosting exclusive species like *Odontophrynus lavillai* and *Lepidobatrachus asper* in Porto Murtinho municipality, Mato Grosso do Sul state (Rosset et al., 2009; Sugai et al., 2013). This region lacks PAs and faces potential biodiversity loss due to activities like cattle ranching. While our insights can inform environmental protection policies in the UPRB, effective conservation strategies require collaboration among scientists, policymakers and local communities (Guisan et al., 2013).

Concerns about Species Distribution Models (SDMs) for climate-induced biodiversity forecasts have been extensively discussed (Guisan et al., 2013), and some uncertainties are quantifiable (Barry & Elith, 2006). We integrated multiple algorithms and generalized circulation models (Diniz-Filho et al., 2009) to assess uncertainty in projected amphibian responses to climate change. Given that limited sampling data can decrease model performance and increase uncertainty (Stockwell & Peterson, 2002), we improved the reliability of our projections using a modelling approach designed for rare species (Breiner et al., 2015, 2018) and fine-scale occurrence data for the UPRB (Neves et al., 2020). Our results show relevant uncertainties mainly in the Dry Chaco and in north-eastern plateaus of UPRB (Figure 2e,f). These highlands exhibited low to moderate richness in our models despite their substantial sampling effort (Neves et al., 2020), which suggests that uncertainties are linked to species underrepresentation rather than to data limitations.

It is not prudent to assume that species distribution will remain unchanged (Klorvuttimontara et al., 2011). We demonstrated the importance of focusing on individual species and specific areas rather than broad patterns for effective conservation planning. This closer examination helped identify the species most affected by future climate change, those at risk due to inadequate protection, and the areas that may serve as future refuges in the UPRB. Despite the importance of PA networks for biodiversity conservation (Ferro et al., 2014; Margules & Pressey, 2000), only 16.05% of the Earth's terrestrial surface is protected (UNEP-WCMC and IUCN, 2023), with substantial gaps in regions like Latin America (Nori et al., 2015), including here the UPRB. Moreover, many PAs in the UPRB were established before comprehensive ecological knowledge were available, resulting in limited coverage of amphibian species ranges. This situation underscores the need for strategic expansion of the PA network, including the assessment of species' responses to climate change to enhance long-term conservation outcomes (Hannah et al., 2007; Nori et al., 2015). While informed-conservation strategies are essential, it is equally important to advocate for measures that mitigate the impacts of agriculture on landscape connectivity and promote educational programs to reconcile societal perception of environmental priorities (Hannah et al., 2007).

## AUTHOR CONTRIBUTIONS

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## CONFLICT OF INTEREST STATEMENT

The authors confirm that they have no conflict of interest to disclose.

## DATA AVAILABILITY STATEMENT

The R-script and raw dataset supporting the results of this work are available at Zenodo Digital Repository https://doi.org/10.5281/zenodo.14247800 (Neves et al., 2024).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Figure S1.** Congruence among the top 30% priority areas for amphibian range conservation under current and future climate conditions. Existing Protected Areas cover 5.85% of the Upper Paraguay River Basin and were included within the top 30% priority areas for both the current climate and future scenarios (SSP245 and SSP585).

**Table S1.** Sørensen's similarity index (Sørensen), area under the curve (AUC), and Boyce index (Boyce) averages for each species and ecological niche modelling method (ANN, artificial neural network; CTA, classification and regression tree; GLM, generalized linear models; and ENS, ensemble model across algorithms).

**Table S2.** Total area in square kilometre and percentage coverage of the potential distribution of 74 species within the 73 Protection Areas analysed in current and in future time under two different shared socioeconomic pathways (SSP)scenarios: the SSP245 representing the business-as-usual scenario, and the SSP585, indicating a non-mitigation scenario. Orange background: 0% coverage.

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