Predicting spatiotemporal bioclimatic niche dynamics of endemic Pyrenean plant species under climate change: how much will we lose?

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Abstract

Species distributions are shifting globally due to environmental and anthropogenic pressures, with mountain ecosystems among the most vulnerable. In such landscapes, the ability of species to track changing conditions is limited, placing narrowly distributed species at risk. As a mountain biodiversity hotspot in southwestern Europe, the Pyrenees harbor many such species, making it a key case study for climate vulnerability assessments.

This study implements a multi-species bioclimatic niche modeling pipeline to evaluate the impacts of climate change on endemic Pyrenean plant species by 2100. Objectives are to (i) map current bioclimatic niche suitability (ii) forecast its future spatial dynamics, and (iii) identify potential climate refugia for conservation. Species occurrences were combined with 19 bioclimatic variables (1x1 km resolution) to characterize current bioclimatic niche suitability, using an ensemble modeling approach integrating five algorithms (MaxEnt, Generalized Linear Model, Generalized Additive Model, Gradient Boosting Machine, and Random Forest). Its future spatiotemporal dynamics were predicted under four climate scenarios (Shared Socioeconomic pathways 126, 245, 370, 585) for 2021-2100 period (2021-2040, 2041-2060, 2061-2080, 2081-2100).

By 2100, nearly all endemic species are predicted to experience severe bioclimatic niche contractions, with half facing complete losses under high-emission scenarios. However, one species may gain suitable areas, highlighting the need for species-specific conservation strategies. Bioclimatic niches are predicted to shift upslope by ~180 m, with hotspots becoming increasingly confined to refugia above 2000 m. These trends intensify after 2060, reflecting escalating climate pressures as the century progresses.

Our findings highlight the profound threat climate change may pose to endemic Pyrenean flora, with widespread bioclimatic niche losses predicted by the end of the century and high elevation refugia emerging as key conservation priorities. Our modeling framework provides a systematic approach for anticipating shifts and informing conservation planning to mitigate high-elevation biodiversity loss in a rapidly changing world.

Keywords: bioclimatic niche, climate change, climate refugia, endemic species, mountain, Pyrenees, species distribution modeling

1 | Introduction

Climate change represents one of the greatest environmental challenges of our time, with a significant and far-reaching impact on world's ecosystems (Li *et al.*, 2018; Intergovernmental Panel On Climate Change, 2022). Among these ecosystems, mountain regions are of special concern as they are experiencing some of the highest and fastest rates of warming, a phenomenon widely recognized as elevation-dependent warming (Pepin *et al.*, 2015). This refers to the tendency for warming rates at higher altitudes to surpass those observed in lowland regions, a pattern identified across multiple mountainous regions worldwide (Qixiang *et al.*, 2018; Pepin *et al.*, 2022). Such warming raises significant concerns for mountain ecosystems, which are particularly sensitive to these rapid changes (Knight, 2022; Intergovernmental Panel on Climate Change (IPCC), 2023). A cascade of ecological consequences follows (Rogora *et al.*, 2018; Dainese *et al.*, 2024), including shifts in species distribution, a well-documented response to climate change (Pearse & Davies, 2019; Rubenstein *et al.*, 2023; Lawlor *et al.*, 2024).

Climate velocity describes the speed and direction in which a species needs to move to stay within its climatic niche as climate conditions change, which, in mountainous contexts, force species to shift to higher elevations (Chan *et al.*, 2024), resulting in shifts upward in their core distribution (Freeman *et al.*, 2018). However, these elevational shifts are unlikely to keep pace with the rapidly changing climate (Carroll *et al.*, 2015; Kellner *et al.*, 2023; Goodwin *et al.*, 2025). Mountain plants, in particular, face even greater challenges than other organisms due to their limited dispersal capacity (Morgan & Venn, 2017; Di Musciano *et al.*, 2020) and weaker ability to compete with other species (Alexander *et al.*, 2015). Their migration is further constrained by the complex topography of mountainous landscapes and habitat fragmentation, which create substantial barriers to movement. Even when they successfully reach climatically suitable habitat, or are already located there, biotic mismatches, such as asynchronies in phenology and distribution with pollinators (Marshall *et al.*, 2020; Vitasse *et al.*, 2021; Dainese *et al.*, 2024; Trunschke *et al.*, 2024), or over-competition of species ascending (Alexander *et al.*, 2015; Schuchardt *et al.*, 2023), may impede their establishment. Moreover, if its establishment occurs within a microclimatic refugia, a common feature in mountainous landscape, prolonged isolation of these persistent populations may compromise their long-term survival by limiting genetic mixing, thereby reducing genetic diversity (Pinto *et al.*, 2024; Turnock *et al.*, 2024). This, in turn, limits their adaptability and resilience to environmental changes (Frankham, 2005; Bijlsma & Loeschcke, 2012; Mathur *et al.*, 2023). On a broader scale, a parallel can be drawn with mountaintop species, which can be described as dwelling in sky islands. A progressive loss of physical space with elevation amplifies extinction risk for these species (Elsen & Tingley, 2015), as they lack alternative areas to persist when facing unfavorable conditions or competition with other

species. This scenario, referred to as “mountaintop extinction”, primarily threatens species with narrow distribution, residing in the upper limits of latitude gradients, or restricted to highest elevation.

The Pyrenees mountain chain, Europe's second-largest biodiversity hotspot with 3,652 indigenous vascular plants, is particularly concerned by the number of mountaintop species, including a panel of endemics and specialized flora (Gómez *et al.*, 2017). The region’s complex climate and geodiversity have historically favored this exceptional diversity (Rahbek, Borregaard, Antonelli, *et al.*, 2019; Körner & Hiltbrunner, 2021) and served as both refuge and corridor for organisms during past climatic changes (Schmitt, 2009; García *et al.*, 2022). However, intensifying global pressures such as climate, land use, and any other environmental or socio-economic factors (OPCC, 2018; Zango-Palau *et al.*, 2024) may compromise its capacity to buffer future environmental shifts (Rahbek, Borregaard, Colwell, *et al.*, 2019). The upslope shift of plant species in the Pyrenees (Lenoir *et al.*, 2008; Pauli *et al.*, 2012; Ameztegui *et al.*, 2016) appears to contribute to increasing species richness on summits (Camarero *et al.*, 2006; Steinbauer *et al.*, 2018). Yet, this dynamic often comes at the cost of endemic and range-restricted species. Endemics represent about 5 % of the Pyrenean flora and species at their upper distribution limits represent another 20 % (Gómez *et al.*, 2017), implying that one quarter of the regional flora could face mountaintop extinction scheme. Parallel observations in the Alps, another European mountain range, underscore this pattern. Red-listed plants have experienced rapid contraction of their elevation margins, resulting in significant habitat loss in lowland areas (Geppert *et al.*, 2023), and endemic ones undergoing substantial range reductions, with projections suggesting that 40 % of their current distribution could become climatically unsuitable by the end of the 21st century (Dullinger *et al.*, 2012). Similar dynamics in the Pyrenees could drive extinctions, altering summit biodiversity and ecosystems. Although alpine plants show traits promoting resilience — adaptation to harsh conditions, diverse thermal microhabitats and clonal nature (Körner & Hiltbrunner, 2021) — these ongoing dynamics call into questions about their ability to adapt or track climatic changes, and raise pressing concern about the consequences for the diversity and structure of mountain ecological communities. In this context, identifying potential responses of species to these changes is essential for anticipating and guiding conservation efforts.

To assess the impact of climate change on plant distributions, the use of modeling tools is a widely adopted approach. Ecological niche, habitat distribution or species distribution models (SDM) are interchangeable terms for mechanistic or correlative approaches that predict and describe habitat suitability or probability of presence of a species, by linking occurrence records with environmental variables across spatial and temporal scales (Vasconcelos *et al.*, 2024). The robust methodological foundations and predictive power of these models have led to their application across diverse fields, including agriculture, public health, and, notably,

conservation biology (Franklin, 2023). In the Pyrenees, SDM has primarily been used for conservation purposes. Research has explored species distribution drivers (Kouba *et al.*, 2011; Williams-Tripp *et al.*, 2012; Dalibard *et al.*, 2021), predicted climate-driven shifts (Martínez *et al.*, 2012; Pérez-García *et al.*, 2013; de Pous *et al.*, 2015; Salvado *et al.*, 2022, 2025; Glad & Mallard, 2022; Russo *et al.*, 2023), and reconstructed distribution over geological time (Bidegaray-Batista *et al.*, 2016; Charbonnel *et al.*, 2016; Gutierrez *et al.*, 2022). Together, these studies underscore the value of SDM in informing management and conservation strategy for many species. By providing insights into species-environment relationships and distribution patterns for past, present and future, SDM becomes relevant tools for anticipating and addressing climate change impact, and, more generally, the impact of global change on biodiversity.

While single-species models have provided valuable insights, there remains a need for an efficient, systematic pipeline (i.e. framework) that integrates all SDM stages and can support multiple species simultaneously. Although various tools exist for each stage of SDM (Kass *et al.*, 2024), fully integrated multi-species framework remains scarce. Such a pipeline enables simultaneous analysis of numerous species, providing standardized outputs that facilitate cross-species comparisons. Moreover, modeling individual species within a cohesive multi-species framework enhances the understanding of spatial and temporal dynamics in biodiversity, which isolated single-species studies might overlook. This approach also refines our ability to detect climate-driven range shifts and predict ecosystem responses to environmental changes. Ultimately, this integrative approach gives natural area managers practical tools to preserve floristic diversity and sustain the ecological resilience of mountain ecosystems in the face of accelerating climate change.

The multi-species approach proposed here is particularly valuable for identifying priority conservation areas and informing management efforts for endemic species. Endemics, often restricted to distinct geographical and climatic niches, serve as key indicators of regional biodiversity and highlight the importance of mountainous ecosystems in enhancing floristic richness and uniqueness. Preserving these species is therefore crucial. Consequently, using SDM, this study aims to: (i) map current distribution of bioclimatic suitable areas for endemic species (ii) forecast future extent and dynamics of these areas by the end of the 21st century under multiple climate scenarios (iii) identify where these species could find refuge by 2100.

2 | Material and methods

Study area and species occurrences data

This study follows the mountain delimitation of Körner *et al.* (2011), updated by Snethlage *et al.* (2022). Within this framework, the Pyrenees span ~40,000 km² along the France-Spain-Andorra border (Figure 1), with over 150 peaks above 3000 m (Gómez *et al.*, 2017). Their steep northern slopes contrast with broader southern

valleys, featuring diverse landscapes. At the Atlantic-Mediterranean-continental interface, this mountain range displays diverse climatic conditions. Mean annual temperatures range from >10 °C in lowlands to <4 °C on peaks, with precipitation varying from >2000 mm (Atlantic slopes) to ~1000 mm (sheltered areas) (Cuadrat *et al.*, 2024).

Endemic species were selected from the Atlas of Pyrenean Flora (2,682 species, Pironon *et al.*, 2022). Excluding endemic subspecies reduced the set to 78 of 84 species. Species with <5 occurrences or highly restricted distributions were also removed, as selected SDM assessment method requires sufficient spatial representation. Ultimately, 59 species were included.

Occurrence data were obtained from the Global Biodiversity Information Facility (GBIF.org, 2025), supplemented with research-grade data from iNaturalist (https://www.inaturalist.org). Occurrences since 1970 within the study area and ≤ 1 km coordinate uncertainty were retained, fitting the resolution of environmental variables. Spatial thinning retained one occurrence per grid cell.

Bioclimatic data

WorldClim 2.1 (Fick & Hijmans, 2017) provided 19 rasterized bioclimatic variables (see Supplemental Information, Appendix A) for the current (1970-2000) and future periods (2021-2040, 2041-2060, 2061-2080, 2081-2100 designated as 2030, 2050, 2070, 2090 in this study). Future datasets based on CMIP6 General Circulation Models (GCMs) at 0.5 arcs/min resolution (~1x1 km at the equator) were combined into median rasters to capture model variability (Song *et al.*, 2024; Carroll & Mahony, 2025). Predictions follow four Shared Socio-economic Pathways (SSP, 126, 245, 370, 585, best to worst-case, respectively), representing socio-economic trajectory and radiative forcing ($W.m^{-2}$) expected in 2100 (O'Neill *et al.*, 2017; Welch, 2024). Under these scenarios, mean annual temperature in the Pyrenees (9.4 °C) is predicted to rise by +18.69 % (11.56°C) to +39.51 % (15.54 °C) in 2081-2100 period while current annual precipitation (975.41 mm) may decrease by -2.18 % (971.85 mm) to -13.57 % (843 mm) (Figure 2).

Highly positively correlated variables (r > 0.8) at presence locations were clustered, selecting in these clusters the most relevant per species, based on a predefined ecological priority list (Appendix A). Depending on species, models include between three and eight bioclimatic variables after the selection process.

Bioclimatic suitability modeling

Model development

A presence/pseudo-absence approach was employed to improve SDM reliability when true absences are unavailable (Mateo *et al.*, 2010). Pseudo-absences were generated following best practices (Barbet-Massin

183 *et al.*, 2012; Thuiller *et al.*, 2024), using environmental constraints sampling to limit inclusion of suitable but
184 unoccupied sites (Broussin *et al.*, 2024). Two sets were created: one equal to the number of presence and
185 another three times larger, both aligned with environmental raster resolution.
186 As modeling algorithms significantly impact SDM outcomes (Buisson *et al.*, 2010; Thuiller *et al.*, 2019) and
187 predictive performance varying across approaches (Norberg *et al.*, 2019; Valavi *et al.*, 2022), bioclimatic
188 suitability was modeled using five algorithms : Maxent (MXT) Generalized Linear Models (GLM) Generalized
189 Additive Models (GAM), Gradient Boosting Machines (GBM) and RandomForest (RF). GBM and RF employed
190 the first pseudo-absence set, while GLM, GAM and MXT used the second. To ensure comparability, probability
191 outputs from GLM, GAM, GBM, and RF were converted into favorability by removing prevalence
192 (presence/absence ratio) effects, as MXT generates suitability instead of probability maps.

193 *Parameters tuning, evaluation and ensemble modeling*

194 An automated workflow tuned model parameters, assessing performance through discrimination,
195 classification, and calibration metrics (Sillero *et al.*, 2021). Block cross-validation was applied, training on k-1
196 blocks and testing on the remaining one. Given limited occurrence data, four-fold repetition was used, setting
197 block size to two thirds of environmentally independent folds, balancing environmental independence and data
198 sufficiency that ensure presence records in each block. Discrimination was assessed via AUC-PR (0–1 scale,
199 with 0.5 indicating random performance), balancing precision and recall, making it particularly relevant for rare
200 species (Sofaer *et al.*, 2019; McDermott *et al.*, 2025). Classification ability was estimated through Sensitivity,
201 measuring true positive rates (0-1 scale, no true positives to perfect classification), crucial given limited
202 occurrences. Calibration was quantified using Boyce Index, assesses alignment between predictions and
203 observed presences (-1 for counter-prediction, 0 for random, and 1 for optimal prediction) (Sillero *et al.*, 2021;
204 Liu *et al.*, 2025). Continuous maps were binarized using MaxSSS threshold, suitable for presence-only data
205 (Liu *et al.*, 2013, 2016).
206 Each algorithm was run 50 times with distinct pseudo-absence sets. Rarefaction curves guided the choice of
207 required runs, selecting the inflection point where adding additional pseudo-absence sets altered predicted
208 suitable areas by <5 % (Appendix C). For each algorithm and iteration (5x50 = 250 models/species), the
209 parameter combination yielding the highest performance score (0.5 Boyce Index, 0.25 AUC-PR, and 0.25
210 Sensitivity) was retained. To ensure calibration quality, only models with Boyce Index > 0.5 were retained,
211 yielding between 58 and 250 models per species. Ensemble model scores were derived from algorithm-
212 averaged evaluation metrics. Algorithms performances were compared using Kruskal-Wallis, with Dunn's post
213 hoc test (Bonferroni correction) identifying pairwise differences.

Ensemble modeling enhances SDM robustness by combining multiple model outputs, effectively improving predictive accuracy by better capturing species distribution patterns (Marmion *et al.*, 2009; Zhu & Peterson, 2017). The median consensus of retained models (Boyce Index > 0.5) forms the median ensemble model, minimizing outliers, biases and aligning with model central tendencies (Marmion *et al.*, 2009; Zhu *et al.*, 2021). As ensemble models do not always outperform individual models in transferability (Zhu & Peterson, 2017), individual models are projected first, and their outputs are then aggregated by median. In total, each species had 17 predictions (1 current, 16 future), represented as continuous distribution maps (Appendix D).

Assessing uncertainty and spatio-temporal dynamics

Uncertainty was quantified using standard deviation across predictions. Pixels with >5 % divergence, indicating inconsistent predictions across algorithms, were masked for visualization on the current distribution map to highlight most reliable regions. To assess SDM reliability under novel conditions (i.e. conditions in future periods deviating from the calibration range), the Multivariate Environmental Similarity Surface (MESS) index (Elith *et al.*, 2010) was applied. Negative MESS values, indicating extrapolation, were masked for visualization on future distribution maps to highlight most reliable predictions.

Suitable bioclimatic extent was quantified from binarized maps for each period and SSP. To assess its spatial shifts, predictions were overlaid with elevation data (CGIAR-CSI, 2018, ~1x1 km at the equator). Continuous suitability maps for the current and 2081–2100 periods for each SSP were averaged across species, identifying suitable persistent pixels as bioclimatic hotspots (areas where the highest number of species could find suitable bioclimatic conditions). Binarized maps were used to extract each species' core elevation range across each period and SSP. Elevation values were then averaged across SSPs to compute a single mean elevation per period for each species, considering only periods in which the species maintained suitable areas across all SSPs. These outputs assess changes in species' bioclimatic niche extent and distribution.

Framework and model characteristics were documented following the ODMAP protocol (Zurell *et al.*, 2020, Appendix B) and summarized in Figure 3.

3 | Results

Models performances

Significant differences in models performances were observed across the five algorithms for all three-evaluation metrics (Kruskal-Wallis, $p < 0.001$). Dunn's post hoc test revealed that i) GBM outperformed significantly GAM ($p < 0.001$), GLM ($p < 0.05$), MXT ($p < 0.01$), as RF ($p < 0.001$, 0.01 and 0.001 respectively)

for AUC-PR; ii) MXT exceeded GAM, GLM and RF ($p < 0.001$), RF outperformed GLM ($p < 0.001$) and GAM ($p < 0.05$) while GBM outperformed GAM, GLM ($p < 0.001$) and RF ($p < 0.01$) for the Boyce Index; iii) MXT outperformed GLM ($p < 0.001$), GBM ($p < 0.05$), and GAM outperformed GLM ($p < 0.05$) regarding Sensitivity. Other comparisons were not significant (Figure 4a). This highlights variation in predictive performance, with GBM and RF generally performing best, and MXT consistently performed well in identifying suitable areas where species are present. GLM exhibited the lowest Boyce Index values, falling under 0.5 for multiple species, indicating weaker prediction consistency.

Ensemble model performance ranged from 0.59–0.98 for AUC-PR, 0.59–0.92 for the Boyce index and 0.86–0.98 for sensitivity (Figure 4b). Poor evaluation metrics were not consistently linked to species with fewer presence points, suggesting additional factors influencing performance.

Predicted bioclimatic niche loss and species vulnerability

The analysis of extent changes in bioclimatic suitable areas for endemic Pyrenean plant species reveals a substantial decline in their availability under climate change (Figure 5). By the end of the century, on average across SSPs, 58 out of the 59 species are predicted to lose a significant part of their suitable bioclimatic niche, with 39 species losing >75 %, 11 losing 50-75 % and 9 experiencing a more moderate loss of 10-50 %. These species are expected to lose on average between -54.98 % (min: +47.77 %, max: -100 %) and -93.73 % (min: -16.12 %, max: -100 %) of their suitable bioclimatic niche by 2081-2100 period under the most optimistic (SSP126) and the worst-case (SSP585) climate scenario, respectively. The severity of loss varies across species. More than half (30 species) are predicted to experience a complete loss (100 %) of their suitable bioclimatic areas by the end of the century for at least one of the SSP, putting them at elevated risk of extinction. *Delphinium montanum*, *Endressia pyrenaica, Silene borderei and Xatartia scabra* appear particularly vulnerable, as models predict a total disappearance of their bioclimatic suitable areas as early as the 2021-2040 period, under all SSPs, suggesting that these species are already present in unfavorable bioclimatic conditions. In contrast, *Pinguicula longifolia* emerges as an exception, showing consistent increase in suitable areas with an average gain of +45.19 % (from +11.05 % under SSP585 to a maximum of +80.79 % under SSP245) by 2081-2100 period. This suggests that shifting climatic conditions may benefit some species, including endemic and threatened ones. The analysis also highlights an accelerating trend in suitable areas loss over time, particularly in more extreme scenarios such as SSP370 and SSP585. Most species experience sharp declines after the 2041-2060 period, reflecting the escalating impact of climate change as the century progresses (Figure 5).

Shifts upward in bioclimatic hotspots and elevational range

The spatial distribution of bioclimatic niche suitability for endemic Pyrenean plant species is predicted to undergo significant changes by the 2081-2100 period under climate change (Figure 6). Currently, bioclimatic hotspots, where most species could find suitable bioclimatic conditions, are mainly above 1000 m, with a maximum favorability of 0.74 (Figure 6a, top panel). By the 2081-2100 period, these hotspots are predicted to shrink in size and shift upward, with the extent of this change strongly linked to the emission scenario. Climate scenarios such as SSP126 show a relatively moderate reduction, with some areas persisting near current locations. In contrast, more extreme scenarios predicted a pronounced contraction of suitable areas, becoming increasingly fragmented. Under SSP585, the maximum favorability value drops to 0.26, with suitable conditions restricted to areas above 2000 m in elevation (Figure 6a, lower panels).

The predicted mean elevation of bioclimatic suitable areas for endemic Pyrenean plant species shows a marked upward shift by the end of the century under climate change (Figure 6b). Currently, mean elevation of suitable bioclimatic area ranges between 739 and 2275 m, depending on the species. By 2081-2100, the average elevation across species is predicted to increase by +189.28 m. While the lower margin remains relatively stable (681 m), the upper margin is expected to reach 2742 m. Species exhibit variable predicted elevation trajectories. For example, *Saxifraga aretioides* shows steep upward shifts exceeding +820 m, while others, such as *Petrocoptis crassifolia*, could display a downward shift (over -750 m), illustrating species-specific responses to climate change. By the 2081-2100 period, most of the 28 species that still have suitable bioclimatic conditions across all SSPs display a clear upward predicted trend, with mean increases ranging from +7.17 % to +45.36 %. Subsets of species that may experience a reduction in their mean elevation could see decreases from -0.07 % to -44.93 %. On average, species show a +21.41 % increase in elevation, while the decrease is about -16.2 %. These results emphasize the significant influence of warming climate on the spatial and vertical distribution of suitable bioclimatic areas, underscoring the increasing vulnerability of endemic Pyrenean flora to rising temperatures.

4 | Discussion

Trends in bioclimatic niche suitability under climate change

This study paints a concerning picture of the future for Pyrenean endemic flora under ongoing and predicted climate change. By the 2081-2100 period, 58/59 of the studied species are predicted to experience substantial reduction in suitable bioclimatic areas (on average -54.98 % to -93.73 % for SSP126 and SSP585 respectively), ranging from moderate contraction in some species to complete losses in others. These findings underline the severe threat posed by changing climate to narrowly distributed species and align with patterns

predicted in similar mountain regions, such as the Alps (Dirnböck *et al.*, 2011; Dullinger *et al.*, 2012; Hülber *et al.*, 2016; Dagnino *et al.*, 2020; Rota *et al.*, 2022), where endemics are acutely sensitive to rapid warming. Parallels with other mountain systems (Manes *et al.*, 2021) underscore the universal challenge that climate change poses to mountain endemism which is, moreover, amplified by topography and human pressures (Elsen *et al.*, 2020). Interestingly, not all species follow the same trajectory. While most of them exhibit severe bioclimatic niche contractions, one species displays consistent gains in suitable bioclimatic areas under all climatic scenarios. This outlier highlights that while some species face heightened risks of extinction, others may find new opportunities under climate change. It also underlines the need for species-specific conservation strategies that account for this ecological variability.

Beyond species-specific patterns, this study revealed notable upward shifts in mean elevations of suitable bioclimatic niche, exceeding 180 m by the 2081-2100 period. If it was consistent over the past century, this trend could explain a part of the upward movement of species already observed in the Pyrenees (Lenoir *et al.*, 2008; Pauli *et al.*, 2012; Ameztegui *et al.*, 2016). However, this observed shift is on average less pronounced than 180 m, potentially reflecting the lag of species' ability to keep pace with climate change, or other factors, such as microclimatic conditions, that influence local-scale dynamics (Maclean & Early, 2023). Nevertheless, the upward shift in species distribution predicted in this study align with trends already documented in various mountain ecosystems (Iseli *et al.*, 2023; Chan *et al.*, 2024). Hotspots of suitable bioclimatic niche, currently located above 1000 m, are predicted to shift above 2000 m. This shift drastically reduces bioclimatic suitable space available for endemic flora, as high elevations cover smaller geographic extent in the Pyrenees (Elsen & Tingley, 2015). Many species risk being squeezed between warming lower slopes and shrinking refugia, exacerbating their risk of extinction. The analysis also revealed fragmentation of bioclimatic suitable areas, which reduced connectivity between them. This loss of connectivity challenges species migration and long-term survival, particularly for low- and mid-elevation ones that may struggle to migrate upward. Regional warming and aridification of the Pyrenees, already documented at a rate of 30 % faster than the global average over the past 50 years (OPCC, 2018), exacerbate challenges already posed by dispersal barriers, topographic constraints, and competition from upslope-moving species that are intensifying pressure on the flora. The severe suitable bioclimatic area reductions predicted under SSP370 and SSP585 scenarios after the 2041-2060 period is particularly alarming and suggests that environmental pressures will intensify in the second half of the century. The urgency of monitoring is reinforced by the identification of high vulnerability of northern Spain's flora, south of the Pyrenees, which is among the most threatened in Europe (Engler *et al.*, 2011).

Strengths and limitations of the modeling framework

Advances in occurrence databases and open-access environmental data have expanded possibilities for studying species–environment relationships. The pipeline developed in this study represents a step forward in addressing mountain biodiversity questions at a broad geographic scale, particularly for multi-species analyses. By integrating five algorithms (GLM, GAM, GBM, RF, and MXT) into an ensemble modeling framework, this approach minimizes model-specific biases and provides robust predictions of potential future species distributions. Moreover, the consistency between our ensemble predictions and previous single-algorithm finding (e.g. *D. montanum*, Salvado *et al.*, 2022) supports the pipeline's robustness. RF, MXT and GBM emerged as particularly strong performers, likely due to their capacity to handle small sample sizes and capture non-linear relationships between species and environmental variables (Valavi *et al.*, 2022). The pipeline effectively addresses challenges posed by sparse data and complex topography, providing consistent and interpretable results for narrowly distributed species. To account for endemic Pyrenean plant species excluded from this study, the pipeline could be applied case-by-case at a smaller spatial scale (in regions of recorded occurrences). This study provides a robust valuable framework adaptable to all endemic species. Moving forward, our pipeline will be extended to species with broader distributions, adapted to biodiversity hotspots worldwide, and optimized for a more extensive multi-species analytical approach. It will provide deeper insights into species and communities' response to climate change, focusing on richness patterns and diversity dynamics.

Despite these strengths, several SDM limitations and considerations warrant caution when interpreting the results (Collette *et al.*, under review), particularly regarding methodological biases and decision-making processes (see Sillero *et al.*, 2021; Bryn *et al.*, 2021; Leroy, 2023). This study presents three main considerations. First, coarse-resolution bioclimatic data, appropriate for broad-scale analyses as they capture general environmental trends, reduce computational costs, and minimize biases from localized data inaccuracies (Mirhashemi *et al.*, 2023), may misestimate habitat suitability by failing to capture fine-scale microhabitat heterogeneity in mountainous environments (Trivedi *et al.*, 2008; Randin *et al.*, 2009; Gottfried *et al.*, 2012; Franklin *et al.*, 2013; Nadeau *et al.*, 2017). This can inflate habitat loss predictions by ignoring microrefugia or overestimate persistence by misrepresenting local threats. However, no systematic bias toward overestimation or underestimation is evident. This absence of directional bias has been highlighted by comparing empirical occurrence data with SDM-based predictions (Tsiftsis *et al.*, 2024). Second, projections beyond 2041-2060 period remain uncertain due to increasing divergence between climate models, particularly for the worst climatic scenarios (SSP370, SSP585) (Goberville *et al.*, 2015; Tebaldi *et al.*, 2021). Although the

366 trajectory for most species aligns across scenarios, notable variation exists in whether favorable bioclimatic
367 niche disappears or persists to a lesser extent, depending on pseudo-absence sets (Appendix C). Long-term
368 monitoring and high-resolution climate data are essential to validate projections and improve predictive tools.
369 Third, the exclusion of biotic interactions (e.g. competition, mutualism, pollination), reduces the ecological
370 realism of projections. Integrating such biotic dynamics into SDMs would enhance the accuracy of projections
371 and offer a more nuanced understanding of species' responses to climate change (Preuss & Padial, 2021;
372 Lee-Yaw *et al.*, 2022; Cosentino *et al.*, 2023).
373 Beyond the limitations of SDM, correlative models based on bioclimatic variables provide valuable insights into
374 species distributions, but fail to capture the complex ecological and evolutionary processes shaping species'
375 responses to environmental changes (Williams *et al.*, 2008). Expansion of bioclimatic suitability areas does
376 not guarantee population growth, as dispersal barriers, establishment limitations, and biotic interactions may
377 restrict species from fully occupying suitable areas. Likewise, suitability contraction does not imply imminent
378 range collapse, as species can persist temporarily in suboptimal conditions before extinction, known as
379 "extinction debt" (Cotto *et al.*, 2017; Nomoto & Alexander, 2021). On the adaptation perspective, rapid
380 environmental changes may outpace the rate at which species can adapt, facing the disappearance of their
381 favorable habitat (Jump & Peñuelas, 2005; Shaw & Etterson, 2012; Cotto *et al.*, 2017). Moreover, fragmented
382 populations may experience divergent selective pressures, fostering local adaptation — often overlooked in
383 SDMs. Integrating local adaptation, phenotypic plasticity (Valladares *et al.*, 2014; Benito-Garzon *et al.*, 2019),
384 and genomic data (Hällfors *et al.*, 2016; Kort *et al.*, 2024) could improve predictions by better accounting for
385 populations' adaptive capacity under environmental stress.

386 **Conservation implications and Policy recommendation**

387 From conservation and management perspectives, our findings underscore the urgent need for conservation
388 strategies that address specific challenges faced by mountain flora in the Pyrenees. High altitude
389 environments, where suitable bioclimatic conditions are expected to persist, represent critical bulwarks against
390 climate change and must be protected as refugia for species to preserve biodiversity. Strengthening
391 connectivity through altitudinal corridors is equally essential to facilitate species migration and genetic flow,
392 mitigating the adverse effects of habitat fragmentation. For species predicted to lose their suitable bioclimatic
393 niche, conservation interventions such as assisted migration, seed banking and translocation may provide
394 options to prevent extinction (Gallagher *et al.*, 2014; Ferrarini *et al.*, 2016). Additionally, re-evaluating their
395 conservation status could help inform adaptive management priorities. Moreover, integrating predictive

modeling tools with field monitoring could enhance the precision of these interventions, ensuring that resources are allocated to areas with the greatest potential for success (Eyre *et al.*, 2022; Elliott *et al.*, 2024).

As climate change reshuffles species distributions, management must account that species could move beyond traditional ranges, crossing administrative or national boundaries. The transboundary distribution of Pyrenean species across France, Spain, and Andorra requires coordinated cross-border efforts to avoid fragmented conservation initiatives, such as inconsistent Natura 2000 habitat interpretation along this frontier (Prud'homme & Ninot, 2018). Adaptive legal frameworks are essential to address these shifts, supported by collaborative efforts that align research, policy, and community engagement for enhanced conservation outcomes. Translating scientific evidence into clear and actionable policy briefs can bridge the gap between research and implementation, fostering informed and, consequently, more effective decision-making (Guisan *et al.*, 2013). Understanding how climate change affects extinction risks and habitat availability is key to prioritizing conservation actions, especially as pressures intensify. This also requires combining ecological modeling, field experimentation, and long-term monitoring to refine conservation strategies and better address species redistributions and their effects on human well-being (Pecl *et al.*, 2017; Bonebrake *et al.*, 2018). Ultimately, preserving mountain biodiversity in an era of rapid change will require collaboration among scientists, resource managers, and local communities, supported by predictive tools to capture the complex realities of a rapidly changing world.

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Figures for:

Predicting spatiotemporal bioclimatic niche dynamics of endemic Pyrenean plant species under climate change: how many will we lose?

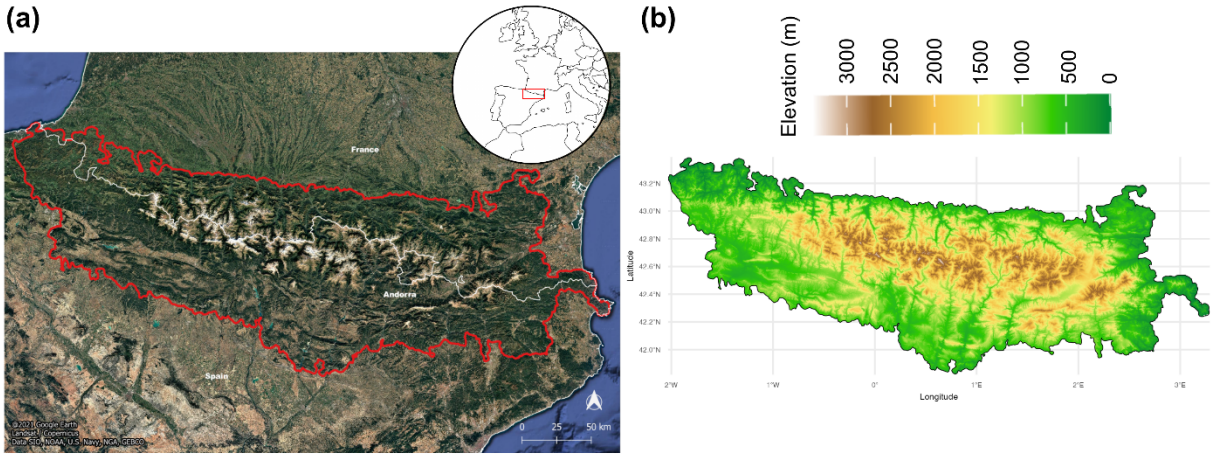

Figure 1. Geographic extent and topography of the Pyrenees. (a) The Pyrenees Mountain range (red outline) spans the border regions of France, Spain, and Andorra. Its delimitation follows the definition set out by Global Mountain Biodiversity Assessment (Körner *et al.*, 2011, updated by Snethlage *et al.*, 2022). The inset map shows the location of the Pyrenees in Europe. Satellite imagery: Google Earth (© Google, Image Landsat/Copernicus, Data SIO, NOAA, U.S. Navy, NGA, GEBCO). **(b)** Elevation gradient from a 90m-resolution digital elevation model (CGIAR-CSI, 2018), showing the region's topographic variation from lowlands (green) to high peaks (brown to white).

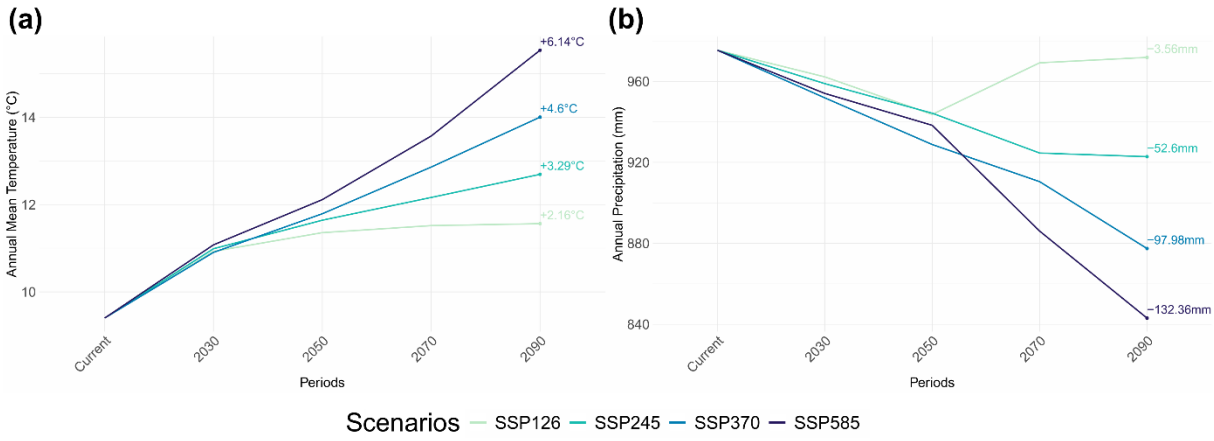

Figure 2. Predicted changes in temperature and precipitation in the Pyrenees under Shared Socioeconomic Pathways (SSP) by 2081-2100 period from WorldClim 2.1. (a) Mean annual temperature (°C) and **(b)** annual precipitation (mm) projections for 2021–2100 under SSP126, SSP245, SSP370, and

SSP585. Values (+/-) reflect differences from the 1970–2000 baseline (current period) for the 2081–2100 period. 2021-2040, 2041-2060, 2061-2080, 2081-2100 periods designated as 2030, 2050, 2070, 2090.

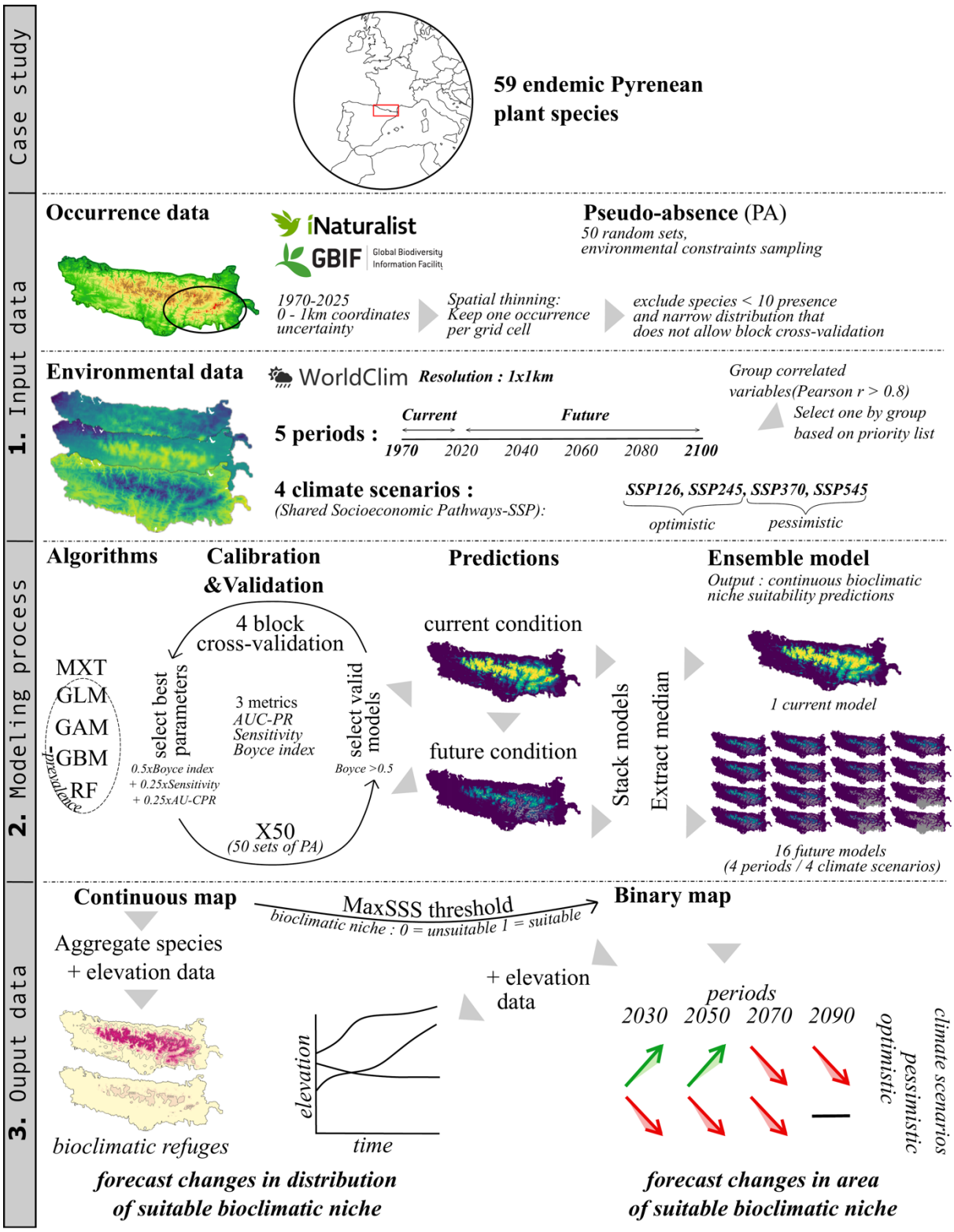

Figure 3: Overview of the species distribution modeling pipeline. The framework consists of three main stages: (**1**) Input data, including occurrence records, environmental data processing, and background sampling; (**2**) Modeling, encompassing model building, performance assessment, prediction, and ensemble

modeling; (**3**) Output processing, manipulating species predictions to assess spatiotemporal dynamics of suitable bioclimatic niches.

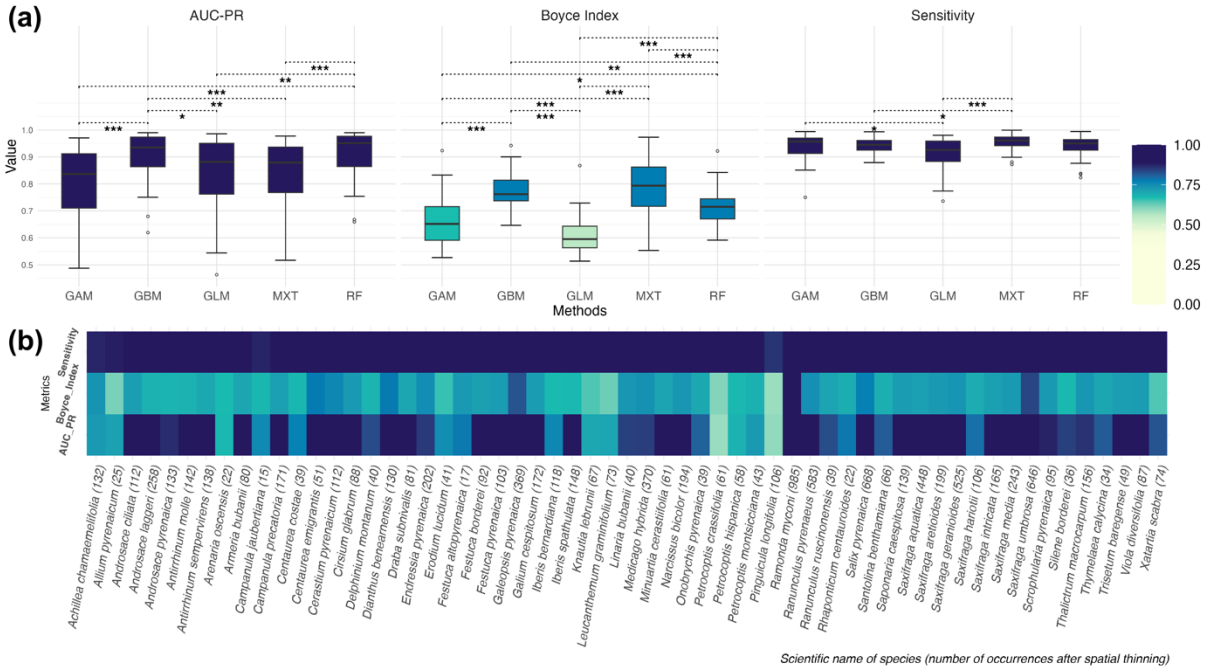

Figure 4: Endemic Pyrenean plant species model performances. (a) Boxplot of three performance metrics — AUC-PR (discrimination), Boyce Index (calibration), and Sensitivity (classification) — across five modeling algorithms (GAM, GBM, GLM, MAXENT, RF). Statistical significance is denoted as: $*p < 0.05$, $**p < 0.01$, $***p < 0.001$. **(b)** Performance of ensemble models across species, computed as the mean of each metric across the five algorithms for each species. Darker shades indicate higher performance.

Figure 5: Predicted extent changes in bioclimatic suitability for endemic Pyrenean plant species under Shared Socioeconomic Pathways (SSP) for the 2021-2100 period. Extent changes in suitable areas under SSP126, SSP245, SSP370, SSP585, relative to the baseline period (1970-2000). Each box represents the extent change in suitable area, with percentage values shown for the 2081–2100 period. Orange indicates a reduction in suitable areas, green expansion, and black a complete loss of suitability. 2021-2040, 2041-2060, 2061-2080, 2081-2100 periods designated as 2030, 2050, 2070, 2090.

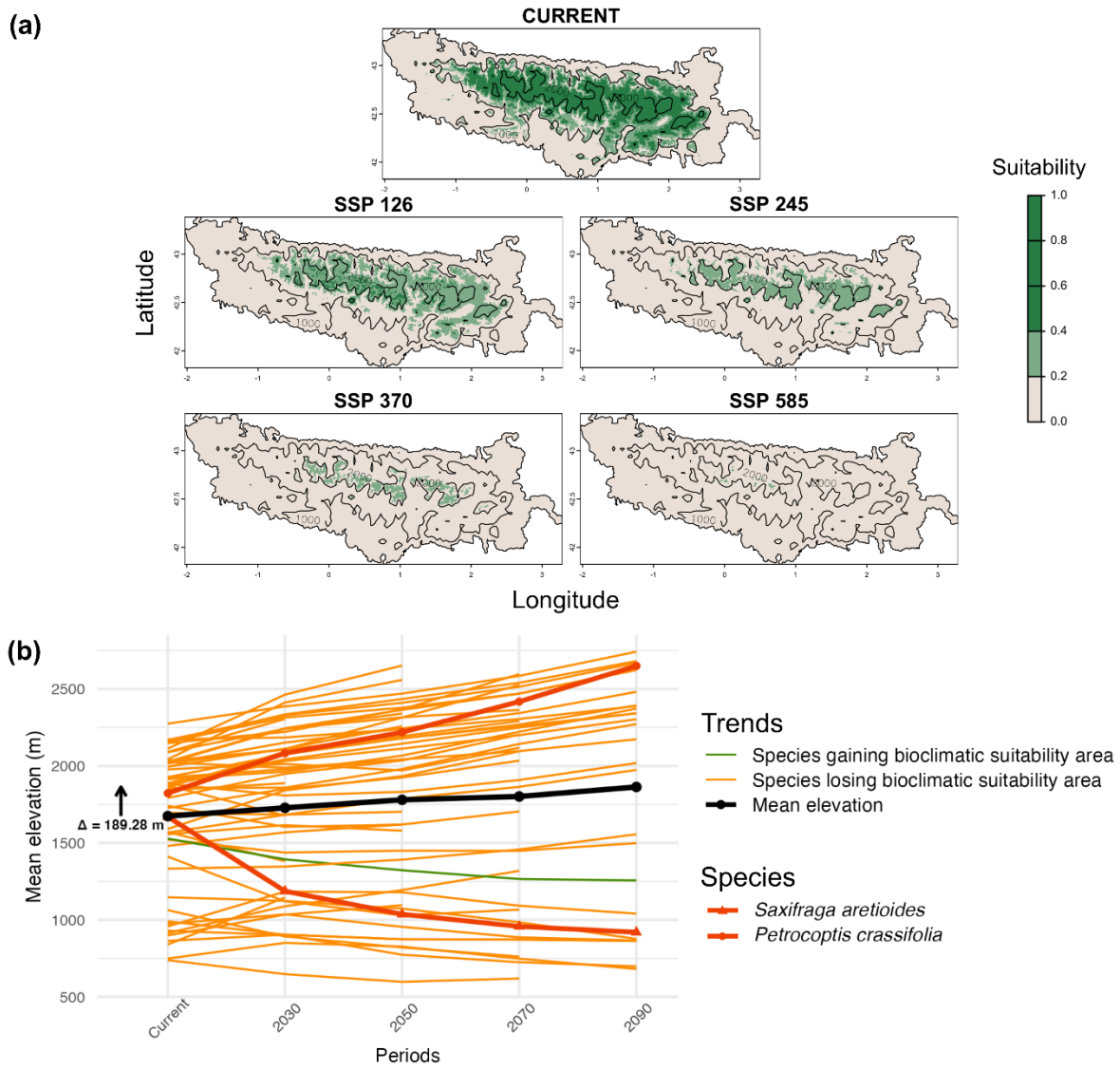

Figure 6. Predicted distribution changes in bioclimatic suitability for endemic Pyrenean plant species. **(a)** Current and predicted (2081-2100) bioclimatic hotspots under Shared Socioeconomic Pathways (SSP). The top panel shows the current distribution, while lower panels display predictions for SSP126, SSP245, SSP370, and SSP585. Darker colors indicate higher bioclimatic suitability. Contour lines mark the 1000- and 2000-meter elevation topography. **(b)** Predicted elevation shift of bioclimatic suitability for the 2021-2100 period, averaged across SSPs. Each line represents the elevation trajectory of an individual species. Orange lines represent species expected to lose part of their suitable bioclimatic niche by the end of the century, while green lines indicate those projected to experience an expansion of it. The black line indicates the overall trend of elevation for species. Two additional highlighted lines correspond to the species predicted to experience the strongest median upward and downward shifts of bioclimatic suitability. 2021-2040, 2041-2060, 2061-2080, 2081-2100 periods designated as 2030, 2050, 2070, 2090.