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Impact of global change on the distribution of mountain mammals and birds

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Abstract

Climate change and land-use changes are key drivers of global biodiversity loss. Many species are shifting to higher elevations or latitudes in response to global warming, often encountering unfavorable land-use conditions during the shift. These changes can lead to reduced range size and increased extinction risks, particularly for mountain species that are often confined to narrow high-altitude habitats. Predicting future distributions of mountain species requires accounting for their bioclimatic responses, topographical distribution, land-use preferences, and ability to colonize new areas via dispersal. We projected the future distribution of 34 mountain mammal and 361 nonmigratory mountain bird species in 2050 under different emission scenarios. Using species distribution models (SDMs) that incorporated topography, climate, and land-use data, we assessed the impacts of global change on species' ranges across mountain regions worldwide and compared different emission scenarios to clarify the contributions of climate, land-use change, and dispersal to shaping future distributions. Species were projected to experience greater range loss under the high-emissions scenario than under the low-emissions scenario (16% higher on average). Dispersal played a key role in range shifts: when dispersal was included in the model, the number of birds that shifted their range increased by 144%. The most severe range losses were projected for species located in Central and South America and Oceania, whereas European mountains showed fewer losses, highlighting substantial regional differences in vulnerability. When land use was also considered, range dynamics remained stable, showing climate as the primary driver of mountain species distribution change. Our findings emphasize the importance of considering dispersal capacity when assessing climatic biodiversity risks in mountains. Our results highlight the urgency of applying regional strategies to establish ecological corridors, improve connectivity, and manage habitats to conserve the unique biodiversity of mountains.

KEYWORDS
climate change, dispersal, distribution, land-use change, mountain biodiversity, scenarios, species distribution model

INTRODUCTION

Human activities have transformed ecosystems globally, driving extensive changes in land cover (Venter et al., 2016), biogeochemical cycles (Battye et al., 2017), and climate (IPCC, 2023). These human-driven changes are key drivers of global biodiversity loss (e.g., IPCC, 2021; Newbold, 2018; Pereira et al., 2024; Scheffers et al., 2016), with substantial impacts on the structure and composition of ecological communities (Di Marco et al., 2019; Gaüzère et al., 2023; Newbold et al., 2015). Biological responses to these pressures are manifold, with species shifting their geographic ranges (Chen et al., 2011;

Di Febbraro et al., 2023; Fialas et al., 2025), experiencing population declines (Stephens et al., 2016), and altering their phenology, which lead to cascading effects across ecosystems (Thackeray et al., 2016).

Mountain ecosystems are especially vulnerable to climate change due to their high relief and elevational gradients, which expose mountain biodiversity to a large amount of change (Diaz et al., 2003; Dragonetti et al., 2024; IPBES, 2019; Pepin et al., 2022). Historical and projected land-use changes in addition to climate change represent a major driver of biodiversity loss (Dragonetti et al., 2024). Almost 60% of global mountain areas are experiencing intense human pressures, especially at lower and intermediate elevations (Elsen et al., 2020). Although mountains cover approximately 20% of the Earth's terrestrial surface (Snethlage et al., 2022), they host one-third of the world's terrestrial species (Körner & Spehn, 2002) and contain half of the planet's biodiversity hotspots (Chape et al., 2008). These ecosystems also provide critical ecosystem services to both mountain and lowland human populations (Locatelli et al., 2017; Martín-López et al., 2019; Viviroli et al., 2020). Human activities in mountains vary considerably across different regions, influenced by economic development and elevation gradients (Dragonetti et al., 2024; Nogués-Bravo et al., 2007; Theobald et al., 2024). In many low-income countries, rapid population growth in mountain areas has intensified land-use changes, including urbanization and agricultural expansion (Capitani et al., 2019; Guarderas et al., 2022; Hailemariam et al., 2016; Liu & Chen, 2006). These pressures affect species in different ways, such as reducing species richness and diversity (Newbold et al., 2015; Vellend et al., 2013) via climate-induced shifts in species distribution (Elsen et al., 2020; Mantyka-pringle et al., 2015). Conversely, in some high-income regions, such as the European Alps, depopulation and land abandonment are leading to the cessation of traditional land-use practices, resulting in dramatic ecological consequences for many species adapted to coexist with those practices (Daskalova & Kamp, 2023; Dragonetti et al., 2024). Patterns of regionalized human impacts are reflected in species risk patterns, yet they are still underexplored globally.

Many mountain species have limited climate tolerances, raising concerns about their capacity to adapt to or to cope with rapid climate changes (Elsen & Tingley, 2015; Pacifici et al., 2018). Mountain species often face a high risk of extinction due to their restricted geographic ranges and narrow endemism (e.g., La Sorte & Jetz, 2010; McCain & Colwell, 2011; Thuiller et al., 2005). These species are increasingly shifting to higher elevations or latitudes to escape rising temperatures (Di Marco et al., 2023; Elsen & Tingley, 2015; Moritz et al., 2008). However, such upward movements frequently result in further range contractions and higher vulnerability, particularly for species confined to isolated, high-altitude habitats, where continued warming can create an "escalator to extinction" (Anderson & Wadgymar, 2020; Freeman et al., 2018; Hetem et al., 2014). Although these upward shifts often lead species into more favorable climates, their movements are frequently limited by topographical barriers—such as steep slopes and rugged terrain—as well as by habitat availability and connectivity (Årevall et al., 2018; Elsen et al., 2020). Even if climatically suitable areas emerge at higher elevations, the projected rate of land-cover change and the presence of fragmented landscapes may act as critical limits, determining whether these potential refugia can be effectively reached and colonized (Årevall et al., 2018; Dragonetti et al., 2024).

Predicting future distributions for mountain species thus requires not only an understanding of species' responses to climate change but also a detailed consideration of their topographical limits and land-use preferences (Elsen et al., 2020; Thuiller et al., 2014). Species distribution models (SDMs) are used to predict species' potential habitats based on environmental preferences and are widely used to project how future environmental changes will impact species distributions (Elith & Leathwick, 2009; Guisan & Thuiller, 2005; Guisan & Zimmermann, 2000). These tools can be used to anticipate future change in the distribution of mountain species and their consequent risk of decline (Mancini et al., 2024). When using these models, it is crucial to account for a species' dispersal capacity to track the shifting climate. Considering dispersal is critical to realistically projecting a species' ability to reach new areas, given the constraints imposed by both natural barriers and human-altered landscapes (Barbet-Massin et al., 2012; Bateman et al., 2013; Thuiller et al., 2019; Visconti et al., 2016).

In this study, we provide a new comprehensive assessment of the distribution change in mountain mammals and birds by 2050 that considers climate change, land-use change, and dispersal constraints. We focused on these taxa because their well-documented distributions allow for more accurate predictions (Pacifici et al., 2017; Visconti et al., 2016). We used ensemble SDMs to analyze the risks posed by different socioeconomic and emission scenarios and explicitly accounted for the regulating effect of dispersal. With our analysis, we intended to provide useful information to support conservation planning and decision-making, such as that related to meeting Paris Agreement targets for certain mountain species and identifying species that could benefit from improved connectivity among protected areas planned for expansion under the Kunming–Montreal Global Biodiversity Framework (CBD, 2021). Although several studies have compared the relative importance of different drivers of change at local or regional scales, no comparable assessments have been conducted at the global scale (Ureta et al., 2022). Our results can help identify potential climate refugia and guide the strategic expansion or adjustment of protected areas, offering practical tools for anticipating species' future needs and informing long-term conservation actions.

METHODS

Selection of species and distribution data

We used SDMs to identify potential suitable areas for mountain mammal and bird species, considering how anthropogenic pressures and topography might affect the size and accessibility of these areas in the future (Figure 1). To map mountainous areas of the world, we used the Global Mountain Biodiversity Assessment inventory (Snethlage et al., 2022). This inventory

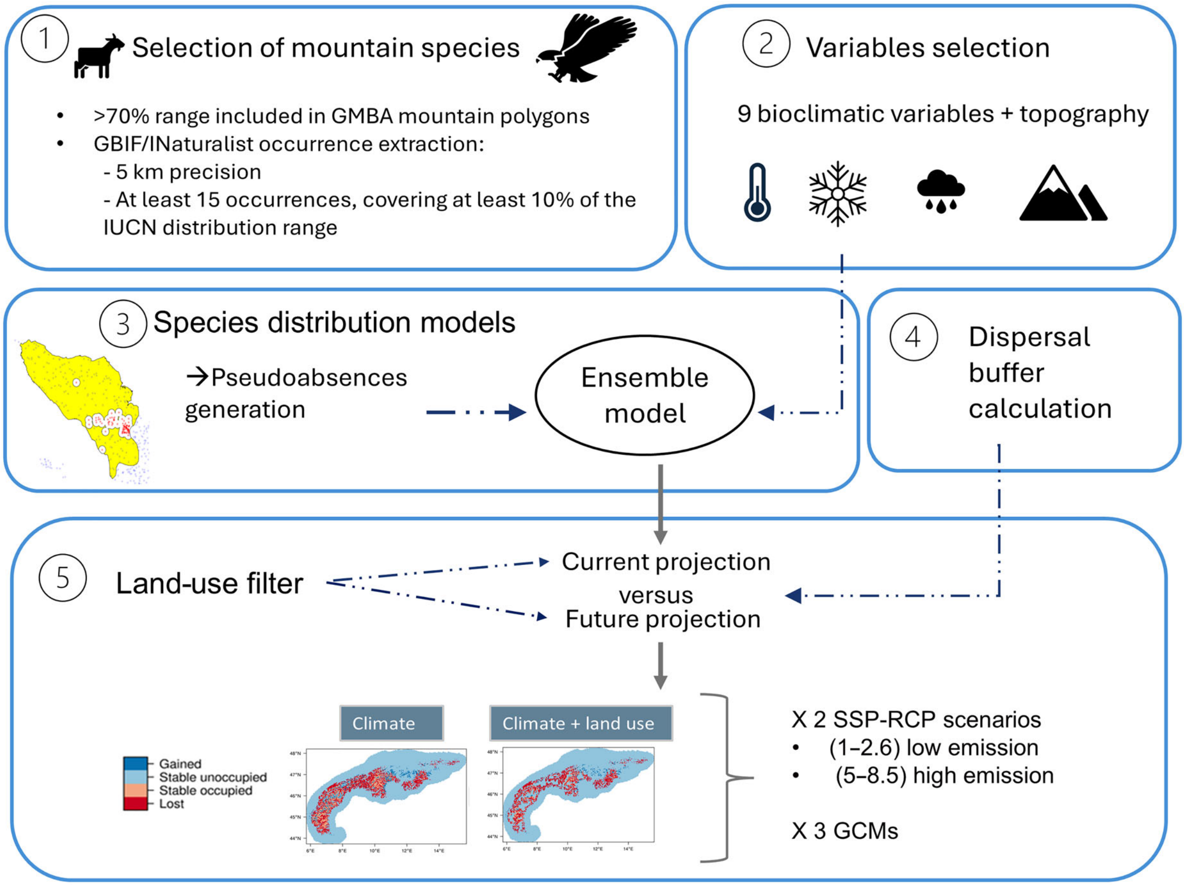

FIGURE 1 Framework of the methodology for projecting climate- and land-use-driven change in mountain species distribution (GMBA, Global Mountain Biodiversity Assessment; GBIF, Global Biodiversity Information Facility; IUCN, International Union for Conservation of Nature; SSP-RCP, Shared Socioeconomic Pathway-Representative Concentration Pathway; GCMs, global circulation models).

defines the ruggedness of terrain by measuring the difference between the highest and lowest elevations (in meters) around specific points, using eight different circular search windows, called neighborhood analysis windows, that range in size from approximately 250 m to 5 km.

We classified mountain ranges into 13 different regions, grouping them by continents and latitude, using the Holdridge life zone classification: America high-latitude mountains in the Northern Hemisphere (high North America); America mid-latitude mountains in the Northern Hemisphere (middle North America); America low-latitude mountains (low America); America mid-latitude mountains in the Southern Hemisphere (middle South America); Europe high-latitude mountains (high Europe); Europe mid-latitude mountains (middle Europe); Africa mid-latitude mountains in the Northern Hemisphere (middle North Africa); Africa low-latitude mountains (low Africa); Africa mid-latitude mountains in the Southern Hemisphere (middle South Africa); Asia high-latitude mountains (high Asia); Asia mid-latitude mountains (middle Asia); Asia low-latitude mountains (low Asia); and Australia and New Zealand (Oceania) (Dragonetti et al., 2024; Nogués-Bravo et al., 2007) (Appendix S1). We then defined mountain species as those with at least 70% of their geographic range (Birdlife International, 2022; IUCN, 2022) included within the above-defined mountain polygons (Snethlage et al., 2022). The 70% threshold ensured that the majority of a species' range falls within mountain areas (Amori et al., 2019), without losing significant taxonomic representation (for instance, applying a threshold of 80% would reduce our initial sample by 494 species). When overlapping species range maps with mountain polygons, we only considered the parts of the ranges considered as extant or reintroduced by the International Union for Conservation of Nature (IUCN) (IUCN, 2022). For birds, we focused on species classified as nonmigratory by the IUCN to allow a more direct comparison with mammal species. We thus obtained an initial sample of 1197 species of mountain mammals and 2159 mountain birds.

For each selected species, we extracted occurrence records from the Global Biodiversity Information Facility (GBIF) and iNaturalist from 1990 to present day (GBIF.org, 2023; iNaturalist, 2023). We used CoordinateCleaner (Zizka et al., 2019) within the R environment (R Core Team, 2024) to clean the occurrences by removing those with latitude and longitude values exchanged and duplicate records, excluding points closer than 10 km to country capitals (to exclude biased occurrences but to retain the reliable ones located in a capital's surroundings), and excluding coordinates farther than 500 km from the species IUCN geographic range and with an uncertainty >5 km. We opted for an uncertainty threshold of >5 km as a compromise between reducing positional error and retaining sufficient occurrence data (Beck et al., 2014). Filtering occurrences in a stricter way (e.g., those with an uncertainty <1 km) would have significantly reduced the number of species analyzed (especially for mammals).

We created a grid of 30 arc-second resolution (~1 km at the equator), matching the resolution of the climatic rasters, and we overlapped it with species occurrences. We then considered presence as all grid cells including at least one occurrence. We selected species with at least 15 presence cells to have a good representation of the suitable habitat of the species and have sufficient quality in the model's predictions (Pili et al., 2025; Santini et al., 2021; van Proosdij et al., 2016; Wisz et al., 2008). This number of occurrences was chosen to ensure sufficient modeling power for mountain species, which are often range-restricted, while retaining as many species as possible in the analyses. We validated the 15-occurrence threshold through a sensitivity test: increasing the N of occurrences to 20 yielded consistent results and model accuracy (Appendix S14).

We further filtered the species to ensure their occurrences were not excessively clustered, leading to biased representation of a small portion of their distribution range (Hernandez et al., 2006; van Proosdij et al., 2016). To implement this action, we created a coarse grid of a 50-km resolution based on species IUCN Red List distributions (IUCN, 2022) and checked how many grid cells contained at least one occurrence point. We only retained species with at least 10% grid cells represented, as a balance between range representation and data availability, thus preventing excessively biased models while maximizing taxonomic and geographic representation.

To ensure the accuracy of our distribution change estimates, we further filtered our species sample by excluding species with highly disjunct ranges if available occurrences did not cover all the isolated portions of the range. Starting from an initial sample of 1197 species of mammals and 2159 species of birds with at least 70% of their range included in mountain polygons, we retained 34 mountain mammals and 361 nonmigratory mountain birds to be modeled.

We examined the elevational distribution of species occurrences to ensure that species were not completely restricted to high-elevation areas poorly accessible by humans. Long-term human activities at lower elevations (e.g., land conversion, habitat loss, and urbanization) can act as a nonrandom selective force, leading to the loss of the low-elevation portion of a species' range while maintaining higher-elevation populations. We calculated the 5th percentile of elevation values across the occurrence points of each species (Appendices S2 & S3). Our selected species were not, in the vast majority of cases, restricted exclusively to higher altitudes, which means the risk of niche truncation (especially in the warmest part of the range) was very low in our sample.

We grouped mountain species based on their presence into the 13 different mountain areas (Appendix S1) depending on where the larger part of the species' range was located to enable comparisons across these regions. Our final selection of 395 species covered 11 out of 13 mountain regions classified by continent and latitude (Appendix S4). We could not select species suitable for high North America, and high Europe was the only mountainous region that lacked mountain species (i.e., species with 70% or more of their range exclusively within its boundaries). Birds were much better represented in our analysis than mammals, showing a higher percentage of mountain species analyzed. The most represented birds orders in our analysis were Passeriformes (n species = 243 out of 1173 total mountain species), Caprimulgiformes (n species = 40 out of 203), and Galliformes (n species = 19 out of 113), whereas for mammals, the most represented orders were Rodentia (n species = 18 out of 711), Primates (n species = 5 out of 72), and Cetartiodactyla (n species = 5 out of 65).

Selection of variables

We focused on variables that have a strong influence ecologically on the distribution of mountain birds and mammals (Mancini et al., 2025). We extracted nine bioclimatic variables from CHELSA v2.1 at a 1-km resolution (Karger et al., 2017): mean annual temperature, temperature seasonality, annual precipitation amount, precipitation seasonality, frost days, growing degree days above 0°C, snow cover days, snow water equivalent, and net primary productivity. Temperature and precipitation are key environmental variables that influence physiological and ecological conditions (Biancolini et al., 2024). Temperature variations can affect metabolic functions and reduce reproductive success (Mitchell et al., 2018; Pendlebury et al., 2004), whereas precipitation directly affects water availability, which is critical for survival. Furthermore, both factors directly influence the abundance of vegetation and prey species (Gillman et al., 2015). Seasonality is crucial in mountain environments, influencing, among other ecological processes, reproductive seasons (Bronson, 2009; Löffler & Pape, 2019; Scridel et al., 2018). We considered snow-related variables as the quality and quantity of snow have a direct impact on organisms by altering the physical environment (Williams et al., 2015). Snow cover acts as an insulator, protecting plants and invertebrates from frost during the coldest months, thus influencing the survival of other species that depend on them (Scridel et al., 2018). Net primary productivity and frost days were instead considered due to their great influence on herbivores, among other taxa (Sanders-DeMott et al., 2018; Schmidt et al., 2018). We also included a topography variable, that is, the coefficient of variation of a digital elevation model at a 1-km resolution, extracted from the CGIAR-CSI SRTM 90 m database (Jarvis et al., 2008). Topographic heterogeneity plays a key role in limiting dispersal and movement in complex landscapes such as mountains (Elsen & Tingley, 2015; Elsen et al., 2020; Li et al., 2016), albeit at different temporal and especially spatial resolutions, depending on the species.

To prevent collinearity among predictors, we performed variance inflation factor (VIF) analysis (Naimi et al., 2014) through a stepwise procedure, retaining only variables with VIF <10 for subsequent modeling (Dormann et al., 2013; Naimi & Araújo, 2016). We fixed mean annual temperature, as this variable is ecologically meaningful for all species and one of the key indicators of global climate change, in the model selection.

We considered 1995 (1981–2010 time interval) as the reference year for the present period, whereas we used 2050 (2041–2060 time interval) for the future, considering three different global circulation models (GCMs: ukesm1-0-ll, mpi-esm1-2-hr, and gfdl-esm4) from the Coupled Model Intercomparison Project 6 (CMIP6) under two emission scenarios, namely, Shared Socioeconomic Pathways (SSP)-Representative Concentration Pathways (RCPs) (i.e., SSP-RCP 1–2.6 and SSP-RCP 5–8.5) (Tebaldi et al., 2021). The three GCMs were selected due to their significant differences in oceanic and atmospheric components that represent a wide range of process responses from moderate (MPI-ESM1-2-HR) to stronger (GFDL-ESM4, UKESM1-0-LL). Their climate sensitivities reflect the broader CMIP6 ensemble, from lower (GFDL-ESM4, MPI-ESM1-2-HR) to higher (UKESM1-0-LL) ends, capturing a diverse array of possible climate responses and uncertainty in future projections (Cimatti et al., 2025).

We chose scenario SSP-RCP 1–2.6 as it depicts a sustainable socioeconomic pathway associated with low emissions, which limit global warming to below 2°C above preindustrial temperatures by 2100 (i.e., compliant with the Paris Agreement). We then selected scenario SSP-RCP 5–8.5 to represent a high-emissions pathway, achieving a global warming of 3.3–5.7°C. We aggregated the binarized future projections of the three GCMs under each scenario through score averaging (i.e., we assigned a final score of 1 when at least two of the three GCMs showed a value of 1, and 0 otherwise).

Species distribution models

We modeled present-day species distributions with an ensemble model using the biomod2 package (Thuiller et al., 2024). We generated a set of pseudoabsences for each species, in proportion equal to 10 times the number of presences outside biomod2 (Mancini et al., 2024) (Appendix S5). We sampled 20% of the pseudoabsences randomly within the species IUCN range and the remaining 80% from outside the species range but in the same biogeographical realm (Olson et al., 2001). For this latter selection, we employed a decay probability function to take into account the spatial sampling bias, where the likelihood of sampling a point is reduced as the distance from the range border increases (Hof et al., 2018):

$$P\text{ sampling} = \frac{1}{\left(\text{distance from range } (m)/1000\right)^2}. \quad (1)$$

This strategy highlighted the contrast between presence areas that include unoccupied areas that are reachable by the species and areas that are unlikely to be colonized in the near future, even if in the same biogeographic realm domain. This approach functions as a form of restricted background or background thickening (Vollering et al., 2019), limiting sampling to areas with comparable effort, and by restricting selection within the same biogeographical realm, this method prevents the inclusion of spurious absences in regions that are outside a species' accessible ecological range (Barve et al., 2011). We prevented the selection of pseudoabsences from within a distance of 10 km around presence points to reduce spatial autocorrelation between presences and absences. We then extracted the values of the bioclimatic variables from each presence and pseudoabsence point for the present (1981–2010) and future (2041–2060).

To assess areas of potential model extrapolation, we used the dismo package to calculate the multivariate environmental similarity surface (MESS) index (Hijmans et al., 2010). The MESS analysis was performed both within the current time period (comparing presence training data against the current climatic data within the area of projection) and under future scenarios (comparing presence training data against future climate projections).

We used species' presence (1) and pseudoabsence (0) as a binary response variable for the following models: generalized linear model (GLM), generalized additive model (GAM), generalized boosting model (GBM) (Burges, 2010), random forest (Breiman, 2001), and MAXNET (Phillips & Dudík, 2008). Using diverse algorithms increases predictive robustness by exploiting their complementary strengths, reducing overfitting, and lowering variance. Regression-based models (GLM, GAM, and MAXNET) provide interpretable ecological relationships, whereas machine learning methods (RF and GBM) better capture complex nonlinear patterns and interactions, improving predictive accuracy in heterogeneous or noisy datasets. Thus, the ensemble better captures complex ecological patterns than single models alone. We used biomod2.0 default settings for individual models because intensive fine-tuning can lead to overfitting in model selection (Cawley & Talbot, 2010).

We performed a spatial block validation, generating four bins based on latitudinal and longitudinal bands that divide occurrence localities as equally as possible (bottom-left, bottom-right, top-left, and top-right) in biomod2 to evaluate model performance (Muscarella et al., 2014). As we did not have true absence data, we used an evaluation metric designed for presence-only data: the Boyce index (Boyce et al., 2002). The Boyce index assesses model performance by correlating predicted/expected (P/E) ratios with suitability bins. Values range from −1 to +1; positive results indicate a strong match between predictions and observed presences, whereas values near 0 or below reflect random or poor performance. We chose the Boyce index because it correlates strongly with presence/absence evaluators while remaining insensitive to species prevalence (Hirzel et al., 2006). Only single models with an index value above 0.5 were retained in the ensemble to ensure that all selected models showed good predictive performance and a reliable positive relationship between predicted suitability and observed presences (Boyce et al., 2002). At this step, we excluded three species (black-headed nightingale-thrush [*Catharus mexicanus*], slaty-backed chat-tyrant [*Ochthoeca cinnamomeiventris*], and the Chilean pigeon [*Patagioenas araucana*]) because the evaluations of four out of five models for these species had a Boyce index <0.5; thus, we were not able to build an ensemble.

To combine the predictions of the selected models into an ensemble within biomod2, we used two different techniques: median, which we reported as the result of the ensemble, and coefficient of variation, to represent the uncertainty across the predictions. Finally, we reported the Boyce index of the aggregated predictions, as well as their true skills statistics (TSS) and F1 score (Allouche et al., 2006; Powers & Ailab, 2011).

The predictive importance of each variable was calculated within biomod2, by comparing two prediction maps, one with the original variables and one with one variable randomly shuffled. The importance was thus calculated as 1 − the correlation between these two maps, calculated with Pearson's coefficient.

To account for potential adaptive capacity to climate change (sensu Foden et al., 2013), after we trained the models using current climate conditions, we projected the suitability of future climate conditions both inside the current species geographic range and in the area around the range that the species could theoretically reach through dispersal. We calculated a buffer of dispersal around each species' range, according to Mancini et al. (2024):

$$\text{Buffer dispersal (km)} = \frac{30\ \text{years}}{\text{age first reproduction}} \times \text{mean dispersal (km)}. \quad (2)$$

For mammals, we extracted the age of first reproduction and mean dispersal from the COMBINE dataset (Soria et al., 2021), whereas for birds, we extracted the age of first reproduction from Bird et al. (2020). Due to lack of mean dispersal information data for birds, we used the model in Weeks et al. (2022) to predict the natal dispersal based on the hand–wing index, which was extracted from the Avonet database (Tobias et al., 2022).

Finally, we compared the binary current projection with the binary future projection with the function BIOMOD_RangeSize in biomod2, using the formula:

$$\text{Future projection} - 2 \times \text{current projection}. \quad (3)$$

Thus, we estimated the change in the range of the species (in terms of range lost or gained) according to both emission scenarios. We identified species with a range shift as the species with both a percentage of range lost and range gained (via dispersal) higher than 20% (Di Marco et al., 2021; Dragonetti et al., 2023). Among these range-shifting species, we selected those with a higher percentage of range loss compared with range gain (≥20%), as these species will experience a minimum range shrinkage of a 20%. This threshold is also ecologically meaningful, as a 20% range reduction can qualify a species as near threatened under IUCN criterion A3 (Mancini et al., 2024).

Species land-use preferences

To understand how land-use change alters climate-driven range change, we added a land-use suitability mask to both the current and future climate projections of each species (Pearson & Dawson, 2003; Visconti et al., 2016). We performed this step using the species versus land-use association from Lumbierres et al. (2022), based on the Copernicus land-use dataset (Buchorn et al., 2020). Specifically, each grid cell with existing or projected land-cover and land-use classes deemed unsuitable according to Lumbierres et al. (2022) was excluded from the suitable climatic range of the species. As Copernicus does not have future projections at the spatial and temporal resolutions we required, we converted the habitat land-cover associations to the GCAM land-use model at a 0.05° spatial resolution (Chen et al., 2020) (Appendixes S6 & S13). In this way, we obtained the land-use preferences of each species, which we resampled at a 1-km resolution, to ensure spatial consistency with the bioclimatic rasters. We then used these layers as a mask to filter the current and future bioclimatic projections. In this case, we used the year 2050 of scenarios SSP-RCP 1–2.6 and SSP-RCP 5–8.5 for future projections, whereas we used the year 2015 from scenario SSP2-RCP 4.5 as the reference for the present because the GCAM database lacks present-day data and this scenario is the most similar to current trends (O'Neill et al., 2017; Riahi et al., 2017). We compared the current projection with the future projection to calculate the change in the percentage range lost and gained, under each emission scenario.

For each species, we obtained four different projections of distribution change: climate-only projection for two scenarios and land use + climate projection for two scenarios (Appendix S7). Each of these four initial projections was replicated under both dispersal and zero-dispersal assumptions, resulting in a total of eight scenarios per species (Appendix S16). We compared the risks faced by species in the two emission scenarios and between projections considering only climate or climate and land use together to determine the role of dispersal.

RESULTS

All models showed high predictive performance during spatial block validation, and the ensemble model showed a median Boyce index of 0.96 (a range from −0.02 to 1), a median TSS of 0.88 (a range from 0.63 to 1), and a median F1 score of 0.72 (a range from 0.40 to 1) (Appendices S8 & S17). The variability across the predictions was quite low, with a coefficient of variation ranging from 0.03 to 0.32 (mean of the coefficients of variation of the three GCMs; Appendices S9 & S18). Mean annual temperature was the most important variable for modeling both birds (importance = 0.48) and mammals (importance = 0.25), followed by growing degree days for mammals (importance = 0.21) and temperature seasonality for birds (importance = 0.17) (Appendix S10).

The MESS analysis showed good environmental similarity between the observation and prediction areas in the present projections, as 95% of the species had positive MESS values in over 50% of their range (i.e., more than half of the prediction area had characteristics similar to locations used for model training) (Appendix S16). In contrast, the future projections revealed a different trend with a high percentage of future nonanalog conditions for most species.

Percentage values of range gained and lost reported in the results section refer to absolute changes (i.e., differences are expressed in percentage points).

Global risk for mountain mammals and birds

For birds, the projected percentage of range loss was substantially higher under the high-emissions scenario than under the low-emissions scenario, with a difference of 16.66% (climate-only projection) (Figure 2). Conversely, the projected percentage of range gained was lower under the high-emissions scenario than under the low-emissions scenario (4.54% lower). Considering only climate change, 89 species experienced a range loss of 70% or more under the low-emissions scenario, whereas 127 species faced similar losses under the high-emissions scenario.

We observed 97 species with a >70% range gain under the low-emissions scenario, decreasing to 83 species under the high-emissions scenario. The number of species showing range shifts (i.e., both high range loss and gain) was 100 under the low-emissions scenario and 96 under the high-emissions one when considering only climate projections. The number of rapidly declining species (i.e., those with a percentage of range lost that exceeds that of range gained) increased from 164 to 207 when comparing the low-emissions scenario with the high-emissions scenario.

Similar to birds, the projected percentage of range loss for mammal was substantially higher under the high-emissions scenario than under the low-emissions scenario, with a difference of 9.20% (climate-only projection) (Figure 2). Conversely, the projected percentage of range gained was lower under the high-emissions scenario than under the low-emissions scenario (1.50% lower). When considering only climate change in the projection, only three mammal species experienced a range loss of 70% or more under the low-emissions scenario, and this number increased to five mammal species facing similar losses under the high-emissions scenario.

Only two species showed range shifts under the low-emissions scenario, whereas five species shifted their range under the high-emissions scenario. The number of declining species increased from 12 to 14 based only on the climate projection.

Risk across mountain regions

A direct comparison across all mountain areas was precluded by the significant imbalance in species representation relative to the total number of mountain species in each area (Appendix S4; Figure 3) and by the low overall sample size for mammals. Consequently, regional comparisons could only be conducted for birds within the areas where avian species were sufficiently represented: high Asia, middle South Africa, and Oceania (more than 80% of mountain species analyzed) as well as middle Europe, middle North Africa, and low America (more than 20% of mountain species analyzed). In these regions, the highest range loss values for birds were 87.72% in high Asia (only a single species, Caucasian snowcock [*Tetraogallus caucasicus*]) followed by 64.03 % in low America and 56.50% in middle South Africa (high-emissions scenario, climate-only projection) (Appendix S11). Conversely, the highest values of range gained under the same scenario for these regions were found in middle Europe (513.60 %), Oceania (29.60%), and middle North Africa (16.76%) (Appendix S12).

Low America hosted the highest number of declining bird species (i.e., the species with range losses that exceeded range gains) under both the low-emissions and high-emissions scenarios (124 and 159 species out of 251, respectively, climate-only projection). The second region with the highest number of declining bird species was low Asia (17 and 22 species out of 43 under the low-emissions and high-emissions scenarios, respectively) followed by Oceania (seven species out of 16 under both scenarios).

In contrast, low America had the highest number of shifting species (82 out of 251 under the low-emissions scenario and 73 under the high-emissions scenario, considering the climate-only projection), and low Asia (five and seven species under the low- and high- emission scenarios, respectively) and Oceania (six species under both scenarios) had the next high number of shifting species.

Climate, land use, and dispersal

We determined the roles of climate, land use, and dispersal in shaping species range change. For birds, projections that included both climate and land-use change showed little difference compared with those that included only climate change. Under the low-emissions scenario, the median range loss increased by 4.49% when land-use change was included, whereas under the high-emissions scenario, the increase was 3.69% (Figure 2). In contrast, when land-use change was added, median range gain decreased by 0.21% under the low-emissions scenario and by 3.85% under the high-emissions scenario.

The result was similar for mammals. When land-use change was included, under the low-emissions scenario, median range loss increased by 2.74%, whereas under the high-emissions scenario, it decreased slightly by 0.31%. Median range gain increased with the inclusion of land-use change by 6.77% under the low-emissions scenario and by 0.70% under the high-emissions scenario.

The inclusion of dispersal led to substantial changes in the predicted range gained for species. Dispersal increased median range gain for birds by 13.68% and 10.15% under the low- and high-emissions scenarios, respectively. For mammals, the increase was 7.55% and 5.72% under the low- and high-emissions scenarios, respectively (climate-only projections). Similar patterns were observed when land-use change was also included in addition to climate change. In this case, dispersal increased median range gain for birds by 11.54% under the low-emissions scenario and by 5.57% under the high-emissions scenario, whereas for mammals, the increase was 9.47% and 6.41%, respectively. The inclusion of dispersal also affected the classification of species as declining or

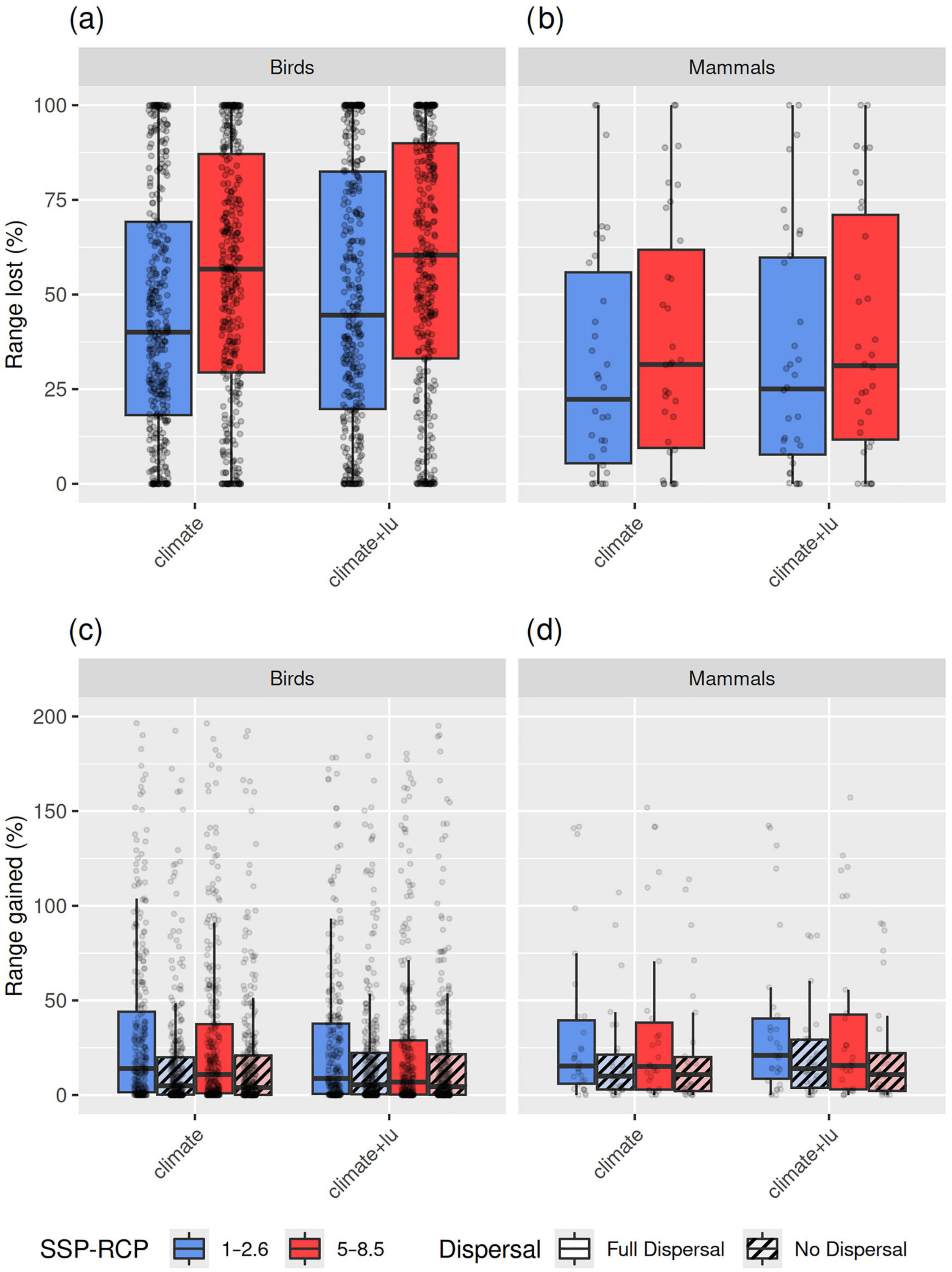

FIGURE 2 Boxplots representing the percentage of range lost (a, b) and gained (c, d) by 2050 for birds and mammals under the two emission scenarios (low-emissions scenario, i.e., SSP-RCP 1–2.6, and high-emissions scenario, i.e., SSP-RCP 5–8.5), calculated considering only climate or climate and land use (indicated on the *x*-axis). Dispersal scenarios are distinguished by visual style in the percentage of range gained (c, d): full dispersal is represented by solid-color boxes, and no dispersal is indicated by a diagonal stripe pattern and increased transparency.

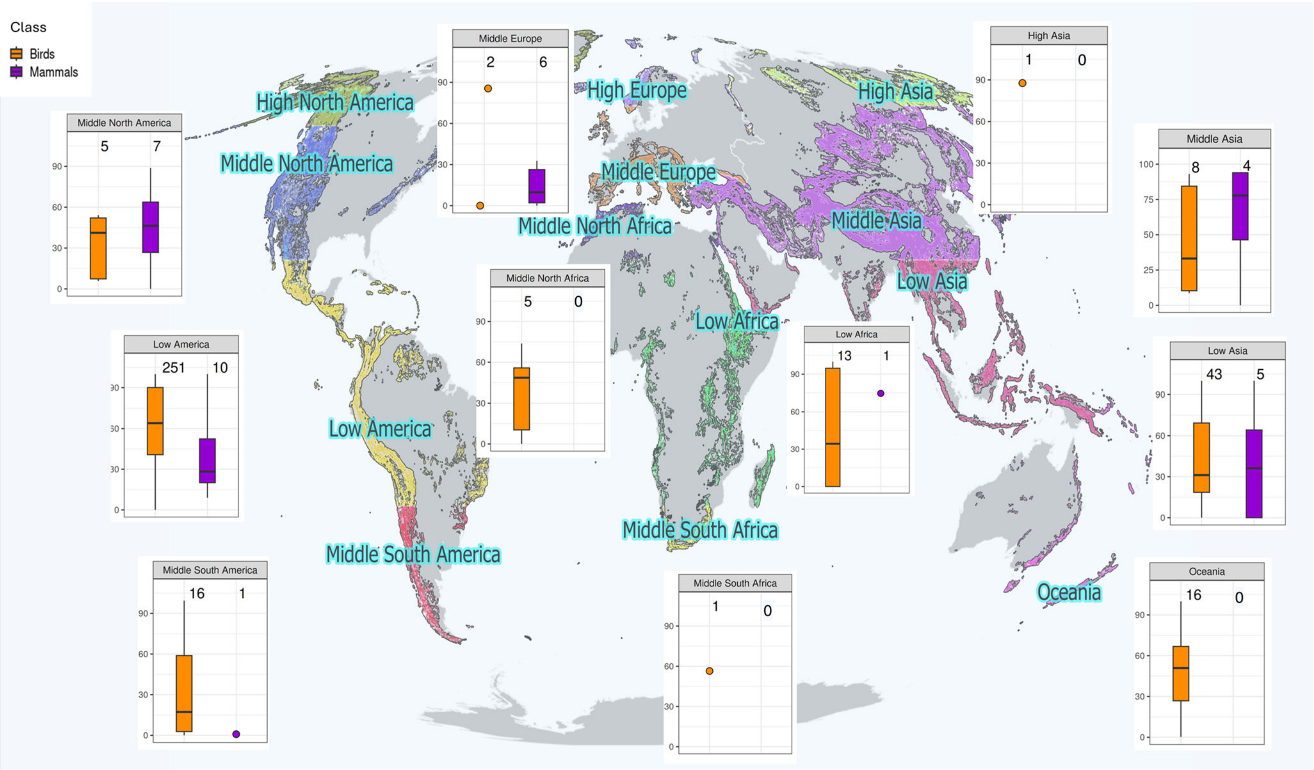

FIGURE 3 Maps of the percentage of range lost for birds (orange) and mammals (purple) in each mountain area under a high-emissions scenario, calculated considering only climate change. The values above each boxplot represent the number of the species analyzed.

shifting. For example, under climate-only projections, when dispersal was considered, the number of bird species classified as declining decreased from 213 to 164 under the low-emissions scenario and from 251 to 207 under the high-emissions scenario (Appendix S15). At the same time, the number of bird species projected to shift their range increased from 41 to 100 under the low-emissions scenario and from 50 to 96 under the high-emissions scenario.

At the regional level, considering only birds from the most represented regions, projections based on climate change alone were broadly consistent with those that also included land-use change. Patterns of range loss and gain were similar across regions, with differences in range loss ranging from −0.3% to 1.89% and differences in range gain ranging from 0% to 9.99% (Appendices S11 & S12).

DISCUSSION

Our analysis revealed that mountain species are particularly vulnerable to global changes. Even under a low-emissions scenario, which was consistent with the Paris Agreement's 2°C target, 28% of the birds and 6% of the mammals analyzed were predicted to shift their range, whereas 45% of bird species and 35% of mammal species were particularly at risk of having a range loss that largely exceeded range gain (≥20%). However, we found that compared with the high-emissions scenario, the low-emissions scenario reduced the percentage of range loss for mountain species by approximately 16%, when considering only climate change. Additionally, much fewer species were at high risk under the low-emissions scenario than under the high-emissions scenario. We demonstrated that pursuing a low-emissions trajectory is therefore essential for achieving the objectives of the Kunming–Montreal Global Biodiversity Framework, including the commitment to halt and reverse biodiversity loss by 2030.

Many of the species we analyzed showed high levels of endemism: 112 out of 361 bird species and 15 out of 34 mammal species are classified as endemic to their region by the IUCN. These species are often habitat specialists with limited dispersal capacity (the mean dispersal ability is 5.86 km for birds and 2.44 km for mammals in our analysis), making them particularly vulnerable to climate change, as the expected pace of climate change is likely to exceed their capacity to migrate (Dirnböck et al., 2011; Pearson et al., 2006). High-altitude species, in particular, have limited capacity to migrate away from unfavorable conditions due to their reduced climatic space, leading to potential population declines and increased extinction rates (i.e., the escalator to extinction phenomenon) (Dirnböck et al., 2011; Freeman et al., 2018; Hetem et al., 2014; La Sorte & Jetz, 2010).

Despite the inherently low mobility of these specialized species, our results indicated that dispersal is a decisive factor in enabling range shifts as an alternative to habitat contraction. This finding is supported by the significant increase in species at risk when dispersal is excluded from projections; for instance, 49 additional bird species faced critical range loss under low-emissions scenarios when their dispersal was not considered. Conversely, accounting for dispersal allowed more species to track suitable climates, as indicated by the 59 bird species that shifted rather than lose area. It is important to recognize, however, that dispersal is not a static trait but can itself be influenced by climate change, which alters movement rates and the effective success of the range shift (Travis et al., 2013). Moreover, our dispersal projections are optimistic, as they assume no geographical and anthropogenic barriers. Therefore, maintaining habitat connectivity and establishing ecological corridors are essential for facilitating species movements, and restoration actions and other interventions that increase permeability will be paramount (Littlefield et al., 2019; McGuire et al., 2016).

Notably, land-use change appears to have a secondary impact compared with that of climate and dispersal, with range dynamics remaining largely stable even when land-use masks were applied. Although this pattern was also observed in previous scenario studies (Di Marco et al., 2019; Newbold, 2018; Pereira et al., 2024), it is important to clarify that the species–habitat relationships are based on broad land-use land-cover classes that are predicted to show limited change through time and do not account for land-use intensity, which might face greater future change. Furthermore, this finding might be partly related to our refined method to account for the climate change driver (as a predictor within our model) compared with land use (used as a mask on future projections).

The percentage of range loss varied greatly across different mountain areas, even if comparisons were conducted only for birds and for the areas most represented in our analysis: high Asia, middle South Africa, Oceania, middle Europe, middle North Africa, and low America. Among these regions, high Asia emerged as an area of concern, even if represented by a single species, *T. caucasicus*. Despite its current classification as a species of least concern, the specialized ecological requirements of *T. caucasicus*, an endemic inhabitant of narrow alpine and subalpine zones of high Caucasus, make it exceptionally vulnerable to climate change. Low America was the most threatened region in proportional terms, with 159 out of 251 analyzed species (approximately 63%) classified as high risk under the high-emissions scenarios. Low America, which includes a vast mountainous region extending from the Central American mountain ranges such as the Sierra Madre Occidental to the Cordillera Central of the Andes, hosts the highest number of species per mountain area (Myers et al., 2000). Central and South America are especially vulnerable to climate change, with high population growth and density and intense land-use change (Castellanos et al., 2023). In the Andes, there is evidence that species have already shifted upslope due to climate change, leading to range contractions for highland species and both contractions and expansions for lowland species (Castellanos et al., 2023; Dragonetti et al., 2023; Fadrique et al., 2018; Freeman et al., 2018). At the same time, the mountains in this region are experiencing increased human population growth and land-use intensification (Chen et al., 2023; Farley et al., 2004; Payne et al., 2020). In the tropical Andes, 72% of all species and 90% of all threatened species are insufficiently covered by protected areas (Bax & Francesconi, 2019). Here, expanding existing protected areas by incorporating priority sites at their boundaries may be the best option, given budget and management constraints of this region. This strategy also improves functional connectivity, supporting species persistence and genetic diversity (Baguette et al., 2013). However, in regions where strict biodiversity conservation is limited by land-use systems and tenure structures, reinforcing sustainable land use through integrated conservation–development initiatives is the most sustainable pathway.

The third most threatened region was low Asia, where over half of the sampled species (22 out of 43) were at risk. We also found birds faced significant range shifts in Oceania. The mountains of Australia and New Zealand are among the most exposed to global climate changes (Lawrence et al., 2023). From 1910 to 2011, Australia warmed by 0.2°C more than the global average (Cleugh et al., 2011), causing major impacts on many natural systems, with some at risk of irreversible change (Hughes, 2003; Lawrence et al., 2023; Shoo et al., 2005). In New Zealand's Southern Alps, glaciers declined rapidly, with a 21% area reduction from 1978 to 2016, and ongoing retreat is projected. Reduced snow cover threatens alpine biodiversity, leading to the loss of alpine vegetation and increased stress on snow-dependent species (Steffen et al., 2009), with a medium to high risk of species losses within Australian alpine ecosystems over the next 50 years (Chambers et al., 2005; Pittock et al., 2003). The montane bird fauna of the region is especially vulnerable, with great population declines predicted even with small amounts of warming (Hughes, 2003; Shoo et al., 2005). In these two regions, climate mitigation and adaptation strategies coupled with restoration and protection from invasive species are essential to allow mountain species survival.

In contrast, middle Europe hosts species that are generally less at risk from climate changes. Previous studies have shown that these areas are generally less exposed to climatic changes than tropical areas and may act as local climatic refugia, offering protection from current climate shifts (Ashcroft, 2010; Dragonetti et al., 2024; Pacifici et al., 2015). Moreover, in certain parts of the European Alps, increasing human depopulation and land abandonment, often leading to the cessation of pastoralism and other traditional land-use practices, could be beneficial for some alpine species (Bachmann et al., 2019; Daskalova & Kamp, 2023).

Our study carries some important caveats. First, we acknowledge that our species set is not fully representative of all mountain taxa and may reflect geographic and phylogenetic biases due to data availability. Consequently, conclusions and conservation recommendations should be interpreted with caution, and direct comparisons between birds and mammals were avoided, with regional analyses limited to birds and well-represented areas.

Although this assessment in mountainous regions represents a significant contribution, it could be further refined by including high-resolution data for additional taxonomic groups. We did not use spatial autoregressive models, but we addressed spatial autocorrelation and sampling bias through different data filtering and spatially explicit block validation. Although a grid subsampling was used to mitigate spatial bias, we recognize it may not fully eliminate environmental sampling bias, which can affect model transferability over time (Pili et al., 2025). Nevertheless, the moderate-to-high performance achieved through spatial block validation suggests that our models maintained robust extrapolation ability.

Although SDMs are designed to approximate a species' fundamental niche—the full range of environmental conditions a species can theoretically occupy (Colwell & Rangel, 2009)—they are built on observed relationships between species occurrences and environmental variables (Guisan & Thuiller, 2005). However, current geographic ranges likely do not represent all the climates a species could inhabit without human influence (Maiorano et al., 2013; Sales et al., 2022; Soberón & Nakamura, 2009). When a species disappears from parts of its geographic range for nonclimatic reasons, only a portion of its potential climatic niche is still occupied (i.e., niche truncation) (Guisan et al., 2014; Martínez-Freiría et al., 2016; Peterson et al., 2018; Soberon & Peterson, 2005). As a result, SDMs may overestimate a species' sensitivity to climate change by failing to account for climatically suitable areas that are no longer occupied (Sales et al., 2022). Mountain species in particular could be forced to move upslope by long-term human activities at lower elevations (e.g., land conversion, habitat loss, and urbanization), reducing their current geographic range to only the colder portion of the climatic space they could tolerate. In our dataset, however, most species still retained occurrences at lower elevations (Appendices S2 & S3), indicating that projected contractions were not solely driven by warm-edge truncation. Moreover, our objective was to compare relative sensitivities across taxa, regions, and scenarios—not to reconstruct the full fundamental niche. Furthermore, by including dispersal, our work represents a bridge between correlative and mechanistic models, which better predicts species responses to climate change (Urban et al., 2016).

Another limitation of our study was the exclusion of certain climate-related factors that may be locally significant for some species, such as microclimatic conditions (Brito-Morales et al., 2018; Körner & Ohsawa, 2005), solar radiation, wind patterns (Scridel et al., 2024), and soil characteristics (Boyle & Martin, 2015; Körner & Spehn, 2002; Nagy & Grabherr, 2009; Viterbi et al., 2013). Although these variables may be relevant for some of our species, we did not include them because their availability is restricted to limited geographic regions and future projections are currently lacking. Biotic interactions, such as the availability of prey, are also important in defining the future distribution of species (Scridel et al., 2024), especially for top predators (but we had only one carnivore, brown palm civet [*Paradoxurus jerdoni*], in our dataset).

Another limitation concerns the dispersal estimates. Although the formula we used has recognized scientific validity, it is still an approximation, partly because it assumes constant species movement, an unrealistic condition in mountain environments. For birds, dispersal estimates are uncertain as they rely on the hand–wing index, a scientifically accepted predictor but with a complex relationship with actual dispersal capacity (Claramunt et al., 2025).

Regarding the MESS analysis, for future scenarios, we provided the full set of uncertainty maps for each species, illustrating where future environmental conditions differ most from current ones (Appendix S16). This decision was driven by the fact that binarizing the MESS results would have led to the exclusion of a substantial portion of the projected ranges, as future climatic conditions in most cases exceeded the training values. Exposure to novel climates is a frequent issue when modeling range-restricted species under future scenarios. Such challenges should not preclude the modeling of climate risk for range-restricted species, but in our case, the results must be interpreted in light of the provided uncertainty maps, which identify areas where model reliability may be lower.

Our findings offer new knowledge that can support conservation planning and inform decision-making processes. The substantial difference between the low-emissions and high-emissions scenarios highlighted the importance of rapidly reducing global emissions to achieving the objectives of the Kunming–Montreal Global Biodiversity Framework, including the commitment to halt and reverse biodiversity loss. The global variability in risks faced by mountain species underscores the need for more localized studies and conservation strategies—especially because many of the most threatened species have small, often endemic ranges (Kraus et al., 2023; Manes et al., 2021). Policymakers should consider these nuances when developing strategies and go beyond climate adaptation alone to support potential range shifts (Parks et al., 2023; Theobald et al., 2024). Our results can also help identify priority mountain regions, for example, in the tropics, where habitat restoration could strengthen the protection of critical habitats for endemic species or areas where potential climate refugia should be prioritized for protection or targeted management. In this sense, expanding protected areas and enhancing ecological connectivity through the creation of wildlife corridors across mountain regions will be essential for facilitating species' movements in response to shifting climatic conditions (Parks et al., 2023).

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SUPPORTING INFORMATION

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