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ARTICLE
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Potential effects of climate change on the threatened Malagasy poison frogs: A multispecies approach

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Abstract

Climate change is exposing ecosystems to novel conditions, and understanding its potential effects on species distributions is crucial. Those effects can significantly affect species with narrow environmental requirements inhabiting closed systems where dispersal is limited. Madagascar is a highly biodiverse island, boasting high levels of amphibian species richness and endemism. The impacts of climate change on Malagasy amphibians are scarcely addressed, with studies focusing on single species or localities. We assessed the potential impacts of climate change on the distributions of the endemic Malagasy poison frogs of the genus *Mantella*, one of the most threatened and best-studied frog genera in Madagascar, which contains species of global interest for the pet trade. We quantified each species' marginality, specialization, and tolerance and modeled their realized niches using the Maximum Entropy algorithm. We projected the models into current and future climates, using five Global Circulation Models, three socioeconomic scenarios, three future periods, and three dispersal scenarios. Our results suggest that 30% of *Mantella* species may gain habitat suitability extent, while 60% are predicted to lose it, with two threatened species forecasted to lose all suitable habitats island wide by 2100. Furthermore, 80% of species are forecasted to lose habitat suitability in currently occupied pixels, with losses exceeding 90%. Range shifts tracking their optimal niche conditions are expected for nearly all species, but the receptor areas are not always suitable. The current distribution extent is a good predictor of both tolerance and marginality, and tolerance can predict the conservation status in the genus *Mantella*. We found a linear relationship with higher marginality and tolerance linked to greater potential losses. We discuss the reliability and severity of the forecasts, the caveats of niche projections, and challenges in planning conservation based on them.

KEYWORDS
amphibians, climate change responses, distributions, Madagascar, *Mantella*, species distribution models, threatened species

INTRODUCTION

Human-induced climate change is exposing ecosystems worldwide to unprecedented climatic conditions over millennia, surpassing the adaptive capacities of many species (IPCC, 2022; Williams et al., 2007). In addition, future projections predict that climate change will become a significant driver of biodiversity loss, with generalized biotic declines and losses in the forthcoming decades (Bellard et al., 2012; Costello et al., 2022; Trisos et al., 2020; Urban, 2015). Climate change is happening at a fast pace (Thompson et al., 2006), acting synergistically with additional anthropogenic impacts, increasing the vulnerability, and reducing the resilience and response time of biodiversity (Botkin et al., 2007; Brodie et al., 2012; Brown et al., 2015; Cohen et al., 2019; Costello et al., 2022).

To persist, individuals, populations, or species must track their current optimal climatic conditions in space or time (Sillero et al., 2022), adapt to the new conditions through genetic, plastic, or behavioral adaptation (Bellard et al., 2012; Nogués-Bravo et al., 2018), or be preadapted to the forthcoming conditions (Chevalier et al., 2024). If none of this occurs, populations will eventually face extinction. Therefore, understanding the potential consequences of climate change on species distributions is crucial, especially as climate change unevenly affects taxa (Warren et al., 2001). Species with poor dispersal ability, low tolerance for ecological changes and acclimation, high specialization, and reduced distributional ranges are expected to be the most vulnerable (Laurance et al., 2011; Sheldon, 2019). Moreover, the effects and consequences of climate change on biodiversity are predicted to vary spatially (Brodie et al., 2012; Wiens, 2016). Tropical ecosystems are expected to suffer relatively smaller climatic changes in absolute terms (Gonzalez et al., 2010; Iwamura et al., 2010). However, these changes will be significant concerning present climatic variability and may have deleterious consequences in tropical species that evolved and adapted in regions with low geographic and seasonal climatic variations (Corlett, 2012; Deutsch et al., 2008; Janzen, 1967; Laurance et al., 2011; Sheldon, 2019; Wright et al., 2009). Assessing the impacts of climate change in the tropics, the world's most diverse and threatened areas, is essential for forecasting and understanding the extinction risks that numerous species face. However, the limited knowledge about tropical species richness and distribution ranges hampers these assessments.

Amphibians are the most endangered vertebrate class, with ca. 41% of described species classified as threatened and an increasing number of species at high risk of extinction (Luedtke et al., 2023), mainly from tropical regions (Ceballos et al., 2017). The recent Global Amphibian Assessment (GAA2) identified diseases, habitat loss, and climate change as primary drivers of conservation status deterioration and highlighted an ongoing shift toward climate change as the leading cause of decline (Luedtke et al., 2023). Amphibians, as ectotherms closely tied to their physical environment, possess traits—such as small body size, restricted distribution ranges, permeable skin, and philopatry—that make them particularly vulnerable to the impacts of climate change and limit their capacity to respond to it (Blaustein et al., 2010). Tropical amphibians are predicted to be among the most affected vertebrates to climate changes, as their narrow thermal tolerances and limited ability to acclimate increase their vulnerability (Deutsch et al., 2008; Gunderson & Stillman, 2015; Parmesan, 2006; Tewksbury et al., 2008; Wake & Vredenburg, 2008). Within this group, understory-dwelling species are expected to be more affected than canopy dwellers, as the former are exposed to smaller temperature fluctuations, possess narrower thermal physiologies, and live closer to their optimum temperature (Kaspari et al., 2015; Sheldon, 2019; and references therein). Given the current conservation status of amphibians and ongoing threats, it is urgent to understand how climate change could affect their distributions.

The tropical island of Madagascar is one of the planet's most biodiverse areas, with extremely high levels of species richness and endemism (Carné & Vieites, 2024; Goodman, 2022). Madagascar ranks among the top biodiversity hotspots for conservation priority (Myers et al., 2000) because its pristine habitats are largely gone, and the future of the island's biodiversity is jeopardized by new threats (Mantyka-Pringle et al., 2015). Habitat destruction and fragmentation continue to be a central conservation problem in Madagascar, which could be exacerbated by climate change, potentially leading to the loss of 17%–50% of the current habitats (Hannah et al., 2008). The rainforests, which harbor ca. 90% of the island's fauna (Harper et al., 2007) and many undescribed species (Carné & Vieites, 2024; Nagy et al., 2012; Perl et al., 2014; Vieites et al., 2009), have suffered severe reductions of up to 44% in the last 70 years (Vieilledent et al., 2018) and are expected to suffer the sharpest declines driven by climate and land cover changes (Brown et al., 2015; Hannah et al., 2008; Hending et al., 2022). The remaining habitats are highly fragmented, leaving little room for low-vagility species to shift their ranges (Andreone et al., 2005; Andreone & Luiselli, 2003; Cushman, 2006). This is especially critical as Madagascar is renowned for its high micro-endemicity rates (but see: Carné et al., 2025), particularly among ectothermic species such as reptiles and amphibians,

TABLE 1 *Mantella* species included in the species distribution models, along with their IUCN category, number of known localities, localities used for modeling, marginality and tolerance values, and model evaluation metrics.

Species	IUCN	Loc	Train	Test	Marg	Tole	AUC_{tr}	AUC_{ts}	TSS_{tr}	TSS_{ts}
M. aurantiaca	EN	91	64	27	2.026	0.063	0.977	0.970	0.864	0.860
M. baroni	LC	73	52	21	2.357	0.072	0.912	0.894	0.704	0.701
M. bernhardi	VU	22	16	6	2.345	0.076	0.963	0.958	0.712	0.821
M. betsileo	LC	43	31	12	1.526	0.567	0.952	0.934	0.705	0.771
M. cowanii	EN	14	10	4	2.758	0.057	0.981	0.942	0.701	0.685
M. crocea	VU	26	19	7	2.082	0.082	0.977	0.970	0.849	0.771
M. ebenaui	LC	76	54	22	2.563	0.682	0.961	0.937	0.803	0.736
M. expectata	EN	40	28	12	1.998	0.118	0.988	0.983	0.935	0.859
M. haraldmeieri	EN	10	7	3	3.015	0.167	0.968	0.940	0.711	0.644
M. laevigata	LC	15	11	4	3.486	0.215	0.983	0.978	0.859	0.836
M. madagascariensis	VU	23	17	6	2.570	0.086	0.932	0.903	0.718	0.656
M. manery	VU	7	5	2	2.483	0.027	0.977	0.966	0.673	0.745
M. milotympanum	CR	28	20	8	2.142	0.032	0.996	0.996	0.834	0.947
M. nigricans	LC	30	21	9	2.989	0.413	0.984	0.965	0.859	0.862
M. pulchra	NT	15	11	4	2.174	0.104	0.870	0.823	0.672	0.537
M. viridis	EN	56	38	18	2.600	0.188	0.994	0.992	0.958	0.909
M. sp. 1	NE	11	8	3	1.690	0.362	0.959	0.939	0.664	0.685

Abbreviations: AUC, area under the curve; Loc, number of 1 × 1 km pixels known for each species; Marg and Tole, marginality and tolerance values for each species, respectively; Train and Test, number of points used for model training and testing, respectively; TSS, True Statistical Skill.

which constitute the most speciose and threatened tetrapod groups (Antonelli et al., 2022; Brown et al., 2016).

Within the richest understory amphibian community of Madagascar, the endemic genus *Mantella* Boulenger, 1882, the Malagasy poison frogs, is probably one of the best-studied frog genera (Andreone et al., 2005, 2011). It comprises 16 currently described species (Frost, 2024) and one undescribed candidate species (Perl et al., 2014; Vieites et al., 2009), with relatively well-known distributions (Glaw & Vences, 2007). All the species are small, aposematic, and generally diurnal active frogs, resembling in morphology and behavior the unrelated neotropical frogs of the family Dendrobatidae, which also exhibit the presence of alkaloid toxins obtained through the arthropod-based diet (Clark et al., 2005; Daly et al., 1996). Because of their bright coloration and diurnal habits, these species have been intensively exploited by the international pet trade, with 264,188 individuals officially reported since 1975, including species of high conservation concern (Andreone et al., 2005; Carpenter & Andreone, 2023). Currently, all species described in the genus are included in Appendix II of the Convention on the International Trade of Endangered Species (CITES) and have been considered flagship species to promote the conservation of specific areas in Madagascar (Andreone et al., 2021). Because of the pet trade and habitat loss, fragmentation, and degradation, the conservation status of the genus *Mantella* is of concern, with 62.5% of the described species catalogued under a threatened IUCN category (Table 1). The good distributional knowledge of the genus *Mantella*, derived from their attractiveness, economic importance in the pet trade, and conservation status, makes this genus an excellent model for understanding the potential effects of climate change on species that are unevenly distributed across the island.

Madagascar is a well-studied biodiversity hotspot (Nori et al., 2020). However, amphibian species inventories and geographical distributions remain incomplete (Carné & Vieites, 2024; Vieites et al., 2008). Consequently, the impacts of climate change on amphibian distributions are scarcely addressed, with most studies to date focusing on single localities (Raxworthy et al., 2008) or species (Dubos et al., 2022; Edwards et al., 2022). In this study, following the GAA2 recommendation to investigate the potential effects of climate change on amphibian species, we examine, for the first time in Madagascar, the current and future habitat suitability for all species within an entire frog genus. We discuss the potential effects of climate change on the geographic distribution of all *Mantella* species and to what extent we can rely on and plan conservation actions based on these predictions.

MATERIALS AND METHODS

Study area

Madagascar is the fourth-largest island in the world, covering a total surface of 587,040 km^2. Situated in the Indian Ocean, between 43° to 51° E and 11° to 25° S, it contains numerous mountain ranges, plateaus, and river valleys. A wide diversity of ecosystems evolved thanks to its complex orography, from rainforests to savannas, ranging from coastal plains to high mountains (up to 2876 m). These heterogeneous environmental conditions have promoted the diversification of numerous species groups (Liu et al., 2024). Its geological history is ancient and complex, with the last continental connection ca. 80 million years ago (Dewar & Richard, 2012). Since then, Madagascar has remained isolated, fostering the evolution of unique flora and fauna, making it possible to consider the island a closed system for biogeographical studies. Therefore, we use the entire island of Madagascar as a study area.

Species and occurrence data

The genus *Mantella* is primarily forest dependent, typically inhabiting the forest floor. While some species, such as *M. expectata* and *M. betsileo*, are found in drier habitats and some, including *M. betsileo*, *M. ebenaui*, and *M. expectata*, can persist in disturbed environments, their reproductive ecology ties them to areas with water bodies. Except *Mantella laevigata*—which presents a peculiar reproductive strategy—*Mantella* species lay eggs outside the water (e.g., in leaf litter or on rocks), relying on rain to wash tadpoles into nearby swamps or streams (Vences et al., 2022).

We gathered distributional data for all 16 currently described *Mantella* species and one candidate species (*Mantella* sp. 1; Vieites et al., 2009) from field surveys conducted during the last two decades and bibliographic data (see list of references in Carné, Vieites, & Sillero, 2025). Taxonomy was defined according to the Amphibian Species of the World (Frost, 2024). After removing duplicates per pixel (with a spatial resolution of ~1 km; see below), we used 589 occurrence records (Table 1). Detailed locality data for some *Mantella* species are restricted and sensitive due to the critical conservation status of several species and their ongoing susceptibility to collection for the pet trade. Therefore, we provide the 1 × 1 km climatic grid centroid coordinates used in all analyses to ensure reproducibility (Carné, Vieites, & Sillero, 2025). Precise coordinates for research purposes are available on request from the authors.

Environmental variables

Our initial set of variables included 23 layers. We downloaded 19 bioclimatic variables, net primary productivity, and growing season length at a 30 arc sec (~1 km) resolution from CHELSA (Booth et al., 2014; Karger et al., 2017). We set this resolution as the working resolution for subsequent analyses. Additionally, we included a 30-m digital elevation model (DEM) from EarthData (https://search.earthdata.nasa.gov/), from which we calculated the slope using the terra package in R (Hijmans, 2024). We then resampled the DEM and slope to match the extent and resolution of the climatic variables. We excluded those highly correlated variables (Pearson's correlation coefficient > 0.7; Dormann et al., 2013), selecting the most relevant variable from a biological perspective for each pair of correlated variables. We also ensured that the remaining variables exhibited no unusual spatial patterns or abrupt changes suggestive of artifacts (Booth, 2022). Our final dataset contained six variables: mean annual air temperatures (bio1), temperature seasonality (bio4), annual range of air temperature (bio7), precipitation seasonality (bio15), net primary productivity (npp), and slope. We used the same set of non-correlated variables for the future forecasts. Since elevation is not expected to change over our time frame, slope was treated as a static variable. We downloaded the remaining environmental layers for the future from CHELSA for three future periods (years 2040, 2070, and 2100), three shared socioeconomic pathways: SSP126 (a lower emissions, "optimistic" scenario), SSP370 (a moderate to high emissions), and SSP585 (a higher emissions, realistic, scenario), and five CMIP6 global circulation models (GCM) to capture the uncertainties in future global climatic projections (GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-HR, MRI-ESM2-0, and UKESM1-0-LL).

Sampling bias correction

Absence data were unavailable for this study, and despite being one of the best-known frog genera in Madagascar, *Mantella* occurrence data might contain sampling biases. We reduced the impact of bias on the ecological niche models by using a background with the same sampling bias as the occurrence records. To do so, we followed the "target-group background" approach suggested by Barber et al. (2022), which uses the collective records of similar taxa across the island to estimate the sampling effort for the focal species. As reptiles and amphibians are sampled together in Madagascar using similar methodologies, we merged 6853 reptile (GBIF.org, 2024a) and 2083 amphibian (GBIF.org, 2024b) occurrence data points from GBIF (http://www.gbif.org), excluding occurrences with an error greater than 1 km and considering human observations, samples, and preserved specimens. Then, we created a two-dimensional kernel density raster to convert single presence points into a continuous probability surface, reflecting the sampling intensity conducted in Madagascar (i.e., the number of specimens per pixel). Finally, we randomly sampled 10,000 background points according to the probability given by the density raster (i.e., more sampling intensity and more background samples at a given locality).

Modeling procedure

We modeled the species' realized niche (sensu Sillero, 2011) following standard procedures (Sillero et al., 2021; Sillero & Barbosa, 2021), using the Maximum Entropy (MaxEnt) algorithm in predicts R package (Hijmans, 2023; Sillero et al., 2023). MaxEnt is a presence-background machine learning method that predicts the species' habitat suitability (the most similar environmental conditions of the study area to the training data; Osorio-Olvera et al., 2019) with the highest entropy (i.e., the most uniform or least biased distribution) while still satisfying the known constraints or observations (Phillips et al., 2006, 2017). MaxEnt estimates the realized niche in the environmental space based on a set of predictor variables included in the model. This niche is then projected onto the geographic space as a habitat suitability index. Because it is impossible to incorporate all variables that define a species' niche, the realized niche is always a partial estimate. Therefore, we use the term "habitat suitability" (e.g., gain/loss of suitable habitat) to refer to the geographic expression of the species' modeled ecological niche (i.e., MaxEnt output maps). MaxEnt is one of the most effective modeling procedures for generating environmental niche predictions from presence- background data (Elith et al., 2006; Valavi et al., 2022) and is capable of producing reliable models with few records (Hernandez et al., 2006; Kremen et al., 2008). MaxEnt output forecasts the habitat suitability and ranges from 0 (unsuitable environmental conditions) to 1 (suitable). We applied MaxEnt's default parametrization to maintain consistency and comparison capability between species. We ran 10 replicates of each model, keeping only one occurrence per pixel (i.e., removing duplicates). We defined the background as the whole island of Madagascar and obtained the background points using the density kernel as a covariate to account for sampling bias (see above). We clamped the response to prevent projecting (extrapolating) the models onto conditions outside the training data range.

Model evaluation and performance

We used the bootstrapping method for model evaluation, as for some species, few localities are known to date (Table 1). We left 30% of occurrence data for testing (Sillero et al., 2021). We used two discrimination metrics: the area under the curve (AUC) of the receiver operating characteristic (ROC; Fielding & Bell, 1997; Zweig & Campbell, 1993) and the True Statistical Skill (TSS; Allouche et al., 2006) to evaluate the accuracy of our models (Sillero et al., 2021). AUC ranges from 0 to 1, and a random model has a value of 0.5; TSS ranges from −1 to 1, and a random model has a value of 0. Both discrimination metrics are correlated (Allouche et al., 2006). As the extent of the study area is the same for all species, the dependence of AUC and TSS values on the extent does not affect the evaluation results (Lobo et al., 2008; VanderWal et al., 2009). We compared the discrimination metrics of the empirical models with those obtained from null models (Raes & ter Steege, 2007). To calculate the null models, we randomly generated pseudo-presence data across the study area, maintaining the same sample size as the species' occurrence data while keeping all other model parameters unchanged. We analyzed whether the discrimination metrics from the empirical models were significantly higher than those from the null models with a Wilcoxon test from the STATS R package (R Core Team, 2023).

We assessed the importance of each explanatory variable by estimating its average percentage contribution across model replicates. Next, we used the Jackknife test (Phillips et al., 2006), which involves recalculating the model in three ways: excluding one explanatory variable at a time, using only that variable, and using all variables together to compare AUC and gain for both the training and test data. Finally, to determine the model's dependence on each variable, we calculated the permutation importance by randomly changing the variable values among the training points and measuring the decrease in AUC.

Species distributions: Current and future projections

We projected the obtained replicated models into the three future periods, three SSP scenarios, and five GCMs. We averaged the 10 current model replicates into a single habitat suitability map for each species. To obtain the future projections, we averaged the projections of the five GCMs, which reduced individual model biases for a more reliable overall prediction (Corlett, 2012). We binarized the continuous predictions into habitat suitable or unsuitable classes to calculate their extent and compare scenarios and species. We used the threshold that maximizes the sum of sensitivity and specificity, as it tends to reflect the species' prevalence well (Jiménez-Valverde & Lobo, 2007).

Range and surface shifts

We assessed the potential habitat change (PHC) between the binarized future projections and the binarized current models for each species to spatially represent the gained/lost regions. We assessed the extent of the potential suitable habitats for each species in each period and scenario by counting the number of suitable pixels (value 1) in the binary models. We determined the gained/lost regions by pairwise comparison of the future scenarios with the current scenario. If a given pixel in the current binary projection is suitable (value $= 1$) and the future binary projection is unsuitable (value $= 0$), we consider it a pixel loss. If the pixel is suitable in both periods, we consider it a stable pixel. If the pixel is unsuitable under current conditions but predicted as suitable in future conditions, we consider it a pixel gain. Finally, if the pixel is unsuitable in both periods, we consider it unsuitable.

We considered three dispersal scenarios following the rationale of Carvalho et al. (2010) to simulate the potential effects of climate change under varying degrees of dispersal capability: (1) unlimited dispersal (UD), assuming that species can disperse to any pixel with suitable habitat within the study area without any dispersal restrictions; (2) limited dispersal (LM), assuming that species can disperse to any pixel with suitable habitat within a given perimetric buffer around current occurrence data; and (3) null dispersal (ND), assuming that the species is not capable of dispersing even if suitable habitat is available (i.e., the species cannot explore new pixels not occupied under current conditions).

To evaluate the change under the UD scenario, we compared each future binary projection with the current binary projection. For the LD scenario, we followed a procedure previously used to reduce the impact of habitat suitability overprediction in Madagascar (Brown et al., 2014, 2016; Kremen et al., 2008). First, we obtained the minimum convex polygon (MCP) of each species based on occurrence data. Next, we calculated the extent of each MCP to determine the buffer radius. Specifically, we used a 20-, 40-, or 80-km radius for MCP extents of 0–200, 200–1000, or >1000 km^2, respectively. Then, we masked all binary projections using the selected buffer and compared them with the current buffered binary projection. Finally, for the ND scenario, we only took into consideration the changes in the currently occupied pixels, herein defined as localities. In this scenario, it is not possible to gain new localities of habitat suitability.

Specialization, tolerance, and marginality

We used the CENFA R package (Rinnan, 2023) to quantify and compare two aspects of the species' niche: specialization and marginality (Hirzel et al., 2002) based on species occurrence and environmental data. Specialization measures the width of a species' niche relative to the study area; higher values indicate a narrower species niche (Hirzel et al., 2002; Rinnan & Lawler, 2019). Marginality measures the position of the species' niche in the available environmental space, that is, the distance between the average conditions used by the species and the average conditions of the study area; higher values indicate a greater ecological distance of the occupied habitat from the available average habitat (Rinnan & Lawler, 2019). Because specialization does not have an upper limit, it cannot be directly compared; therefore, we used its inverse, the tolerance, which ranges from 0.0 for species with a narrow niche to 1.0 for species with a wide niche (Hirzel et al., 2002).

We tested the relationship between marginality and tolerance as predictor variables of the PHC by 2100 using generalized linear models (GLMs) from the *stats* R package (R Core Team, 2023). Additionally, we analyzed with GLMs the extent of the occurrence-MCP and the current suitable extent as predictor variables of marginality and tolerance. Finally, we tested with ANOVA whether marginality and tolerance can predict the IUCN Red List endangered categories, represented both as a categorical variable (threatened: Yes/No) and the IUCN categories. To account for normality in model residuals, we transformed the extent variables and the tolerance using the natural logarithm and the PHC using the Yeo-Johnson transformation in the VGAM package (Yee, 2020), setting the lambda parameter to the value that maximizes the Shapiro–Wilk test p value of the variable.

RESULTS

Tolerance and marginality

Mantella manery, *M. milotympanum*, *M. cowanii*, and *M. aurantiaca* have the lowest tolerance values ($T \leq 0.06$). By contrast, *Mantella ebenaui*, *M. betsileo*, *M. nigricans*, and *M.* sp. 1 have the highest tolerance ($T > 0.360$). Marginality values are more similar between species, ranging from 1.2 to 3.5 for all species. *Mantella laevigata*, *M. haraldmeieri*, *M. nigricans*, and *M. cowanii* have the highest values, while *M. betsileo*, *M.* sp. 1, and *M. expectata* have the lowest (Table 1; Appendix S1: Figure S1). We found no correlation between tolerance and marginality ($R^2 = -0.079$, $p = 0.761$). We found linear trends for both tolerance (non-significant:

$p_{\mathrm{UD}} = 0.808$; $p\text{-value}_{\mathrm{LD}} = 0.843$) and marginality ($p_{\mathrm{UD}} = 0.045$; $p_{\mathrm{LD}} = 0.037$) as predictor variables of PHC in both UD and LD scenarios by 2100 under SSP585, while in the other two scenarios (SSP370 and SSP126), they were non-significant. Higher marginality and tolerance values led to a higher predicted loss of species' habitat suitability surface, while low values led to species surface gains (Appendix S1: Figure S2). We found a significant linear relationship between the current suitable extent as predictor variables of tolerance (MCP $p = 0.002$; current model $p = 0.001$) and marginality (MCP $p = 0.091$; current model $p = 0.098$), where smaller extents led to a higher marginality and lower tolerance values (Appendix S1: Figure S3). Finally, we found a significant relationship between tolerance ($p = 0.003$), but not with marginality ($p = 0.987$), as predictor variables of the IUCN endangered categories, with those species with lower values of tolerance being cataloged in endangered categories (Appendix S1: Figure S4).

Model performance

We produced reliable models (AUC > 0.8; TSS > 0.5) for all species included in the study. All empirical models presented significantly higher discrimination metrics than null models (Appendix S2: Table S1). The overall empirical mean values were as follows: $\mathrm{AUC}_{\mathrm{Train}} = 0.96 \pm 0.03$, $\mathrm{AUC}_{\mathrm{Test}} = 0.95 \pm 0.04$, $\mathrm{TSS}_{\mathrm{Train}} = 0.78 \pm 0.10$, and $\mathrm{TSS}_{\mathrm{Test}} = 0.77 \pm 0.11$ (Table 1; Appendix S2: Table S2; Appendix S1: Figure S5). We found considerable variation in the contribution of environmental variables explaining the occurrence data of the different species, with no consistent pattern (Carné, Vieites, & Sillero, 2025).

Range shifts on *Mantella* species

Climate change is expected to drive range shifts in *Mantella* species due to changes in habitat suitability. The extent and magnitude of these shifts will vary depending on the species, projected timelines, SSPs, and dispersal scenarios. Overall, 7 species are predicted to gain suitable climatic areas, while 10 are predicted to lose them by the year 2100 (Figures 1 and 2, Table 2; Appendix S1: Figures S8–S75; Appendix S2: Table S3).

Among the species predicted to gain habitat suitability extent, *Mantella madagascariensis*, *M. milotympanum*, and *M.* sp. 1 are forecasted to increase their current extent by more than 50% in all six evaluated scenarios by 2100. In the latter two species, habitat suitability is predicted to increase in the northern part of their distribution without any loss of currently suitable areas, a pattern also shared with *M. expectata* (Appendix S1: Figures S58–S59 and S70–S71, respectively). Conversely, in *M. madagascariensis*, gains in habitat suitability in the north will be accompanied by losses in the southernmost part of its range (Appendix S1: Figures S50 and S51), a pattern also predicted in *M. ebenaui*, *M. nigricans*, *M. pulchra*, and *M. viridis* (Appendix S1: Figures S34, S35, S62, S63, S66, S67, S74, and S75).

Among the species predicted to lose habitat suitability, *Mantella crocea*, *M. viridis*, and *M. nigricans* are forecasted to face reductions of over 50% in their current habitat suitability extent across all scenarios, with the first two species losing all suitable areas under SSP585 (Appendix S1: Figures S28–S31, S60–S63, and S72–S75). By 2100, under SSP585 and both UD and LD scenarios, *M. laevigata*, *M. cowanii*, *M. aurantiaca*, and *M. nigricans* are predicted to have the smallest suitable areas (Table 2; Appendix S2: Table S3).

Seven species, *Mantella baroni*, *M. bernhardi*, *M. cowanii*, *M. crocea*, *M. haraldmeieri*, *M. laevigata*, and *M. manery*, are predicted to suffer range contractions toward their suitable cores, losing peripheral suitable areas. For the first four species, this coincides with an altitudinal shift toward higher altitudes (Appendix S1: Figures S12–S18, S24–S31, S40–S47, and S52–S55).

Considering the ND scenario, *Mantella milotympanum* and *M.* sp. 1 are forecasted to keep all occupied pixels by 2100 under all SSP scenarios and *M. expectata* almost all of them. By contrast, the remaining *Mantella* species are expected to lose currently occupied pixels in different degrees depending on the SSP scenario and year of projection (Table 3; Appendix S2: Table S3). By 2100, eight *Mantella* species are predicted to lose over 50% of their currently occupied suitable pixels in at least one SSP scenario, with *M. crocea* and *M. viridis* losing all pixels under SSP585, and *M. cowanii*, *M. laevigata*, and *M. nigricans* losing more than 90% of them (Figure 3).

DISCUSSION

Without urgent lifestyle and systemic changes to reduce environmental impacts, ecosystems will face climatic conditions that approach or exceed their recent historical limits, leading to biotic distributional readjustments (Hampe & Petit, 2005; IPCC, 2022; Parmesan & Yohe, 2003; but see: Chevalier et al., 2024). In this study, we applied niche ecological models to explicitly assess, for the first time, the potential effects of climate change on the distribution of a whole well-studied and threatened genus of Malagasy frogs, the genus *Mantella* (Andreone et al., 2005, 2011).

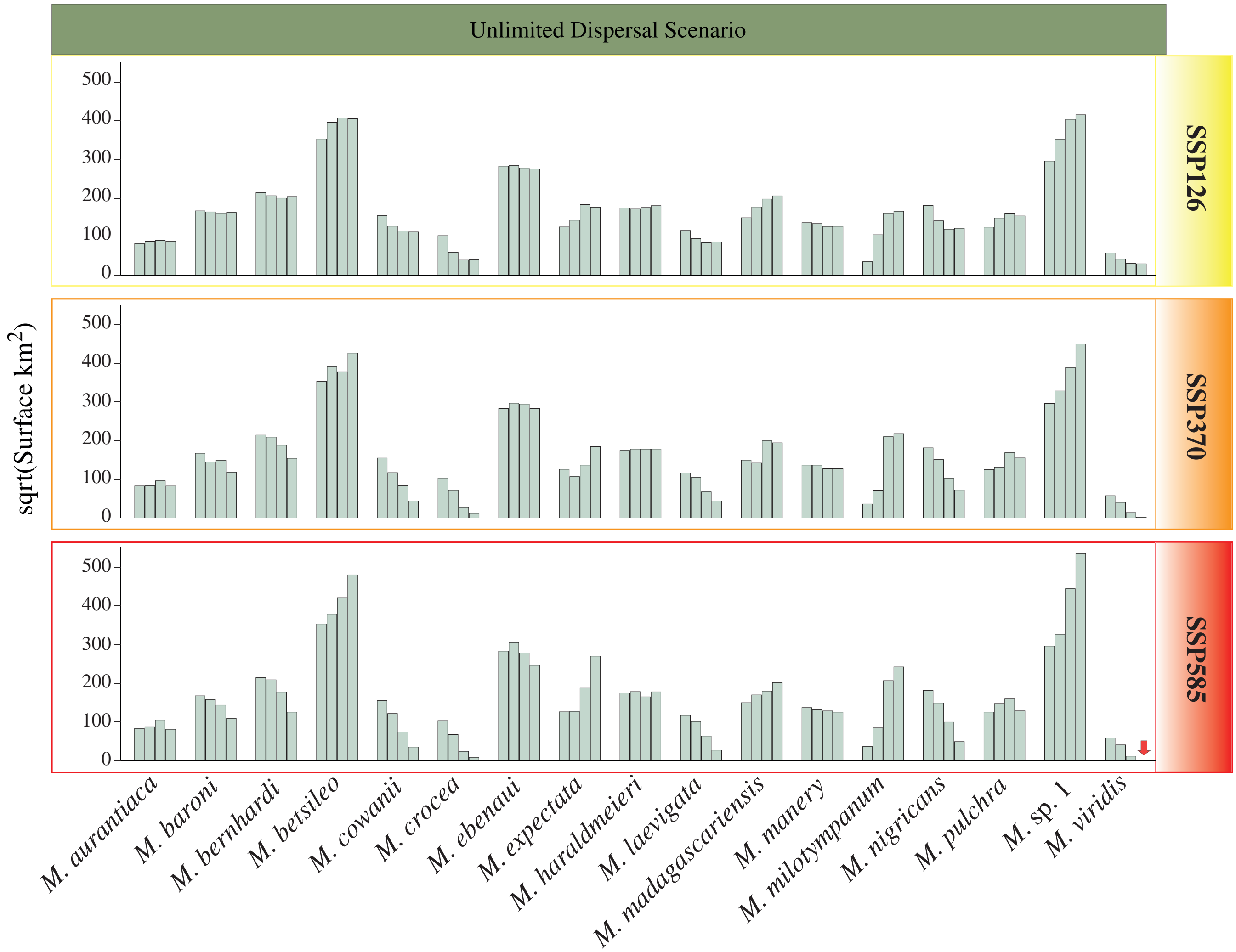

FIGURE 1 Predicted surface area changes in the species distributions of the genus *Mantella* under three shared socioeconomic pathways (SSP126, SSP370, and SSP585) and the unlimited dispersal scenario. For each species, each histogram bar represents a different period: current, 2040, 2070, and 2100 (from left to right). Red arrow indicates predicted species extirpations.

Our results suggest that even under the most optimistic emission scenario, climate change could drive large-scale shifts in *Mantella*'s distributional ranges. Not all species will respond equally: 30% of the species are forecasted to gain suitable habitat area, while 60% are predicted to lose it, as found in previous multispecies studies addressing the impacts of climate change in Madagascar (e.g., Brown et al., 2015).

Species' range, tolerance, marginality, and IUCN category

Mantellinae species generally occur in natural, undisturbed habitats and show low resistance to even minor habitat disturbance (Vallan, 2002; Vallan et al., 2004). The genus *Mantella* includes small-bodied frogs with active behavior, inhabiting various habitats. Most *Mantella* species are rainforest-dependent specialists, except *M. betsileo*, *M. ebenaui*, and *M. viridis*, which are generalists and adaptable species capable of persisting in degraded habitats, and *M. expectata* and *M. cowanii*, which can also be found in other habitats, such as rocky areas or savannas (Glaw & Vences, 2007).

Our results suggest that rainforest-restricted species (e.g., *M. manery* and *M. milotympanum*) are the most specialized, except *M. cowanii*, which is also found in Antoetra's rocky savannas (but see ongoing local extirpations in Edmonds et al., 2024). These species have specialized environmental requirements and, consequently, the narrowest niches. By contrast, the most generalist species, such as *M. betsileo* and *M. ebenaui*, show the least specialization. Habitat-specialized species are particularly vulnerable, as changes to their specific requirements can threaten their persistence (Sheldon, 2019).

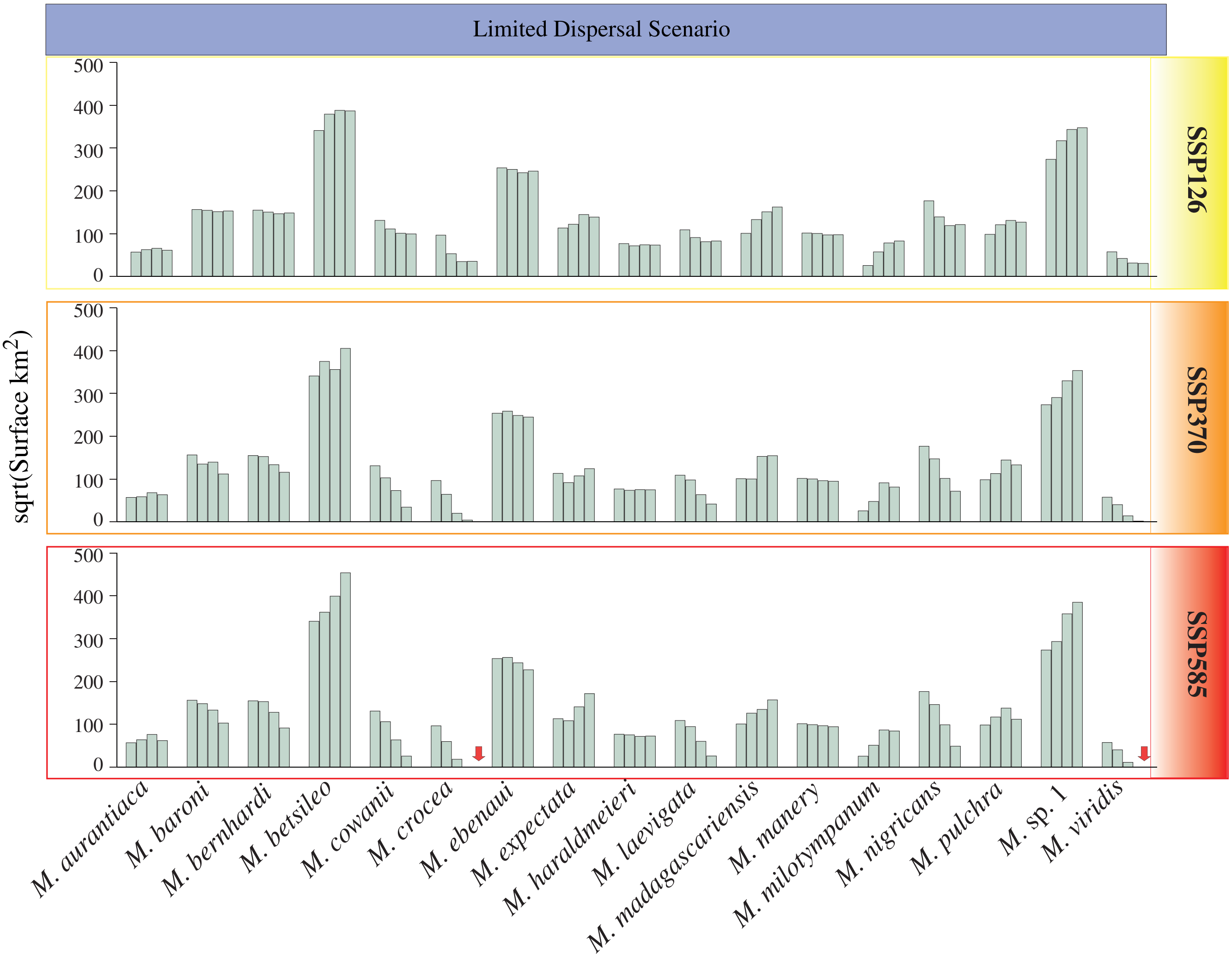

FIGURE 2 Predicted surface area changes in the species distributions of the genus *Mantella* under three shared socioeconomic pathways (SSP126, SSP370, and SSP585) and the limited dispersal scenario. For each species, each histogram bar represents a different period: current, 2040, 2070, and 2100 (from left to right). Red arrows indicate predicted species extirpations.

Our results suggest that the conservation status of the studied species can be partially predicted by their specialization values. The higher the specialization, the worse the conservation status, which may be linked to their current range extent, which also showed a significant relationship with marginality. Species with narrow distributions tend to be more specialized (or vice versa) because they utilize only a limited portion of the available environmental range. In contrast, marginal species often have narrow ranges because their suitable habitat is marginal and, therefore, far from the mean environmental conditions.

Our results suggest that high specialization may be linked to gains in suitable habitat extent. Counterintuitively, some analyzed specialized species might benefit from climate change, as their specific requirements could become more prevalent in the study area. However, habitat availability needs to be considered. For example, *M. aurantiaca* is predicted to gain suitable habitats by 2100 under the SSP585 scenario, but this newly suitable area is currently deforested, making colonization and long-term survival unlikely. Conversely, our data indicate that higher marginality values are associated with greater predicted surface losses, suggesting that species' marginal environmental conditions in the studied region are expected to decrease, reducing their habitat suitability.

Environmentally suitable areas versus suitable habitats

For the UD and LD scenarios, our results predict that the suitable areas for some species (i.e., *Mantella milotympanum* catalogued as CR; *M. expectata* as EN;

TABLE 2 Habitat suitability area (in kilometers) where each *Mantella* species is currently predicted to occur (current) and percentage of potential habitat change under different shared socioeconomic pathways (SSP) and projection years considering the unlimited dispersal scenario (UD).

		SSP126			SSP370			SSP585		
Species	**Current**	**2040**	**2070**	**2100**	**2040**	**2070**	**2100**	**2040**	**2070**	**2100**
M. aurantiaca	6887.0	14.1	19.9	14.8	0.8	34.4	−0.4	11.2	60.2	−5.2
M. baroni	27,971.6	−3.2	−6.4	−4.9	−25.1	−20.5	−49.9	−11.2	−26.7	−57.5
M. bernhardi	45,871.8	−7.2	−12.7	−9	−4.7	−23.1	−48.1	−5.2	−31.4	−65.8
M. betsileo	124,597.4	25.7	32.7	31.8	22.4	14.5	45.7	14.6	41.5	84.9
M. cowanii	23,980.9	−32	−44.8	−46.9	−42.7	−70.8	−91.9	−38.5	−77	−94.9
M. crocea	10,679.5	−65.9	−84.8	−84.2	−52.6	−93.1	−98.7	−57.6	−94.7	−99.3
M. ebenaui	79,992.6	1.2	−3.3	−5.2	10.0	8.3	0.1	16.2	−3.3	−24.3
M. expectata	15,851.8	29.1	112.6	96.8	−27.9	18	114.6	1.9	121.1	359.5
M. haraldmeieri	30,437.0	−2.7	1.7	7.3	4.2	4.1	4.3	4.2	−11	3.6
M. laevigata	13,613.4	−32.9	−46.9	−44.7	−19.6	−66.3	−85.9	−25.1	−70.4	−94.7
M. madagascariensis	22,337.8	40.8	75.1	90.1	−9.7	77.9	68.8	28.7	44.1	81.8
M. manery	18,716.7	−3.4	−13.6	−13.2	−0.2	−13.2	−13.1	−6.5	−12.1	−16.3
M. milotympanum	1309.6	751.4	1894.1	2008.2	280.2	3269.3	3529.3	446	3157.3	4371.7
M. nigricans	32,863.8	−38.9	−56.2	−54.4	−30.7	−68.3	−84.4	−32.5	−70	−92.7
M. pulchra	15,700.0	41.2	64.9	51.3	9.9	81.1	53.5	38.4	64.2	5
M. sp. 1	87,543.0	41.9	86.1	97.2	22.9	72.7	130.3	21.7	125.3	226.8
M. viridis	3344.7	−46.4	−70.2	−71.9	−51.1	−94	−99.9	−50.6	−96.1	−100

Note: Negative values represent habitat suitability losses, and positive values indicate gains. For the limited dispersal scenario or the surface figures, see Appendix S2: Table S3.

M. madagascariensis as VU; *M. pulchra* as NT; and *M.* sp. 1 as NE) will increase by more than 50% by 2100 in almost all SSP scenarios. For *M. aurantiaca*, catalogued as EN, our results suggest a 15% increase in suitable areas, contrasting with Dubos et al. (2022), who predicted a complete extirpation by 2070 using different predictor variables and modeling algorithms. In parallel, the ND scenario suggests that these species will lose less than 50% of their currently occupied pixels. Overall, these findings suggest that if these species can colonize any suitable area and face no biotic or abiotic dispersal barriers, their populations might expand and potentially improve their conservation status.

However, a significant difference exists between gaining suitable areas and actually occupying them (i.e., fundamental vs. occupied niche). The occupied niche is the environmental space with the biotic and abiotic conditions for a species to survive and persist over time, accessible through dispersal (Hutchinson, 1957). A species will not expand its range if it cannot disperse into suitable areas or if other habitat requirements (not considered in the model) are unmet. Biotic interactions should be considered when drawing conclusions involving natural dispersal. Rich and complex communities, such as those in Madagascar (Goodman, 2022), are often in delicate equilibrium with their environment (Stone, 2018). Thus, assuming dispersal and colonization solely because an area becomes suitable is overly simplistic (Urban et al., 2012, 2013). Moreover, an increase in suitable areas for declining species may not lead to range expansion due to their population dynamics. Improved environmental conditions may slow their decline but not necessarily reverse it (Harrison et al., 2006). This can lead to overestimating and drawing optimistic conclusions when modeling niches based on a reduced set of variables (Costello et al., 2022). Although our results suggest colonization possibilities in regions that may become suitable for certain species within their current expressed environmental tolerances, we cannot conclude that they will successfully colonize these areas. For example, while *M. expectata* is forecasted to gain substantial suitable areas, these new areas lack the seasonal streams, wet canyons, and narrow gallery forests that the species inhabit (IUCN SSC ASG, 2017). This is why it is important to consider several dispersal scenarios (Carvalho et al., 2010). The ND and UD scenarios represent unrealistic extremes of dispersal, while the LD scenario, though not entirely realistic, is closer to reality than the other two.

TABLE 3 Number of currently occupied pixels (1 × 1 km) and projected percentage of currently occupied pixel loss for each *Mantella* species under different shared socioeconomic pathways (SSP) and projection years.

		SSP126			SSP370			SSP585		
Species	**Current**	**2040**	**2070**	**2100**	**2040**	**2070**	**2100**	**2040**	**2070**	**2100**
M. aurantiaca	91	6.59	10.99	13.19	10.99	20.88	41.76	6.59	18.68	48.35
M. baroni	73	16.44	17.81	20.55	24.66	24.66	41.10	21.92	23.29	53.42
M. bernhardi	22	18.18	22.73	22.73	18.18	40.91	54.55	18.18	45.45	59.09
M. betsileo	43	18.60	16.28	18.60	18.60	34.88	30.23	18.60	32.56	23.26
M. cowanii	14	28.57	35.71	35.71	35.71	50.00	85.71	35.71	71.43	92.86
M. crocea	26	76.92	88.46	88.46	53.85	96.15	100	61.54	92.31	100
M. ebenaui	85	9.41	12.94	12.94	9.41	10.59	10.59	9.41	9.41	14.12
M. expectata	40	12.50	2.50	5.00	25.00	22.50	12.50	20.00	2.50	0.00
M. haraldmeieri	10	20.00	20.00	20.00	20.00	20.00	20.00	20.00	30.00	40.00
M. laevigata	15	26.67	26.67	26.67	20.00	46.67	80.00	26.67	60.00	93.33
M. madagascariensis	23	17.39	8.70	4.35	34.78	4.35	4.35	30.43	26.09	4.35
M. manery	7	28.57	28.57	28.57	28.57	28.57	42.86	28.57	28.57	42.86
M. milotympanum	28	3.57	0.00	0.00	0.00	0.00	0.00	3.57	0.00	0.00
M. nigricans	30	20.00	30.00	30.00	20.00	40.00	73.33	20.00	43.33	96.67
M. pulchra	15	86.67	80.00	86.67	86.67	80.00	86.67	86.67	80.00	86.67
M. sp. 1	11	0.00	0.00	0.00	27.27	0.00	0.00	9.09	0.00	0.00
M. viridis	56	19.64	48.21	51.79	21.43	85.71	100	23.21	91.07	100

Amphibians are generally poor active long-distance dispersers with high philopatry and homing tendencies (Fonte et al., 2019; Vences & Wake, 2007). Although no studies exist on the long-dispersal capabilities of *Mantella*, their small size and reliance on ponds or streams for reproduction suggest that they are unlikely to be effective long-distance dispersers, especially if unsuitable habitats separate suitable patches. For example, *M. crocea* persists in the Ambohitantely Special Reserve, a small forest (~170 km^2) surrounded by grasslands, but is absent from smaller nearby forest patches likely due to the unsuitable habitat between fragments impeding dispersal (D. R. Vieites, personal observation). Therefore, habitat quality and a suitable network for connectivity are essential for dispersal, survival, and persistence. These conditions are already scarce in Madagascar, and the future outlook is not promising. Deforestation has reduced forest cover by 44% since 1970 (Vieilledent et al., 2018), exacerbated by the unsustainable slash-and-burn agriculture expected to continue and intensify (Brown et al., 2015; Hannah et al., 2008; Hending et al., 2022; Morelli et al., 2020). This technique involves clearing forests, burning debris, briefly cultivating the depleted soil, and then moving to a new forest patch (Klanderud et al., 2010). Even after 30 years, significant ecological and structural gaps remain between cleared and secondary or primary forests, jeopardizing the future of forest-dependent species (Klanderud et al., 2010). Combined with the rapid population growth in rural areas (CIA, 2024; FAO, 2024) and Madagascar's low UN Human Development Index rank (UNDP, 2024), these factors will reduce suitable habitats and connectivity, leaving little room for forest-dwelling species to disperse and persist. Unfortunately, currently available land cover future projections (Hou et al., 2022) are not useful for modeling, as they fail to account for these forest threats and, contrary to observed trends, unrealistically predict a forest increase.

Habitat suitability loss versus population extirpations

Our results suggest that by 2100, 60% of *Mantella* species will lose substantial amounts of their current suitable habitats. Particularly concerning, under both UD and LD scenarios, two threatened species, *M. crocea* and *M. viridis*, are predicted to lose all suitable habitats. Additionally, *M. bernhardi* and *M. cowanii* (both threatened according to the IUCN), and *M. nigricans*, *M. laevigata*, and *M. baroni*, catalogued as LC, are forecasted to lose over 50% of their suitable habitats. Even

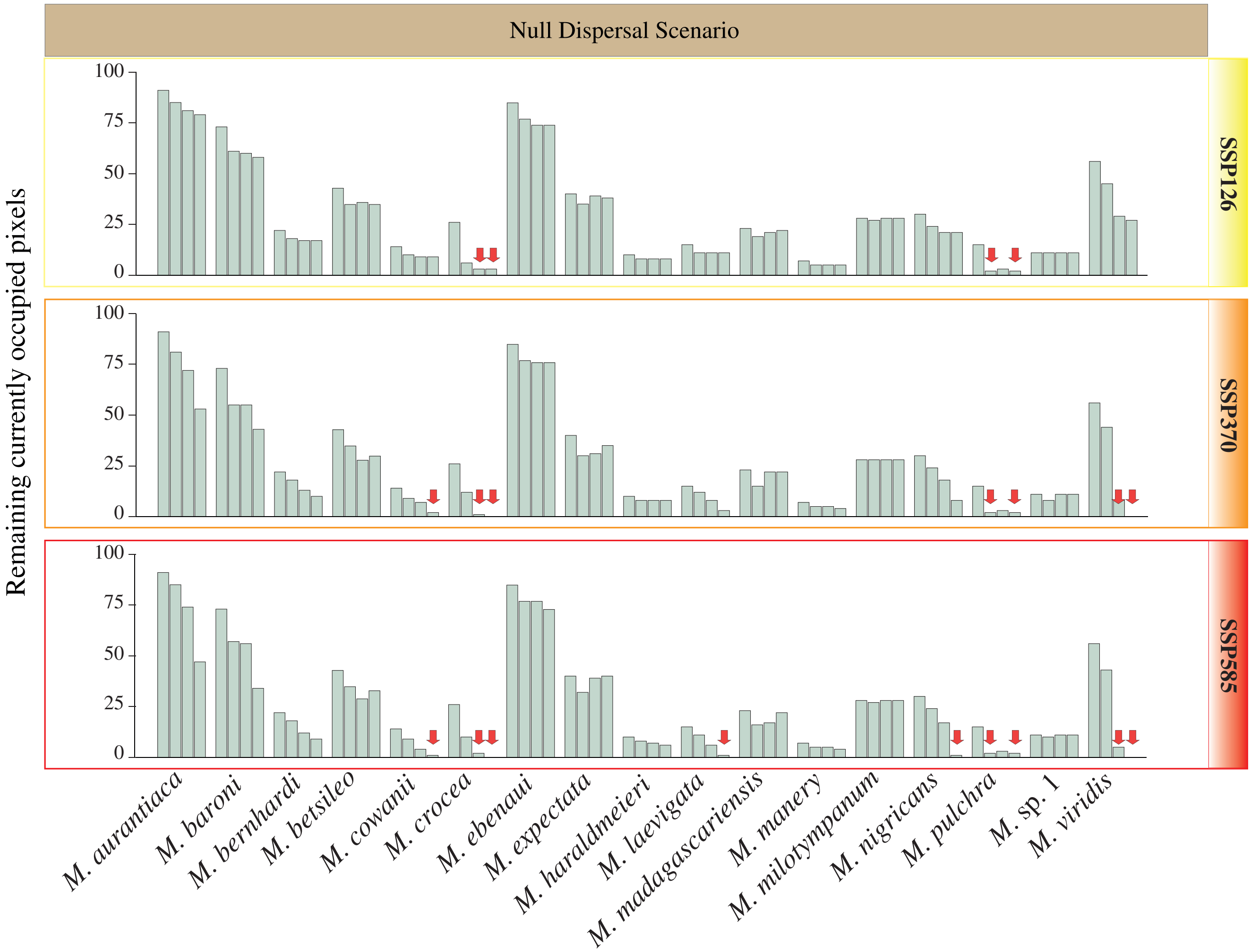

FIGURE 3 Predicted loss of currently occupied pixels in the species distributions of the genus *Mantella* under the null dispersal scenario (ND) and three shared socioeconomic pathways (SSP126, SSP370, and SSP585). For each species, each histogram bar represents a different period: current, 2040, 2070, and 2100 (from left to right). Red arrows indicate species predicted to lose >85% of currently occupied pixels.

more concerning, some species are predicted to lose 90% of currently occupied pixels, such as *M. cowanii*, *M. crocea*, *M. laevigata*, *M. nigricans*, and *M. viridis*—a phenomenon that has already begun (Edmonds et al., 2024). Thus, except for *M. crocea* and *M. viridis*, which might lose all suitable conditions on the entire Island, population survival and persistence would require dispersal.

Amphibians are ectothermic, low-vagile, philopatric, and closely tied to their physical local environments and microclimates (Wake & Vredenburg, 2008). We have modeled species distributions using downscaled macroclimatic coarse-gridded projections. These downscaling techniques cannot capture the microclimatic variations caused by topography or habitat structure (Dobrowski, 2011). In consequence, some populations predicted to become extinct might persist in enclave microrefugia microclimates (Frey et al., 2016; Potter et al., 2013), softening the forecasted species losses (IPCC, 2022). The genus *Mantella*, known for being seasonally abundant and hard to find during certain periods of the year that are spent underground, may benefit from both behavioral adaptations and microrefugia, thus reducing the forecasted losses. However, if the macroclimate changes drastically and rapidly, microclimates will also change, potentially reducing the effectiveness of behavior and microrefugia.

Recently, Chevalier et al. (2024) noticed that approximately 50% of Earth's species, particularly in the tropics, show niche contiguity. This means that their current ecological niches touch existing climatic boundaries, suggesting that they could potentially expand as new conditions become available. Although amphibians have the lowest contiguity prevalence, this could translate into persistence or even range expansions rather than extirpations for some species, as they could be preadapted to the upcoming climatic conditions (Klinges et al., 2024). However, it is risky assuming that a species' realized niche could be larger because it has been estimated using current climatic limits and because the species has not yet experienced conditions at the extremes of its known environmental gradient. This assumption may lead to overly optimistic conclusions and underestimate potential losses that we might later regret.

Range shifts

Our results suggest that range shifts are expected in species predicted to both lose and gain suitable areas. Despite disparities among species (see *Results*), two patterns emerge: latitudinal shifts toward lower latitudes, where species gain area in the north and lose it in the south, contrary to the isotherm-tracking hypothesis that predicts poleward shifts tracking cooler temperatures (Lenoir et al., 2024); and altitudinal shifts, with species losing low-altitude areas and gaining at higher altitudes.

Altitudinal and latitudinal range shifts of species tracking their optimal climatic conditions have been globally predicted and observed during the last decades (Chen et al., 2011; Freeman et al., 2018; Parmesan, 2006; Sillero, 2021; Sillero et al., 2022; Urban, 2018). In a recent comprehensive review, Rubenstein et al. (2023) demonstrated significant differences between observed and predicted shifts, finding that amphibians are not shifting their ranges as expected, with overall shift rates not differing from zero. This is concerning because amphibians are the most threatened vertebrate group (Luedtke et al., 2023), and a lack of range shifts could indicate a higher extinction risk. Alternatively, it might suggest that other processes, such as (pre)adaptation, are preventing these expected shifts.

To effectively plan species conservation based on predicted range shifts, we need to better account for and predict what species are expected to shift and by how much (Rubenstein et al., 2023), ideally considering distinct dispersal scenarios or incorporating empirical dispersal data to account for uncertainty. Without more evidence supporting ongoing amphibian range shifts in Madagascar, we prefer not to explicitly suggest new protected areas or conservation actions. However, we provide empirical data and detailed maps to account for it.

Study caveats

We recognize that several factors can influence range changes. For example, we did not directly include factors such as future land cover changes, dispersal ability, biotic feedbacks (e.g., declines in arthropod abundance due to climate change; Lister & Garcia, 2018), population dynamics, or other anthropogenic threats (e.g., fire regimes, land and watershed pollution, river diversion for agriculture, or pond drainage) in our models due to data, species' ecology knowledge, and methodological limitations. Some of these data are not available for the future. These threats are already concerning in Madagascar and are expected to increase in the near future partly due to feedback loops between climate change and human responses (Watson, 2014). Consequently, some projections may overestimate habitat suitability or the likelihood of a species reaching new areas. Conversely, not accounting for species preadaptation might lead to overestimating habitat reductions (Chevalier et al., 2024).

Disparities between observed and predicted species responses to climate change are common (Rubenstein et al., 2023; Vilà-Cabrera et al., 2019). Over the past few decades, many species have been predicted to become extinct due to climate change (e.g., Thomas et al., 2004; Trisos et al., 2020; Urban, 2015), yet relatively few have become extinct (Botkin et al., 2007; Vilà-Cabrera et al., 2019). This discrepancy partly arises because (1) the predictor variables determining a species' current distribution are often unknown or tentatively hypothesized; (2) unconsidered behavioral adaptations; (3) the predictor variables based on downscaled coarse-gridded projections may fail to capture the micro-habitats used by many species (i.e., we do not truly understand the niches of many species); and (4) population dynamics, influenced by factors such as competition, (pre)adaptation, ecological interactions, and resource availability, are challenging to account for in modeling due to knowledge gaps and methodological limitations. Moreover, in niche-based forecasts, species are treated as entities responding uniformly to environmental conditions with static spatiotemporal environmental tolerances. This approach assumes that any area with conditions outside a species' current ecological niche limits is unsuitable (Guisan & Thuiller, 2005; Thomas et al., 2004). However, populations within a species may be physiologically and/or genetically preadapted to specific ecological conditions (Harte et al., 2004; Herrando-Pérez et al., 2019), influencing how individuals or populations perceive and respond to climatic stress, ultimately determining the species' fate.

Our study analyzes the potential effects of climate change on the distribution of the genus *Mantella*, a well-known and threatened frog genus from Madagascar. By 2100, most species are predicted to lose suitable areas across all SSP and dispersal scenarios, though some may benefit by gaining new suitable areas. Latitudinal and altitudinal range shifts are expected for nearly all species, but the limited dispersal capabilities, coupled with Madagascar's rapid habitat degradation, could impede their spatial reorganization, leading to underestimations of local extirpations in our models. Conversely, predicted losses may be overestimated due to limitations in microhabitat detection and may be offset by behavioral changes or by preadaptation. Given these uncertainties, and considering that the amphibian community of Madagascar comprises 435 described species and many candidate species (Carné & Vieites, 2024; Frost, 2024), recommending specific conservation actions requires more comprehensive evidence to ensure that scarce resources are allocated in a way that benefits the highest number of species.

AUTHOR CONTRIBUTIONS

Conceptualization: Albert Carné, Neftalí Sillero, and David R. Vieites. *Data curation*: Albert Carné. *Formal analysis*: Albert Carné and Neftalí Sillero. *Validation*: Albert Carné, Neftalí Sillero, and David R. Vieites. *Writing original draft*: Albert Carné. *Writing—review and editing*: Albert Carné, Neftalí Sillero, and David R. Vieites.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Carné, Vieites, & Sillero, 2025) are available on Figshare: https://doi.org/10.6084/m9.figshare.28939010.v1.

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SUPPORTING INFORMATION

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

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