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The Miners of South America: Impacts of Climate Change on the Distribution of *Geositta* Miners Along Elevational Gradients

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ABSTRACT

Range shifts along elevational gradients are a common response of species to changing climate, particularly in tropical regions where temperature decreases sharply with elevation. In this study, we investigate the current and future distribution of seven *Geositta* species (Furnariidae), which inhabit arid and semi-arid open habitats across different elevations in South America. Using ecological niche modeling, we assessed climatic suitability under two climate change scenarios: an optimistic scenario with reduced emissions and a pessimistic scenario with continued high emissions. Species distribution models were generated with the MAXENT algorithm, using 100 replicates per species. Future projections, based on two General Circulation Models (2061–2080), evaluated the influence of elevation on climatic niche availability. Our results indicate that six of the seven *Geositta* species will likely face significant habitat loss under all scenarios, with the pessimistic scenario causing the most severe reductions. Climatic suitability patterns differed between lowland and highland species, influenced by vegetational and elevational zonation of the Andean slopes. For highland species, suitable conditions were mostly restricted to higher elevations within their current ranges, reflecting the geographic constraints that limit their ability to shift upslope. These findings highlight the vulnerability of *Geositta* to climate change, stressing the urgency of conservation efforts. Protecting mid- to high-elevation habitats and transitional zones, while reducing anthropogenic pressures, will be key to safeguarding species with limited dispersal abilities. Although our models suggest most species are likely to retain substantial portions of their climatically suitable range, their future persistence may still depend on habitat availability, dispersal capacity, and other ecological constraints.

RESUMO

Mudanças na distribuição ao longo de gradientes altitudinais são uma resposta comum das espécies às alterações climáticas, especialmente em regiões tropicais, onde a temperatura diminui rapidamente com a elevação. Investigamos a distribuição atual e futura de sete espécies de *Geositta* (Furnariidae), que ocupam habitats abertos áridos e semiáridos em diferentes altitudes na América do Sul.

Utilizando modelagem de nicho ecológico, avaliamos a adequação climática sob dois cenários: otimista, com redução das emissões de gases de efeito estufa, e pessimista, com emissões contínuas elevadas. Os modelos de distribuição foram gerados com o algoritmo MAXENT, utilizando 100 réplicas por espécie, e projeções futuras baseadas em dois Modelos de Circulação Geral (2061–2080) permitiram avaliar o efeito da altitude na disponibilidade do nicho climático. Seis das sete espécies provavelmente sofrerão perdas significativas de habitat em todos os cenários, sendo o pessimista o mais severo. Padrões de adequação climática diferiram entre espécies de baixada e de altitude, influenciados pela zonação vegetacional e altitudinal das encostas andinas. Para as espécies de altitude, as condições adequadas restringiam-se principalmente a altitudes mais elevadas dentro de suas áreas de distribuição atuais, refletindo as limitações geográficas que restringem sua capacidade de migrar para altitudes mais elevadas. A proteção de habitats de elevação média e alta e de zonas de transição, junto à redução de pressões antrópicas, será crucial para a conservação de espécies com dispersão limitada. Embora a maioria das espécies deva manter áreas climaticamente adequadas, sua persistência futura dependerá da disponibilidade de habitat, capacidade de dispersão e outras restrições ecológicas.

1 | Introduction

Changes in the geographic range of species along latitudinal and elevational gradients provide compelling evidence of potential effects of climate change (Grabherr et al. 1994; Boisvert-Marsh et al. 2014; La Sorte et al. 2014). For tropical species, however, latitude has a relatively small impact on driving range shifts due to its minor effect on temperature when compared to elevation (La Sorte et al. 2014; Perillo et al. 2021). As a result, species seeking more suitable climatic conditions tend to move to higher elevations, leading to a reduced geographic range. This process can potentially threaten these species (Raxworthy et al. 2008; Freeman et al. 2018) including those living in open habitats, whose future remains uncertain (Marini et al. 2009; Borges et al. 2019; Meireles et al. 2023).

According to the latest report of the Intergovernmental Panel on Climate Change (IPCC 2022), the rise in temperature in the coming years will be decisive for the future of species found in open habitats, contributing to large-scale extinctions and losses in the functional diversity of these ecosystems. Grasslands, one of the ecosystems most at risk, are disturbance-dependent systems maintained by natural fires, grazing by large herbivores, and seasonal climatic fluctuations. Without effective mitigation measures, these ecosystems are expected to undergo severe biodiversity losses (Gibson and Newman 2019; Hidasi-Neto et al. 2019; Hofmann et al. 2021). This finding is particularly concerning, since some of these ecosystems harbor unique assemblages of endemic species that are undergoing exceptional loss of habitat, thereby qualifying them as biodiversity hotspots (Myers et al. 2000).

Species inhabiting open habitats along a large elevational gradient are good candidates to be studied regarding the impacts of climate change on their geographic range. Among those species, we highlight members of the genus *Geositta* (Furnariidae, Sclerurinae) as an ideal model. This genus contains eleven species widely distributed in South America, all exhibiting similar behavior and ecological requirements (Fjeldså and Krabbe 1990; Remsen Jr 2003; Ridgely and Tudor 2009; Machado et al. 2017; Gómez 2019). Members of *Geositta* are closely associated with open and dry habitats, such as open grasslands, arid shrublands, deserts and barren rocky areas (Fjeldså and Krabbe 1990; Remsen Jr 2003; Ridgely and Tudor 2009). These terrestrial birds are mostly insectivorous, breeding within cavities excavated in the soil by the birds themselves or by other animals (Fjeldså and Krabbe 1990; Remsen Jr 2003; Ridgely and Tudor 2009; Machado et al. 2017; Gómez 2019). Five species of the genus have declining populations, but only *G. poeciloptera* is currently recognized as threatened with extinction and classified as globally vulnerable (IUCN 2024).

In this study, we used ecological niche models to investigate the effects of climate change on the distribution of members of *Geositta* along a large elevational gradient. For that, we evaluated the effects of climate change based on different greenhouse gas emission scenarios and policies for the next 50 years. As species of the genus occur from sea level to more than 5000 m a.s.l., with some species predominantly distributed in lowlands and others in highlands (Remsen Jr 2003), we expect distinct responses in their adaptation to climate change. We predict that all miner species will experience reductions in climatically suitable areas in the future, irrespective of their elevation range, scenario, or emissions policies adopted. Nevertheless, the magnitude of these losses is expected to vary among species, with lowland taxa being disproportionately affected, as climate change impacts are projected to be more pronounced in lowland regions than in high-elevation areas. We also investigated the relationship between elevation and climatic suitability for species occurrence. We expect that lower regions within each species' range will exhibit less climatic suitability compared to higher regions. Although no direct evidence exists of ongoing range shifts in *Geositta* due to recent climate change, the distribution of these species is strongly constrained by climatic factors through their association with dry environments such as deserts, puna grasslands, and Cerrado plateaus. Thus, while land-use change also plays a major role, we consider climate to be a key determinant of their current and future ranges.

2 | Methods

2.1 | Study Species

Seven out of the 11 species of *Geositta* are year-round residents, with the other four species performing seasonal long-distance or elevational movements. The seven resident species were selected for this study (see Table 1), with the four migratory species being excluded due to limited information about their breeding and wintering grounds, as well as their migratory timing (Remsen Jr 2003). Furthermore, migrant species are often composed of multiple populations, each one exhibiting distinct migratory strategies and timing (Rappole 2013), biasing data analysis for these species and making relevant conclusions difficult or even unfeasible.

TABLE 1 | Species of *Geositta* miners included in this study, countries of occurrence, elevational range, conservation status, and population trends according to the IUCN Red List (2024).

Species	Countries	Elevational range	Status	Population trend
G. crassirostris	PE	L (300–3500)	LC	Decreasing
G. maritima	CL, PE	L (0–2600)	LC	Stable
G. peruviana	PE	L (0–700)	LC	Stable
G. poeciloptera	BO, BR, PY	L (500–1250)	VU	Decreasing
G. punensis	AR, BO, CL, PE	H (3050–5000)	LC	Stable
G. saxicolina	PE	H (3700–4900)	LC	Stable
G. tenuirostris	AR, BO, CL, EC, PE	H (2500–4600)	LC	Stable

Note: Elevational range: L, lowland; H, highland. Countries: AR, Argentina; BO, Bolivia; BR, Brazil; CL, Chile; EC, Ecuador; PE, Peru; PY, Paraguay. Status: LC, least concern; VU, vulnerable.

The seven species of *Geositta* studied here are distributed along a large elevational range, but in a small latitudinal range (between 0 and 30 degrees south, mostly) (Table 1). For easy data interpretation, we will call the predominantly coastal species as "lowland species," including those with a strong foothill component. *Geositta poeciloptera*, a species endemic to the central Brazilian Cerrado grasslands (Lopes et al. 2024), was also considered a lowland species. The species predominantly distributed along the Andes will be called "highland species" (Table 1).

2.2 | Bird Occurrence Data

To access the current distribution of each species, we searched for occurrence records of members of *Geositta* in the Global Biodiversity Information Facility database (www.gbif.org), an open access platform that provides data on all types of life on Earth. We also searched for occurrences in eBird (www.ebird.org), a global platform for sharing bird occurrence records. We filtered the gathered data to eliminate duplicates and points without geographic coordinates. We also eliminated points outside known areas of occurrence or that happened to be at sea. For filtering guidance, we used as a reference the distribution maps of each species produced by BirdLife International and the Handbook of the Birds of the World (available at www.iucnredlist.org). Once filtered, we spaced occurrence records using a 10 km radius around each presence. This distance was chosen as a compromise between reducing spatial autocorrelation and retaining sufficient occurrences for model calibration. This scale corresponds to the typical resolution of bioclimatic data (≈5–10 km) and has been commonly adopted in species distribution modeling studies to avoid pseudo-replication while preserving environmental representativeness (e.g., Fourcade et al. 2014; Aiello-Lammens et al. 2015). We implemented this thinning in the spThin package (Aiello-Lammens et al. 2015) in R 4.4.1 program (R Development Core Team 2024) to avoid occurrence clustering in the same pixel (see Climate data topic).

Because reliable absence data are not available for *Geositta* (e.g., non-detections in eBird or GBIF often reflect lack of observer effort rather than true absence), we used presence-only models with background points (pseudo-absences), as commonly applied in MaxEnt. Although this procedure reduces the raw number of presence records, spatial thinning was implemented to minimize geographic bias and ensure independence of occurrences, thereby avoiding overrepresentation of well-sampled sites. While other approaches (e.g., bias files or weighted background sampling) could also be used, thinning provided a transparent and conservative method to reduce sampling bias while maintaining sufficient records for robust model performance.

2.3 | Climate Data

We used 19 bioclimatic variables extracted from the WorldClim v2 database (Fick and Hijmans 2017) with a resolution of 5 arc-minutes. To minimize multicollinearity in the data, we performed Variance Inflation Factor (VIF) analysis tests (the default threshold of 10 was used) using the *usdm* package (Naimi et al. 2014) implemented in the R 4.4.1 program (R Development Core Team 2024), selecting only variables with the lowest values of correlation. For each species, we use a specific mask to crop variables to countries of species occurrence.

2.4 | Predicting the Current Climatic Suitability Areas of the Species

To create the current projections, we utilized the 'sdm' package (Naimi and Araújo 2016) in R 4.4.1 (R Development Core Team 2024) to train models using the Maximum Entropy model (MAXENT) (Phillips et al. 2006). The models were trained with 10,000 background points randomly generated within each species' study area and involved 100 independent runs through subsampling. In presence-only approaches such as MaxEnt, the algorithm does not use true or pseudo-absences; instead, it contrasts occurrence records with randomly sampled background points. These points represent the range of environmental conditions available in the study area and help reduce biases that could result from arbitrarily generating pseudo-absences. We evaluated the predictive performance of the models by using 70% of the data for calibration and the remaining 30% for evaluation. Model performance was assessed using a threshold > 0.7, based

on the average true skill statistic (TSS) (Allouche et al. 2006) and area under the curve (AUC) (Fielding and Bell 1997). For each species, we constructed ensemble models that maximized sensitivity and specificity, resulting in a single consensus map by averaging the binarized projections from the determined TSS threshold (Meireles et al. 2023).

2.5 | Predicting the Future Climatic Suitability Areas of the Species

To build the future projections for each species, we used two General Circulation Models (GCM), both classified as good performers for the Andes and Cerrado regions (Ortega et al. 2021), namely MPI-ESM1-2-HR and MRI-ESM2-0. The temporal scale encompasses the period between 2061 and 2080. We also evaluated two different climate policy scenarios for greenhouse gas emissions based on Shared Socio-Economic Pathways—SSP: (1) Optimistic (ssp245), with climate policies to reduce greenhouse gas emissions over the years and limit warming to ~2.5°C; and (2) Pessimistic (ssp585), with a substantial increase in greenhouse gas emissions (~5°C) (Riahi et al. 2017; Gidden et al. 2019). All models generated were based on the Coupled Model Intercomparison Project Phase 6 (CMIP6) (Eyring et al. 2016). The future data were also taken from the WorldClim v2 database (Fick and Hijmans 2017) with the same mask and resolution as the current scenario variables.

2.6 | Assessing Current and Future Environmentally Viable Areas

We used ArcGis 10.5 (ESRI 2016) to calculate changes in the extent of environmentally viable areas between the current and future projections (including the different scenarios and climate models) for all seven miner species. We selected areas with climate suitability greater than 40% since the predominance of records occurs in this range. For this, we used niche models (i.e., suitability maps) generated for each species as vectorized maps, calculating their dimensions (> 40%) in km^2 and estimating lost and gained areas based on the current projection.

2.7 | Statistical Analysis

To assess differences in area loss in relation to elevation for each climate model and emission scenario, species were grouped according to their elevational distribution (lowlands and highlands). The average area loss was calculated for each group and a *t*-test was performed to compare these averages between groups (Zar 1996).

To investigate the relationship between elevation and climate suitability, values of these variables were extracted for all species occurrence records in current and future climate models. The distribution of these values was analyzed, and the model fit was verified through residual analysis, as described by Crawley (2012). For each species, we examined how climatic suitability varied across its entire elevational range, testing whether suitability was greater in the lower versus upper portions of the range for lowland species, and conversely, whether it was greater in the upper versus lower portions for highland taxa. Elevation data were obtained from the WorldClim v2 database (Fick and Hijmans 2017) at the resolution of 5 arc-minutes.

3 | Results

A total of 1478 records were compiled for the seven species evaluated in this study after applying spatial rarefaction (Table 2). The VIF analysis revealed that the bioclimatic variables investigated contributed distinctly to predicting climate niches for each species. However, two common variables were identified: Precipitation of Wettest Month (Bio13) and Precipitation of Driest Month (Bio14). There was a significant difference in the relative contribution of these variables for the models, with Bio13 ranging from 0.85% to 21.30% and Bio14 ranging from 0.80% to 64.30% (Table 2).

The performance of all models was deemed satisfactory and superior to the usual TSS threshold of 0.7, with its average ranging from 0.73 to 0.89 for TSS and 0.91 to 0.97 for AUC (Table 3). Similarly, the suitability models for all species in the current scenario proved to be well adjusted and matching known occurrence records for each species (Figure 1 and Figure S1).

For future predictions, all GCM models (MPI-ESM1-2-HR and MRI-ESM2-0) and scenarios (ssp245 and ssp585) showed a considerable reduction of suitable climatic areas for each species between the years 2061 and 2080. Exception is made for *G. peruviana*, a species for which models showed an increase in climatically suitable areas (Figure 2). The projections based on scenarios without mitigation policies of greenhouse gas emissions (ssp585), and consequently greater global warming, showed a greater reduction in area (Figures 2–4, Table 4). The *t*-test indicated that there was no significant difference in the loss of climatically suitable area between lowland and highland species ($t = 0.639$, $df = 5.605$, $p = 0.547$) (Figure 4).

The climatic suitability values extracted for all occurrence records for the lowland and highland species groups in the current scenario showed a significant relationship with elevation for lowland ($\chi^2 = 28.0$, $df = 1$, $p < 0.001$; $\beta = -0.000073 \pm 0.000014$, $t = -5.30$) and highland ($\chi^2 = 76.7$, $df = 1$, $p < 0.001$; $\beta = +0.000108 \pm 0.000012$, $t = 8.76$) species, revealing different patterns for each group. Lowland species exhibited higher suitability in lower areas and lower suitability in higher areas, while highland species presented the opposite pattern. For *G. poecilloptera*, the only non-Andean species, although included among the lowland species, the pattern resembled that of the highland species (Figure 5).

The relationship between climate suitability and elevation was significant for both future scenarios and GCMs, maintaining the same patterns presented by each species in the current period. For highland species, suitability increased strongly with elevation ($\chi^2 = 836.3$, $df = 1$, $p < 0.001$; $\beta = +0.000180 \pm 0.000006$, $t = 28.92$). For lowland species, suitability decreased with elevation, although the effect was weaker ($\chi^2 = 4.0$, $df = 1$, $p = 0.045$; $\beta = -0.000016 \pm 0.000008$, $t = -2.00$). Climatic scenarios also had a strong effect (highland: $\chi^2 = 87.7$, $df = 3$, $p < 0.001$; lowland: $\chi^2 = 80.2$, $df = 3$, $p < 0.001$). Compared to the optimistic baseline

TABLE 2 | Selected environmental variables and relative contribution to predict climate niches for each of the seven species of *Geositta* miners.

Variables	Description	Percent contribution (%)						
		***G. crassirostris* (30)[a]**	***G. maritima* (219)[a]**	***G. peruviana* (168)[a]**	***G. poeciloptera* (66)[a]**	***G. punensis* (519)[a]**	***G. saxicolina* (81)[a]**	***G. tenuirostris* (395)[a]**
Bio 1	Annual mean temperature	—	—	—	36.3	—	—	—
Bio 2	Mean diurnal range (Mean of monthly)	—	—	—	—	0.45	7.60	0.40
Bio 3	Isothermality	—	8.55	15.4	6.15	31.10	15.2	18.60
Bio 4	Temperature seasonality	5.00	—	—	—	—	4.65	—
Bio 5	Max temperature of warmest month	—	12.75	—	—	—	—	—
Bio 6	Min temperature of coldest month	—	—	3.65	—	—	—	—
Bio 7	Temperature annual range	3.30	8.10	1.25	0.50	—	—	—
Bio 8	Mean temperature of wettest quarter	—	7.60	10.45	—	—	78.25	44.60
Bio 9	Mean temperature of driest quarter	—	—	3.30	—	26.95	—	—
Bio 10	Mean temperature of warmest quarter	—	—	—	—	—	—	—
Bio 11	Mean temperature of coldest quarter	—	—	—	—	—	—	—
Bio 12	Annual precipitation	—	—	—	13.70	—	—	—
Bio 13	Precipitation of wettest month	21.30	11.00	3.75	3.70	0.85	18.75	2.20
Bio 14	Precipitation of driest month	64.15	17.40	64.30	20.00	0.80	5.80	0.80
Bio 15	Precipitation seasonality	3.80	—	2.45	—	13.30	0.15	12.50

(Continues)

TABLE 2 | (Continued)

Variables	Description	Percent contribution (%)						
		G. crassirostris (30)[a]	*G. maritima* (219)[a]	*G. peruviana* (168)[a]	*G. poecilioptera* (66)[a]	*G. punensis* (519)[a]	*G. saxicolina* (81)[a]	*G. tenuirostris* (395)[a]
Bio 16	Precipitation of wettest quarter	—	—	—	—	—	—	—
Bio 17	Precipitation of driest quarter	—	0.45	—	—	—	—	—
Bio 18	Precipitation of warmest quarter	—	—	—	14.65	—	22.7	8.45
Bio 19	Precipitation of coldest quarter	16.65	33.10	—	15.55	0.55	—	11.05

[a]Number of occurrences.

TABLE 3 | Average of true skill statistic (TSS) and area under the ROC curve (AUC) values to evaluate model performance for the seven *Geositta* miner species.

Species	TSS	AUC
G. crassirostris	0.73	0.91
G. maritima	0.81	0.94
G. peruviana	0.89	0.97
G. poeciloptera	0.82	0.95
G. punensis	0.87	0.96
G. saxicolina	0.86	0.97
G. tenuirostris	0.82	0.95

(ssp245MPI), suitability was consistently lower under other scenarios: for highland species, decreases were $\beta = -0.020 \pm 0.008$ (ssp245MRI), $\beta = -0.044 \pm 0.008$ (ssp585MPI), and $\beta = -0.073 \pm 0.008$ (ssp585MRI); for lowland species, decreases were $\beta = -0.071 \pm 0.015$ (ssp245MRI), $\beta = -0.082 \pm 0.015$ (ssp585MPI), and $\beta = -0.136 \pm 0.015$ (ssp585MRI). These results indicate that climatic suitability will be consistently lower under pessimistic greenhouse gas emission scenarios (ssp585) compared to optimistic ones (ssp245) for all species, except for *G. peruviana* (Figure 6).

4 | Discussion

Our current projections showed great similarity with those of Ribeiro et al. (2017), who trained ecological niche models to explore the diversification of the genus *Geositta*. The climatically suitable areas predicted by both studies agreed with the occurrence records for each species, however some discrepancies between projections in the two studies were found, with different extrapolations for the climatically suitable areas. This can be explained by the fact that Ribeiro et al. (2017) used the entire South America as a mask to predict the most suitable locations for species occurrence, identifying areas outside the distribution limits. Contrastingly, we used only the countries where the species occur as a mask to train the models. In our view, including the entire South America as a mask certainly overestimated the range of the studied species. This is because the Andes, due to its large elevational gradient, steep relief and deep valleys, can be viewed as a series of isolated sky islands; furthermore, its complex vegetation, composed by different types of forests, shrublands, grasslands, and deserts distributed along elevational zones (Fjeldså and Krabbe 1990; Borsdorf and Stadel 2015; Hazzi et al. 2018), create barriers that prevent colonization of some areas (Haffer 1967; Vuilleumier 1970). However, we must acknowledge that the small number of species per elevational group constrained the statistical power of our tests; thus, results should be interpreted as exploratory rather than conclusive. Also, although we modeled the relationship between suitability and elevation linearly, we recognize that nonlinear responses are possible, especially across broad elevational gradients. Our intention, however, was to detect general trends of increasing or decreasing suitability within each group, providing a first-order assessment of elevational effects.

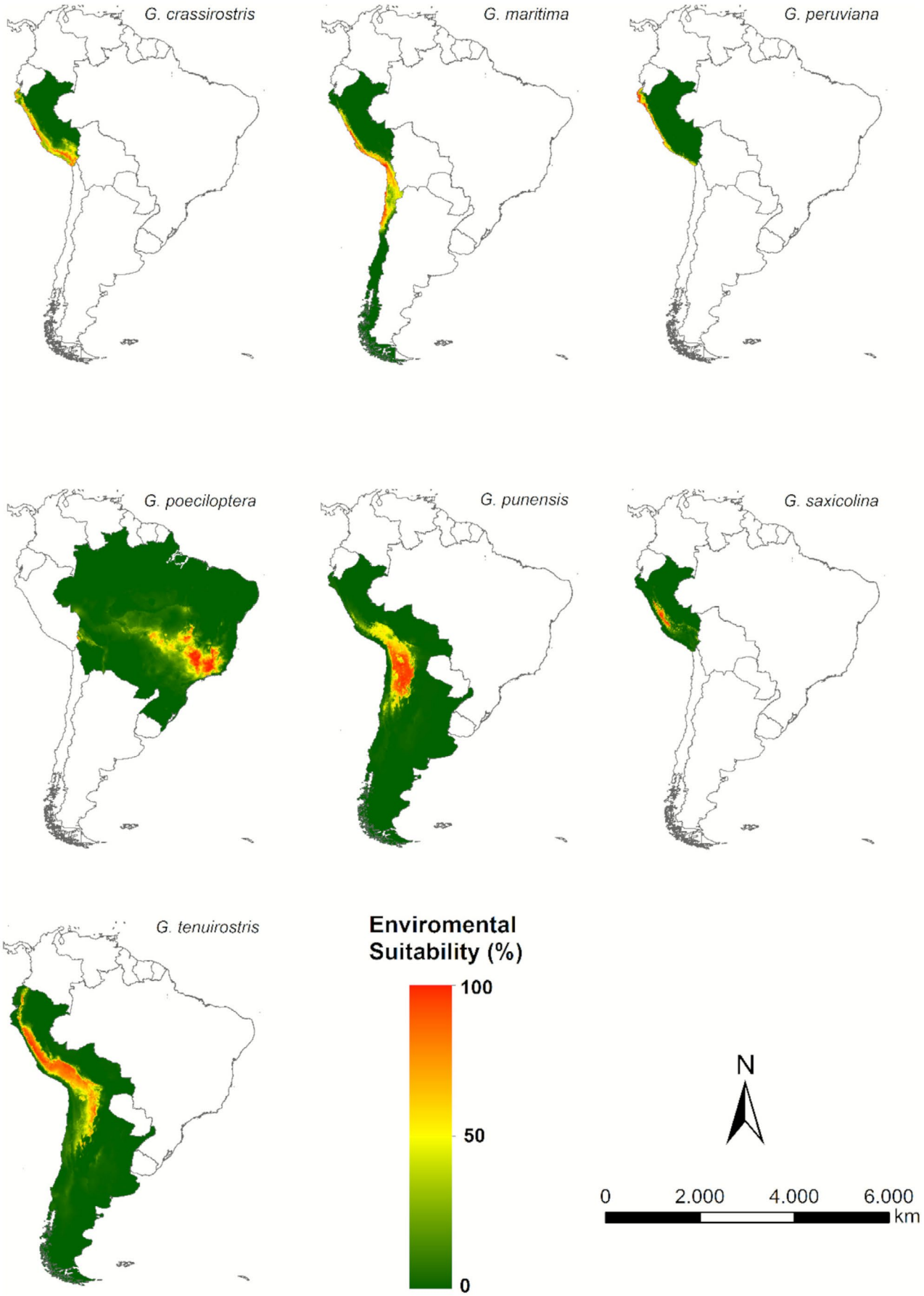

FIGURE 1 | Ensemble projections generated for the prediction of the current suitable areas for the occurrence of seven species of *Geositta* miners in South America. The maps of occurrence records can be found in the Supporting Information (Figure S1).

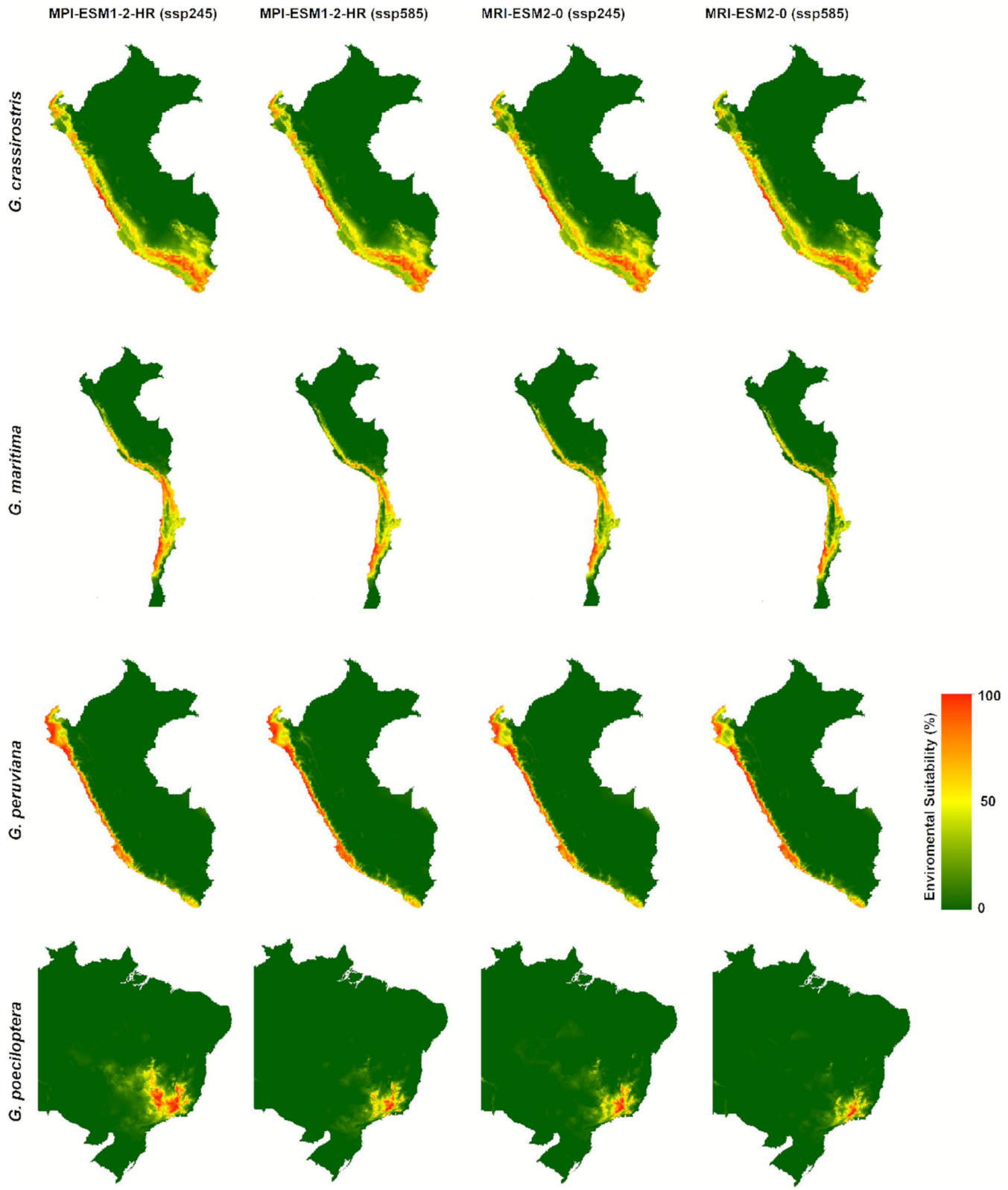

FIGURE 2 | Ensemble projections of future predictions (2061–2080) of suitable areas for the occurrence of lowland species of *Geositta* miners in South America for the optimistic (ssp245) and pessimistic (ssp585) scenarios. Models for all species in large size (including the current model) can be seen in Supporting Information (Figures S2–S5).

Other studies using different approaches found results similar to ours. Meireles et al. (2023) in their study on the distribution of *G. poeciloptera*, used a more restrictive filter for the occurrence data (e.g., data with exact coordinates and records after 1990), and more than one algorithm, but encountered similar projections to those generated in this study. Another example is the study of Arana et al. (2014), in which authors analyzed the current and future distribution of *G. peruviana*, finding projections

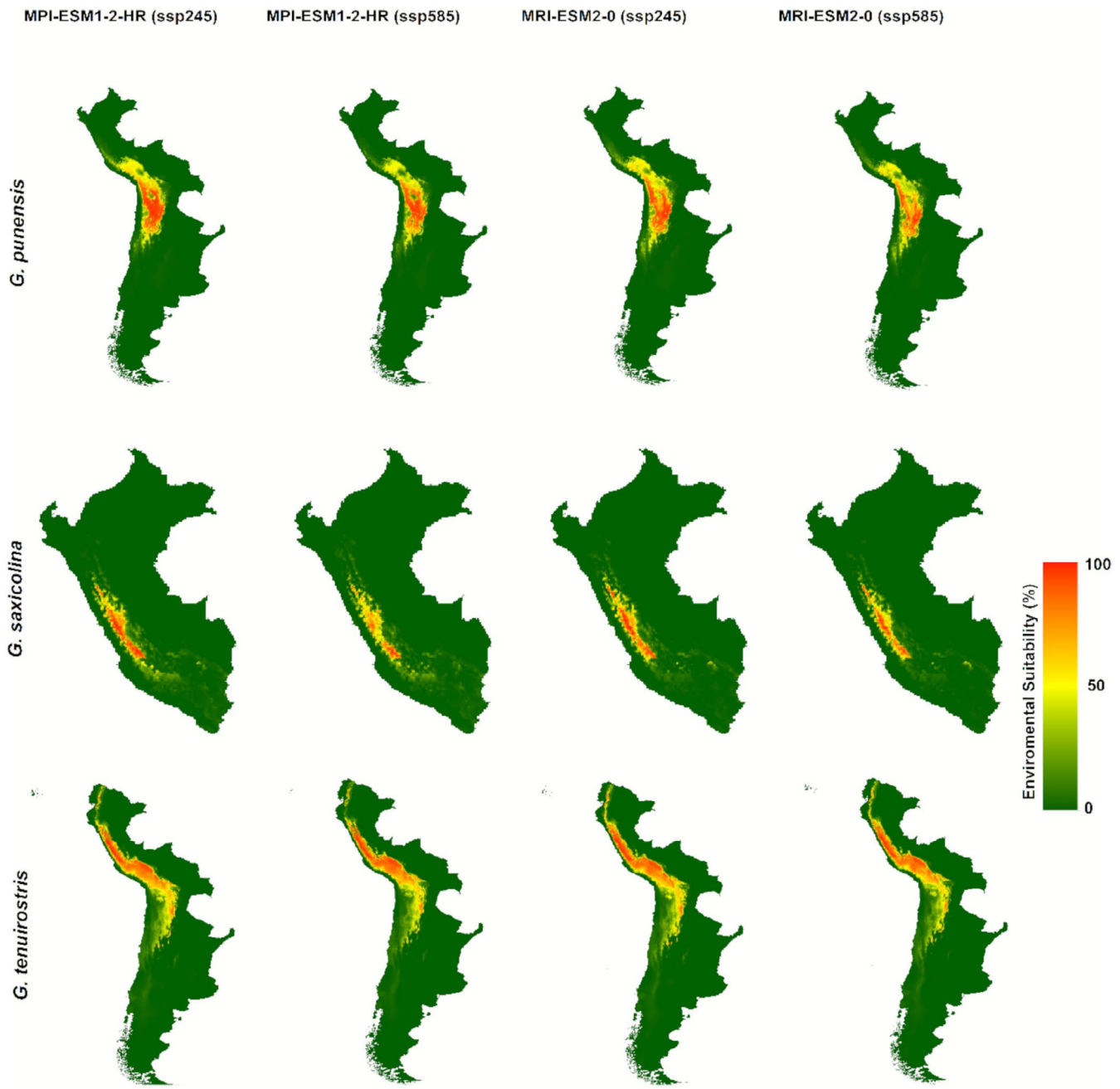

FIGURE 3 | Ensemble projections of future predictions (2061–2080) of suitable areas for the occurrence of highland species of *Geositta* miners in South America for the optimistic (ssp245) and pessimistic (ssp585) scenarios. Models for all species in large size (including the current model) can be seen in Supporting Information (Figures S6–S8).

similar to those produced in our study, including an increase in environmentally suitable areas for the species.

Although our models predict that nearly all species will lose suitable areas, highland species forced to shift to higher elevations, where available area is limited, may face an elevated risk of extinction (Raxworthy et al. 2008; Freeman et al. 2018). While this prediction is concerning, species responses must be assessed individually, taking into account not only climatic factors, but also interactions between species, human impacts (such as land use changes for agriculture and livestock), and geographic barriers (Terborgh 1971; Terborgh and Weske 1975; Borges et al. 2019; Meireles et al. 2023).

Besides climate and land use, biotic factors may also shape the distribution of *Geositta* miners. For instance, South American grasslands are strongly influenced by fire regimes and grazing, which help maintain open habitats (Gibson and Newman 2019; Hidasi-Neto et al. 2019; Hofmann et al. 2021; Borsdorf and Stadel 2015). In addition, vegetation zonation and ecological interactions may further restrict realized distributions (Fjeldså and Krabbe 1990). These aspects were not modeled here but should be considered in future studies.

The need to analyze species-specific responses to climate changes exhibited by each member of *Geositta* is illustrated by two contrasting examples. *G. peruviana*, as previously noted,

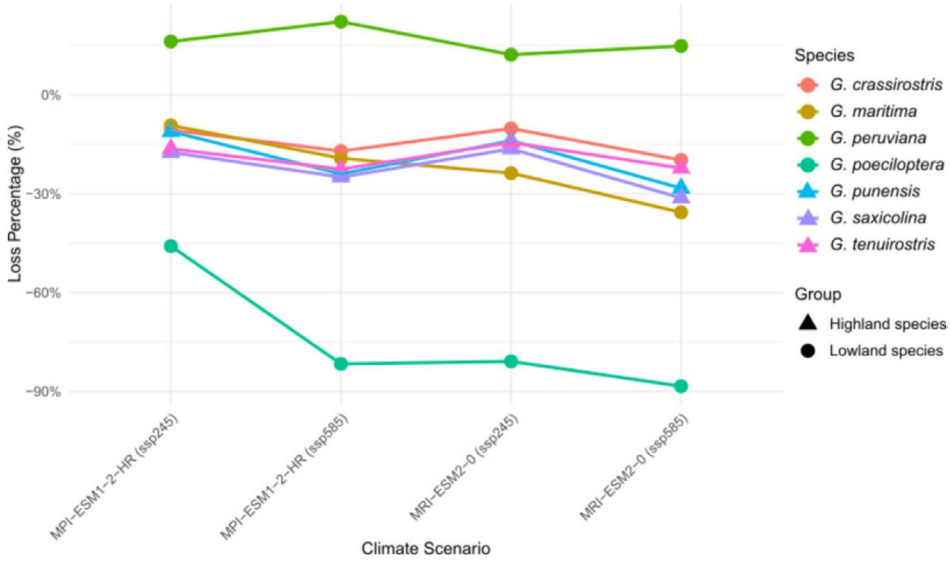

FIGURE 4 | Percentage of loss of climatically suitable area for the seven *Geositta* miners under two General Circulation Models (MPI-ESM1-2-HR and MRI-ESM2-0) and two greenhouse gas emission scenarios (Optimistic—ssp245 and Pessimistic—ssp585) in relation to the current scenario model.

TABLE 4 | Areas above 40% threshold of current and future climate suitability produced by two General Circulation Models – MPI-ESM1-2-HR and MRI-ESM2-0—in two different climate scenarios—Optimistic (ssp245) and Pessimistic (ssp585)—for the seven species of *Geositta* miners.

		Future area (km²)			
Species	**Current area (km²)**	**MPI-ESM1-2-HR (ssp245)**	**MPI-ESM1-2-HR (ssp585)**	**MRI-ESM2-0 (ssp245)**	**MRI-ESM2-0 (ssp585)**
G. crassirostris	188,530	168,321 (89.2%)	156,332 (82.9%)	169,231 (89.7%)	151,204 (80.2%)
G. maritima	278,048	252,182 (90.7%)	224,487 (80.7%)	211,961 (76.2%)	178,860 (64.3%)
G. peruviana	78,757	91,489 (116.1%)	96,243 (122.2%)	88,355 (112.1%)	90,429 (114.83%)
G. poeciloptera	518,056	280,229 (54.1%)	94,901 (18.3%)	98,858 (19.1%)	59,833 (11.6%)
G. punensis	588,612	522,955 (88.8%)	447,361 (76.0%)	506,770 (86.1%)	421,688 (71.6)
G. saxicolina	46,155	38,094 (82.5%)	34,630 (75.0%)	38,591 (83.6%)	31,698 (68.7%)
G. tenuirostris	692,296	578,718 (83.5%)	536,018 (77.4%)	592,025 (85.5%)	538,265 (77.7%)

was the only species for which models consistently predicted an expansion of its distribution under all future climate scenarios. As a species closely tied to deserts, often inhabiting areas with little or no vegetation (Fjeldså and Krabbe 1990; Gómez 2019), its range may be increasing due to desertification of neighboring habitats (Arana et al. 2014). In contrast, *G. poeciloptera*—the best-studied species in the group (see Machado et al. 2017; Meireles et al. 2018, 2021, 2023; Lopes et al. 2021, 2022) and the one most strongly associated with mesic habitats (Ridgely and Tudor 2009)—is the only species in the genus considered threatened with extinction (IUCN 2024), and is already extinct in its lowest elevational range (Meireles et al. 2023). This local extinction is driven not only by climate change but also by the widespread conversion of its grassland habitats into pastures and croplands.

The contrasting patterns of climatic suitability observed between lowland and highland species appear to be linked to vegetation zonation along the Andean elevational gradient. Highland species (*G. punensis*, *G. saxicolina*, and *G. tenuirostris*) all exhibited the expected pattern, with higher suitability in upper elevations and lower suitability in lower areas. This pattern reflects their close association with the dry puna, a montane grassland and shrubland that occurs above the wetter tree line (Fjeldså and Krabbe 1990; Ridgely and Tudor 1994; Schulenberg et al. 2010). Such vegetation zonation in the Andes along elevation is what underlies the ascending gradient of climatic suitability observed in these species.

Contrastingly, lowland species (*G. cassirostris, G. maritima* and *G. peruviana*) showed an inverse pattern, with higher suitability in lower areas and lower suitability in higher areas. These species occur at much lower elevations along the Peruvian coast and Andean foothills (Fjeldså and Krabbe 1990; Ridgely and Tudor 1994; Schulenberg et al. 2010). On the dry western slopes of the Andes, their distribution is interrupted by the Lomas formations, a fog-dependent vegetation belt that extends from Peru to Chile between 200 and 1000 m of elevation (Dillon

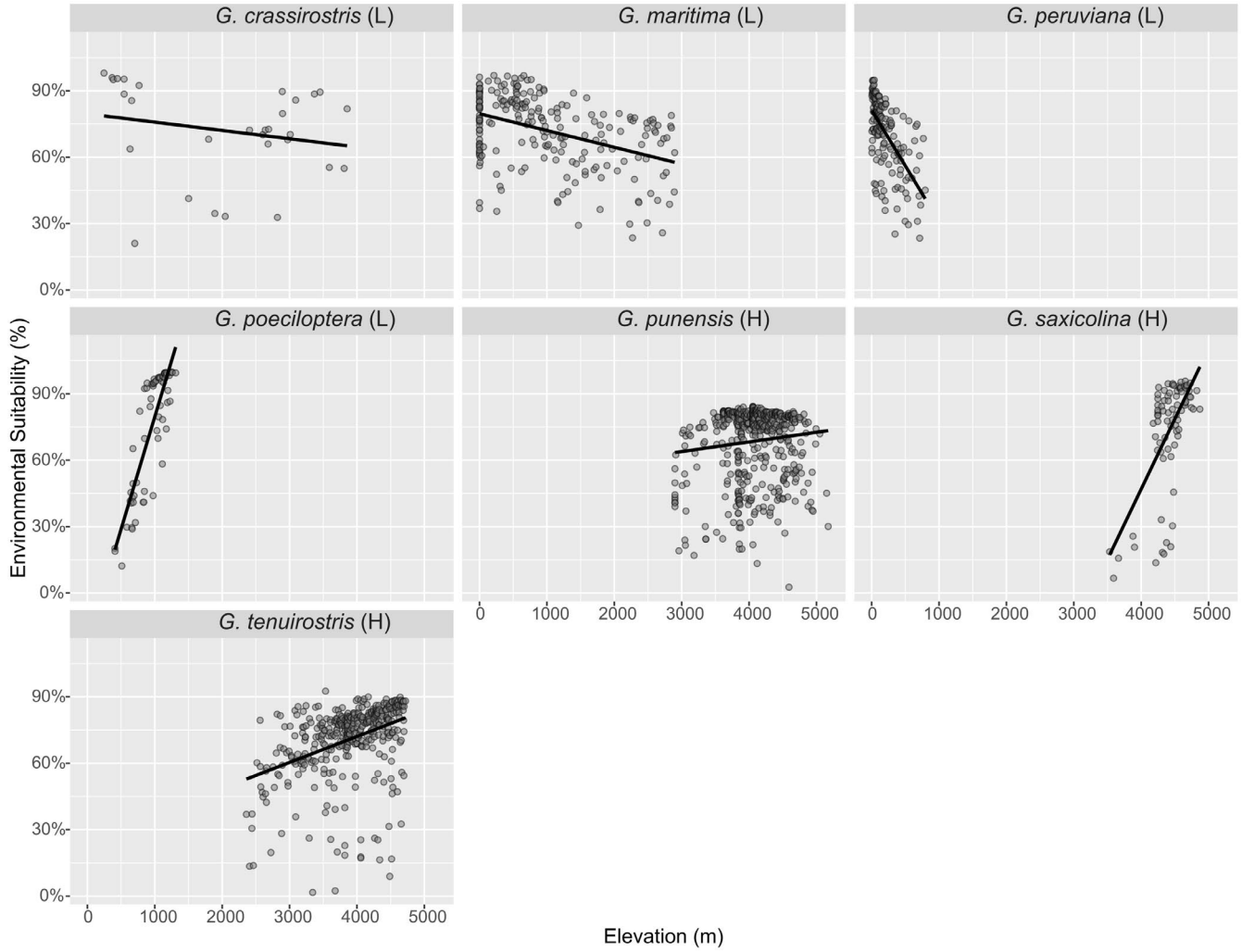

FIGURE 5 | Current climate suitability for all occurrence records of the lowland (L) and highland (H) species of *Geositta* miners studied in relation to elevation.

et al. 2003; Borsdorf and Stadel 2015). Characterized by greater humidity and distinct plant communities, the Lomas act as a biogeographic barrier, separating the dry coastal lowlands and foothills from the deserts, shrublands, and grasslands of the high Andes. This isolation helps explain the divergent patterns of climatic suitability between lowland and highland *Geositta* species.

G. poeciloptera, although recorded at lower elevations, showed the same pattern as its highland congeners, with more climatically suitable areas located at higher elevations. This pattern occurs because the areas inhabited by the species are geographically distant and shows different ecological characteristics from the Andes Mountains. The higher elevations in the Cerrado were originally covered by seasonally dry natural grasslands and savannas, with less fertile soils and little woody vegetation. Contrastingly, the lower areas were originally covered by seasonal forests, with more fertile soils (Meireles et al. 2018; Lopes and Silva 2024).

Members of *Geositta* miners are associated with dry environments, such as the seasonally dry open grasslands of the Brazilian Cerrado (Machado et al. 2017; Meireles et al. 2023) and deserts, semi-deserts, and dry grasslands along the Pacific Coast and the Andes (Fjeldså and Krabbe 1990; Remsen Jr 2003; Ridgely and Tudor 2009). In the Cerrado, the drier open grasslands are usually found at the top of the central plateau, where the elevation, shallow soils, and exposure to the sun create more arid conditions favorable to these species. On the western slope of the Andes, the mountain's topography and weather patterns create a more varied distribution of dry environments. On the coast, cold currents generate coastal deserts that are home to lowland species from arid climates. At the top of the mountains, arid conditions occur at much higher elevations than those observed in the central plateau of Brazil (Borsdorf and Stadel 2015), providing habitats for highland species. Between these two zones, the middle range of the Andes is characterized by a wetter climate, due to increased precipitation, creating a significant contrast with the dry areas at the extremes (Rundel et al. 1991; Péfaur 1982; Dillon et al. 2003; Borsdorf and Stadel 2015).

5 | Conclusion

This study highlights the urgent need for coordinated and evidence-based actions to protect the biodiversity of open

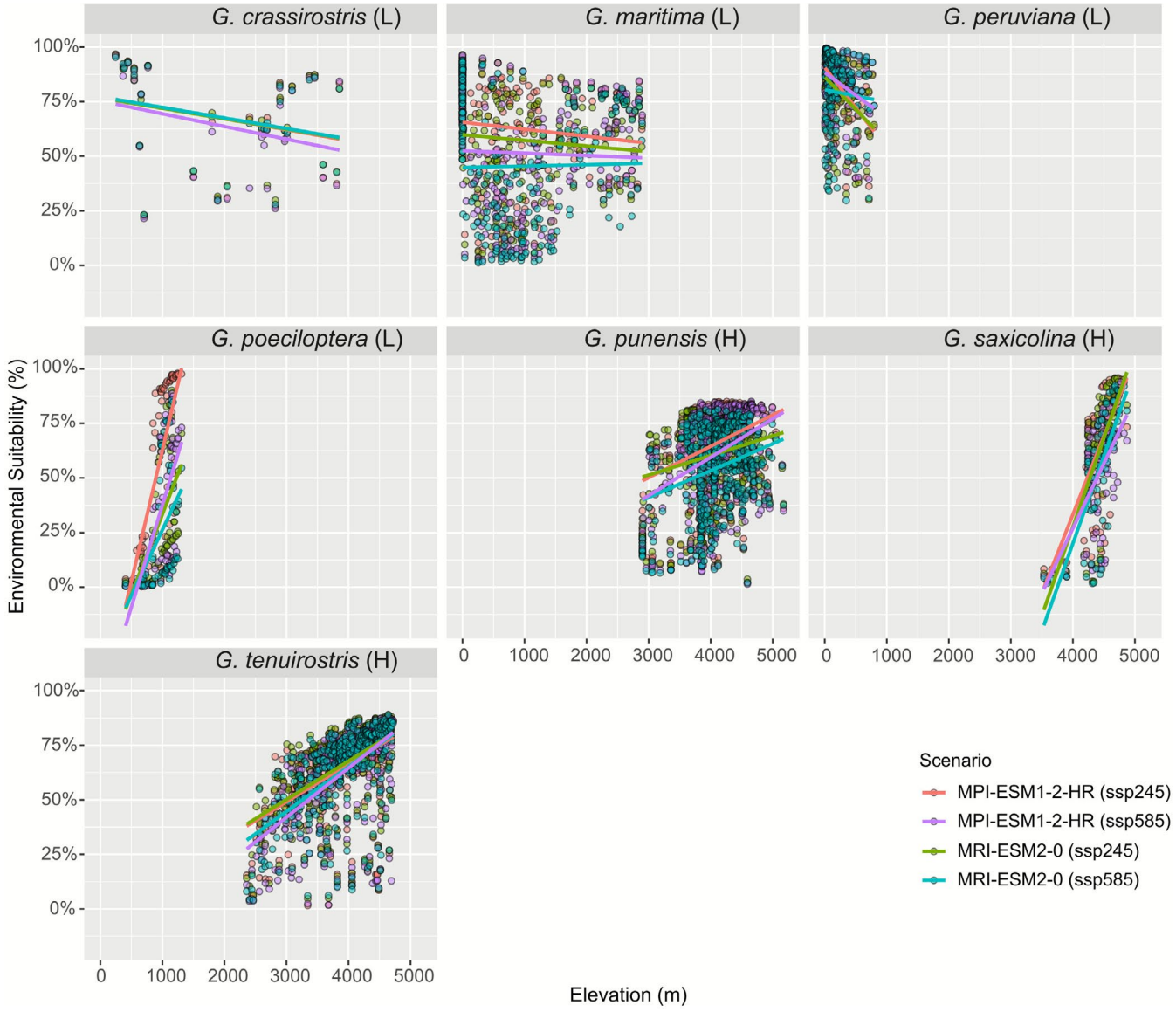

FIGURE 6 | Future climate suitability for all occurrence records of lowland (L) and highland (H) species of *Geositta* miners in relation to elevation for two GCMs (MPI-ESM1-2 and MRI-ESM2-0) and two greenhouse gas emission scenarios (Optimistic ssp245 and Pessimistic ssp585).

habitats in face of climate change, as demonstrated by species in the genus *Geositta*. Our findings reveal that most species in this genus are expected to experience significant reductions in climatically suitable areas in the near future, with the extent and speed of these losses directly depending on the effectiveness of greenhouse gas reduction policies (IPCC 2022).

Highland species suffer from higher risk of extinction due to geographic constraints, limiting their ability to migrate beyond mountain tops and find suitable areas (Raxworthy et al. 2008; Freeman et al. 2018). For instance, *G. poeciloptera* illustrates this vulnerability by having already lost crucial low-elevation habitats and now being restricted to middle and high elevations in the Brazilian Cerrado. Future projections suggest that the species will increasingly be confined to higher elevations existent in its distribution (Marini et al. 2009; Meireles et al. 2023).

In the Andean region, the complex elevational zonation creates a mosaic of vegetation types that significantly influences species distribution and climate suitability (Rundel et al. 1991; Péfaur 1982; Dillon et al. 2003; Borsdorf and Stadel 2015). Lowland species, which prefer drier environments, may struggle to adapt to wetter conditions of higher elevations due to these variations (Fjeldså and Krabbe 1990; Remsen Jr 2003; Ridgely and Tudor 2009; Machado et al. 2017).

Analyzing climatic niches for each species individually is crucial, but it is also necessary to consider the complex interplay of climatic, anthropogenic (e.g., land use changes), and biotic (i.e., species interactions) factors to fully understand the threats these birds face (Borges et al. 2019; Meireles et al. 2023; Forero-Medina et al. 2011). Future research should focus on long-term monitoring of climate change impacts and explore strategies beyond habitat restoration to ensure the

conservation of these species. However, we can conclude with this study that to mitigate the impacts of climate change on *Geositta* miners, it is essential to implement immediate and effective environmental policies. Prioritizing the protection and management of high-elevation habitats is critical due to the dispersal capacity of these species. Additionally, preserving transitional vegetation zones and reducing anthropogenic pressures such as land conversion and habitat manipulation are vital actions to safeguard these species.

Author Contributions

R.C.M., L.E.L., G.R.B. and R.S. conceived the ideas and designed the methodology; R.C.M. and G.R.B. collected the data; R.C.M., G.R.B. and R.S. analyzed the data; R.C.M., L.E.L. and R.S. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in the Zenodo repository https://doi.org/10.5281/zenodo.14270576 and on public data platforms stated in the methods.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figures S1–S8:** btp70136-sup-0001-FigureS1-S8.docx.