Climbing invasions or climatic refugees: how many and to which extent non-native plant species could reach the Pyrenees mountains under climate change?

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Abstract

Under climate change, the status of invasive species is becoming complex, as taxa considered invasive in one region may become threatened in another, experiencing simultaneous expansion and decline across their range. In this context, mountain systems may act both as barriers to spread and as climatic refuges for these species. The Pyrenees, a longitudinal barrier separating the Iberian Peninsula from the rest of Europe, are increasingly exposed to alien plant species spreading from lowlands. Several invasive species have already reached high elevations in the massif, raising concerns about how many more may follow and to what extent under future climate change.

This study assesses future invasion risks for 35 non-native plant species recognized as invasive on both sides of the Pyrenees. We project future dynamics of their bioclimatic niche suitability to identify which are likely to become widespread and where by 2100. Combining occurrence data with 19 bioclimatic variables at 1×1 km resolution, we model current bioclimatic niches and project its future distribution using an ensemble framework integrating five algorithms under four climate scenarios covering the 2021–2100 period.

Projections indicate that 80 % of invasive plant species in the Pyrenees would not be climatic winners under future warming. The centroid of suitable climatic conditions is projected to shift upslope to more than 87 % of species. This upward movement would tend to stall around 2,000 m, as suggested by future hotspot patterns, effectively squeezing suitable areas and constraining future invasions within mountain zones, as climatic pressure increases at lower elevations. Such redistribution would not necessarily imply negative outcomes, and overlapping with endemic species would remain very limited.

These results raise a broader question: could today's invasive species become tomorrow's mountain flora? Although climate projections cannot capture the full complexity of invasion processes, they provide a basis for prioritizing surveillance and early action.

Keywords: Invasive species, Climate change, Mountain, Range shifts, Invasion risk, Species Distribution Models

Introduction

Biological invasions are a defining feature of the Anthropocene (Essl *et al.*, 2011 ; Seebens *et al.*, 2017). The unprecedented acceleration of international trade (Hulme, 2021) and tourism (Anderson *et al.*, 2015), supported by expanding transportation networks (Hulme, 2009 ; McGrannachan *et al.*, 2021), have intensified species introductions worldwide, while climate change facilitates the establishment and spread of non-native organisms (Hellmann *et al.*, 2008 ; Hulme, 2017 ; Stachowicz *et al.*, 2002 ; Walther *et al.*, 2009 ; Willis *et al.*, 2010). Among these, invasive species, defined as established non-native alien taxa that spread and form successive populations beyond their introduction points (Soto *et al.*, 2024), are reshaping ecological communities (Bellard *et al.*, 2016 ; Pysek *et al.*, 2020b ; Vila *et al.*, 2011). In addition, global syntheses have confirmed that they generate substantial economic costs across all continents (Ahmed *et al.*, 2023 ; Diagne *et al.*, 2021 ; Zenni *et al.*, 2021), with no sign of slowing down. However, these costs are not evenly distributed, as damages can outweigh management expenditures (Bradshaw *et al.*, 2024). This growing concern surrounding invasive species, together with their increasing ecological and economic impacts, raises practical questions about which species are most likely to expand and where management attention should concentrate (Cuthbert *et al.*, 2022), as it remains uncertain whether climate change will promote invasive species or instead lead to contrasted outcomes (Bellard *et al.*, 2013 ; 2018 ; Cao Pinna *et al.*, 2024 ; Finch *et al.*, 2021 ; Lopes *et al.*, 2023).

In this global context, invasive plants deserve special attention, as vascular plants dominate recent introductions worldwide (Haubrock *et al.*, 2023 ; Seebens *et al.*, 2017). Experimental evidence demonstrates that warming legacies enhance invasive plant growth (Ivison *et al.*, 2025 ; Lembrechts *et al.*, 2016) while it may simultaneously reduce enemy performance (Zhou *et al.*, 2025), creating synergistic advantages for colonization success. Mountain regions were historically considered relatively protected from plant invasions due to climatic constraints and limited propagule pressure (i.e. the number and frequency of introduction events) (Alexander *et al.*, 2016 ; Zefferman *et al.*, 2015). However, these filters weaken under multiple anthropogenic pressures (Kueffer *et al.*, 2013 ; Pauchard *et al.*, 2009 ; 2016), facilitating the establishment of invasive plants at higher elevations (Larson *et al.*, 2021 ; Steinbauer *et al.*, 2018). In particular, expanding infrastructure and tourism development, including roads, hiking trails and ropeway corridors, increases both the frequency and magnitude of introductions by improving human accessibility, thus intensifying propagule pressure and facilitating the upslope spread of non-native taxa into montane and subalpine environments (Barros & Pickering, 2014 ; Hemp, 2008 ; Koyama *et al.*, 2024 ; Liedtke *et al.*, 2020). Observations across mountain ranges worldwide provide clear evidence of accelerating plant

invasions at high elevations (ISELI *ET AL.*, 2023) accompanied by thermophilization patterns reflecting the progressive recruitment of a low-elevation pool of warm-adapted alien taxa (GOTTFRIED *ET AL.*, 2012 ; HAMID *ET AL.*, 2020 ; ISELI *ET AL.*, 2025) as well as high rates of species turnover (ISELI *ET AL.*, 2023 ; KALWIJ *ET AL.*, 2015 ; ZU *ET AL.*, 2022). However, despite growing evidence of invasive plant spread at high elevations, invasion risk is rarely assessed across entire mountain ranges and multiple species simultaneously, leaving climate-driven redistributions of invasive species along elevational gradients poorly understood.

As a major European mountain range, the Pyrenees present a valuable case study for assessing climate-driven invasion risks in mountain ecosystems. Spanning France, Andorra, and Spain between the Atlantic and Mediterranean regions, this range is located at the crossroads of several climatic and biogeographic influences. It is considered among the top biodiversity hotspots in Europe, with 3652 indigenous vascular plant species, of which about 5% are endemic (GÓMEZ *ET AL.*, 2017). Historically, the Pyrenees have acted both as refugia and dispersal corridors during past climatic fluctuations (GARCÍA *ET AL.*, 2022 ; SCHMITT, 2009). However, under ongoing climate warming, it remains unclear whether they will primarily function as a biogeographic barrier constraining the further spread of invasive species or instead emerge as a climatic refuge for species displaced from warmer regions. Across France and Spain, biological invasions already entail massive economic costs and projections suggest a steep increase toward 2040 (HENRY *ET AL.*, 2023). As a transboundary mountain range, it is interconnected by dense transport and tourism networks that facilitate species introductions from multiple biogeographic sources. Most alien plants in the Pyrenees occur at lower elevations, where human activities and associated anthropogenic corridors have facilitated their introduction and establishment, with valleys historically acting as the primary entry points into the mountain range (AYMERICH & SÁEZ, 2019 ; JANTZI *ET AL.*, 2021 ; NINOT *ET AL.*, 2017). Although few species are currently invasive at high elevations, factors such as second-home development, intense touristic and commercial connectivity, and ongoing climate warming may foster the future spread of some non-native species (AYMERICH & SÁEZ, 2019 ; SOTO *ET AL.*, 2025).

Although projections tend to predict an intensification of invasion impacts under future climates (ADHIKARI *ET AL.*, 2022 ; CARBONI *ET AL.*, 2018 ; PETITPIERRE *ET AL.*, 2016) and be intuitive to imagine, recent evidence suggests that the trajectories of non-native species may be more complex than uniformly expansive. Range dynamics often involve both gains and losses, with some taxa thriving under new conditions, while others experience local declines or even face extinction risks within their native range (PAUDEL *ET AL.*, 2025 ; STAUDE *ET AL.*, 2025). This contrasts the traditional perception of invasive species as systematic “winners” of global change and instead highlights a dynamic continuum of biogeographic responses shaped by regional

climates, human influence, and ecological constraints (HONG *ET AL.*, 2025). Notably, one quarter of naturalized plant species are themselves threatened within their native range (STAUDE *ET AL.*, 2025), illustrating that invasion success in one region can coincide with conservation concerns in another (GARZÓN-MACHADO *ET AL.*, 2012 ; MARKOVÁ *ET AL.*, 2020). This paradox, increasingly recognized across taxonomic groups (ROBUCHON *ET AL.*, 2025 ; TEDESCHI *ET AL.*, 2025), raises fundamental questions about whether non-native populations of threatened species should be conserved, and to what extent naturalization may act as inadvertent *ex situ* refuges under accelerating global change.

In this context of contrasting invasion trajectories, a spatially explicit assessment of future climatic suitability is needed to clarify patterns in mountain systems. Rather than assuming uniformly expansive responses, we hypothesize that future climatic suitability within the Pyrenees will exhibit species-specific and spatially heterogeneous dynamics, reflecting interspecific differences in climatic niches and pronounced environmental gradients within this mountain chain. Consequently, invasion risk cannot be captured by a simple “winners versus losers” framework (GOURY *ET AL.*, 2025) but requires examining how suitable conditions may expand, persist, or contract across space and time, with direct implications for future management efforts and associated economic costs. We therefore assess dynamics of future bioclimatic suitability for 35 non-native plant species classified as invasive on both sides of the Pyrenean range, documenting species-specific potential shifts and identifying areas most likely to become vulnerable to invasion by 2100 under multiple climate scenarios. We provide a rare range-wide, spatially explicit assessment of both climatic and economic dimensions of invasion risk across a complete mountain chain. By combining species-specific climatic niche projections with a range-wide spatial synthesis and linking these patterns to the temporal dynamics of invasion-related economic costs, this study identifies contrasting invasion trajectories and reveals where invasion risk is likely to persist, shift, or emerge under future climates.

Spatially explicit tools, such as species distribution models (SDMs), provide a well-suited framework to address these objectives. SDMs are widely used in invasion ecology to project how climate change may expand suitable areas to non-native species (BARBET-MASSIN *ET AL.*, 2018 ; RENTERIA *ET AL.*, 2021 ; SRIVASTAVA *ET AL.*, 2019). SDMs also provide a valuable framework to flag species with high expansion potential, helping managers anticipate which taxa are most likely to spread and where preventive efforts should concentrate. However, their application remains challenging, as invasive species often occupy only a subset of their potential environmental and geographic ranges, owing to the combined effects of human-mediated introductions, intraspecific variability, novel biotic interactions and niche shifts (FENOLLOSA *ET AL.*,

2025). Nevertheless, climate remains a primary driver of broad-scale invasive species distributions (BARROS *ET AL.*, 2025 ; BELLARD *ET AL.*, 2018 ; WALTHER *ET AL.*, 2009), such that our approach deliberately focuses on large-scale patterns of climatic suitability to capture general trends rather than fine-scale processes, following the framework developed in COLLETTE *ET AL.*, 2025. By illustrating species-specific dynamics of climatic suitability and by mapping emergent hotspots of suitability, we provide an operational foundation for coordinated surveillance and prevention across jurisdictions. While climate constitutes only one facet of the invasion process, assessing its suitability provides a valuable baseline for identifying locations where environmental conditions are becoming suitable for invasions. This baseline can subsequently be integrated with complementary information on land use patterns, corridor connectivity and management feasibility to refine priorities and guide proactive management across the Pyrenean range.

Material and methods

Species occurrences and bioclimatic data

We focused on plant species officially listed as invasive with a major impact (i.e. widely distributed taxa forming dense populations, according to French classifications) on at least one regional list of areas adjacent to the Pyrenees (see Supporting information). All selected species occur in both France and Spain, ensuring that each taxon is of recognized concern across the Pyrenean range.

For each species, post-1970 occurrence data were obtained from the Global Biodiversity Information Facility (doi: 10.5281/zenodo.18114751). To minimize spatial sampling bias, records with coordinate uncertainty > 1 km were removed, and spatial thinning was applied to retain a single occurrence per grid cell. Species lacking GBIF occurrence records in regions adjacent to the Pyrenees were excluded, as were species with insufficient occurrences to ensure representation across all spatial blocks required by the spatial cross-validation scheme. After these filtering steps, 35 species remained out of the 41 initially identified.

Bioclimatic predictors were obtained from the WorldClim v2.1 database (FICK & HIJMANS, 2017), which provides 19 variables describing temperature and precipitation regimes for both the baseline period (1970–2000) and four futures (2021–2040, 2041–2060, 2061–2080, and 2081–2100, referred to as 2030, 2050, 2070, and 2090). Future projections were generated under four Shared Socioeconomic Pathways (SSPs, SSP126, SSP245, SSP370, and SSP585), covering a range of potential climate trajectories (O'NEILL *ET AL.*, 2017).

Bioclimatic suitability modeling and spatial dynamics of invasion risk

Bioclimatic suitability modeling

We adopted the ensemble modeling framework described in COLLETTE *ET AL.*, 2025, integrating five algorithms into an ensemble model: generalized linear models (GLM), generalized additive models (GAM), generalized boosted models (GBM), random forest (RF), and maximum entropy (MaxEnt). Because invasive plants typically have broader and more extensively documented distributions than rare endemic taxa, occurrence data are less extremely imbalanced. Model performance was therefore evaluated using the Area Under the Receiver Operating Characteristic Curve (AUC-ROC), a widely used discrimination metric, instead of Area Under the Precision–Recall Curve (AUC-PR). In addition, the spatial cross-validation scheme was adjusted by increasing the number of spatial blocks to five, with an adjusted block size. These methodological adaptations specific to this study are detailed in the ODMAP protocol (Overview, Data, Model, Assessment and Prediction), a standardized framework for transparent SDMs reporting (ZURELL *ET AL.*, 2020, Supporting information).

Model calibration was conducted within the smallest bounding box that maximized GBIF data coverage while preserving computational efficiency. The chosen extent included climatically extreme regions (e.g., northern Europe and the Alps) to ensure a broad representation of environmental conditions. This approach is consistent with evidence that models calibrated on invaded ranges outperform those built across entire distributions (BARBET-MASSIN *ET AL.*, 2018). Future projections were restricted to a bounding box encompassing the Pyrenean range, and all suitability maps for analyses were subsequently cropped to the Pyrenees following the mountain delimitation proposed by KÖRNER *ET AL.* (2011) and updated by SNETHLAGE *ET AL.* (2022) ; all maps are available in the Supplementary Material.

Spatial and temporal dynamics of bioclimatic suitable area

To quantify changes in suitable bioclimatic areas, continuous suitability maps were binarized for each period and SSP using the maximum sum of sensitivity and specificity (maxSSS) threshold (LIU *ET AL.*, 2013 ; 2016). Suitable area was then calculated for the current period and for each future period–SSP combination. Spatial overlap between present and future binary maps was computed to estimate the proportion of currently suitable areas projected to remain suitable under each scenario. Each taxon was classified according to whether it showed a consistent increase (“winner”) or display decrease (“loser”) in suitable bioclimatic areas throughout the century across all SSP scenarios. Latitudinal, longitudinal and elevational shifts between the current period and 2081–2100 were quantified by overlaying binarized projections with elevation data from CGIAR-CSI (2018; ~1 × 1 km resolution at the equator) and corresponding geographic coordinates. For each species, elevational, latitudinal and longitudinal centroids, defined as the mean elevation, latitude and longitude of suitable pixels, were calculated for the current period and for each SSP. Only species retaining

suitable areas under all SSPs were used to estimate overall centroid shifts between present and future conditions. Species-specific shifts under each SSP are reported in Supporting information.

Mapping bioclimatic invasion hotspots and their overlap with endemic biodiversity.

Continuous suitability maps for the current and future (2081–2100) periods were averaged across species to identify bioclimatic hotspots, defined as areas where the highest number of invasive taxa is projected to find suitable climatic conditions in the future. To further assess potential spatial conflicts between biological invasions and native biodiversity, bioclimatic hotspots identified for invasive species were compared with hotspots previously found for endemic plant species of the Pyrenees, using the same framework (COLLETTE *ET AL.*, 2025b). Hotspot maps of all SSPs were binarized using a threshold of 0.2, corresponding to the lowest non-zero class of the legend, thereby retaining all areas showing any hotspot signal. Spatial overlap between invasive and endemic hotspots was then quantified using the Jaccard similarity index (spatial overlap index; (JACCARD, 1901)). This index ranges from 0 (no overlap) to 1 (complete overlap), providing a standardized metric to evaluate the degree of spatial congruence between invasion risk hotspots and areas of high endemic suitability.

Altitudinal distribution and economic impacts of invasive species in the Pyrenees

Distribution of invasive species across the altitudinal belts of the Pyrenees

Occurrence records were intersected with a classification of four elevation belts corresponding to the main vegetation zones of the Pyrenees: foothills and lower montane (0–900 m), montane (901–1 800 m), subalpine (1 801–2 300 m), and alpine zone above 2 300 m (SAULE *ET AL.*, 2018). For this analysis, we used the full set of occurrence records (i.e., non–spatially thinned data). For each belt, we quantified species richness, identified the taxa present and their relative proportions, and summarized species composition by life form, using life-form information compiled from the FloraVeg.EU database (CHYTRÝ *ET AL.*, 2024). Life forms were harmonized into four categories: trees, shrubs, herbs, and aquatic species (Supporting information). Six species with no recorded occurrences within the Pyrenees (*Cabomba caroliniana, Crassula helmsii, Lindernia dubia, Pistia stratiotes, Elodea nuttallii, and Hydrocotyle ranunculoides*) were excluded from these analyses.

Economic cost assessment of invasive species

Economic cost data associated with invasive plant species were extracted from the InvaCost package (LEROY *ET AL.*, 2022). Records were filtered to retain only observed costs with high methodological reliability reported for France and Spain, which were used as a proxy to infer the temporal dynamics of invasion-

related economic costs potentially relevant to the Pyrenean region. This approach was adopted because cost data specifically attributable to mountain systems are scarce, while France and Spain encompass the entire Pyrenean range and provide the most comprehensive and comparable datasets available. Only species with cost data available for at least three distinct years were retained, resulting in 19 of the 35 invasive species being included in the economic analysis.

For each species, annual costs pooled across France and Spain were summarized and analyzed using *invacost* (Supporting information). Multi-year cost entries were expanded into annual values, and all costs were standardized to 2017 USD. Temporal trends in economic costs were assessed using generalized additive models (GAM) fitted to log-transformed yearly costs, as implemented in *invacost*, and projections were extended to 2050 to describe potential future trajectories.

Results

A strong decline in invasive species richness with elevation

Intersecting occurrence records with the four elevational belts revealed a clear concentration of invasive taxa at low elevations. Invasive occurrences were clustered along valleys and low-elevation depressions, especially in the northeastern Pyrenees (Figure 1a).

The foothill and lower montane belt (0–900 m), which represents the largest portion of the mountain system (45.8 % of the Pyrenees surface), hosted 28 species, accounting for 77.26**%** of all occurrences, making it by far the richest zone (Figure 1b). Species richness then declined steadily with elevation: 20 species in the montane belt (901–1 800 m), 10 species in the subalpine belt (1 801–2 300 m), and 5 species in the upper alpine zone (> 2 300 m). After standardizing by belt area, species density followed the same decreasing trend with elevation (Appendix E). Five species are recorded in the upper alpine zone, *Elodea canadensis, Fallopia baldschuanica, Helianthus tuberosus, Impatiens balfourii, Senecio inaequidens*. Within the subalpine belt, most species were rare; among the 10 species present, eight reached this elevation only marginally (0.11–2 % of their occurrences), suggesting that their distribution there remains marginal or incidental. Two species stood out, with much higher proportions of occurrences. *Heracleum mantegazzianum* reached about 36 % of its records in this belt, and *Elodea canadensis* is around 11 %, revealing a marked capacity for establishment in colder, high-mountain environments. Overall, these results show that invasive plants in the Pyrenees are primarily concentrated at low elevations, yet several taxa already demonstrate the ability to colonize high-mountain environments.

Life-form composition also shifted markedly with elevation (Figure 1c). Herbs dominated all belts and represented most invasive taxa throughout the gradient, reflecting their broad ecological tolerance. Shrubs

and trees were concentrated in the lower and mid-montane belts, and their richness declined sharply with altitude. Trees were entirely absent from the upper alpine zone (> 2 300 m), indicating that woody invasive species are currently unable to establish in the most climatically constrained environments of the range. This consistent dominance of herbs combined with the restricted altitudinal reach of woody species highlights the strong filtering imposed by climate and habitat conditions along the Pyrenean gradient.

Future bioclimatic suitability declines for most species, with only 20% potential winners

Projections indicated marked variation in future bioclimatic suitability across the 35 invasive taxa (Figure 2). Overall, 80 % of species were projected to experience a reduction in suitable climatic areas by 2081–2100 under at least one SSP scenario. Losses were substantial for several species: six were projected to lose more than 75 % of their suitable area, ten lost 50–75 %, one lost 33–50 %, and eighteen lost less than 33 %. Averaged across species, changes ranged from −8.33 % under the most optimistic scenario (SSP126; min: +222.6 %, max: −92.9 %) to −82.24 % under the most pessimistic one (SSP585; min: −0.7 %, max: −100 %). Two species (*Paspalum dilatatum* and *Heracleum mantegazzianum*), experienced a complete loss of suitable bioclimatic area in at least one scenario.

In contrast, seven species (20 %) were identified as potential “winners” of climate change, with average gains of +191.42 % under SSP126 (min: +22.8 %, max: +476.5 %) and up to +380.83 % under SSP585 (min: +22.6 %, max: +819.9 %). More species could appear as winners based on their consistent increases in suitable areas under the mid and intermediate scenarios (SSP126 or SSP245), but these apparent beneficiaries ultimately shifted to the “loser” category by experiencing sharp reductions in suitability under other more pessimistic scenario.

Across the five algorithms (GLM, GAM, GBM, RF, MaxEnt), cross-validated model performance was consistently high, with AUC averaging 0.82 ± 0.07, Boyce index 0.82 ± 0.13, and sensitivity 0.87 ± 0.04 (Supporting information). Between 6 and 50 models depending on species were used for predictions.

Climate-driven upward, northward and westward shifts of climatically suitable areas with complete spatial reorganization

Across species retaining suitable conditions across SSPs during the 2081-2100 period, the centroid of climatically suitable areas shifted upward on average by 161 m (range -309.9 to +562.1 m), a northward shift of ~11 km (range -34.7 to +56 km) and a western shift of ~59 km (range −222.3 to +25.6 km) (Figure 3a). By 2081-2100 period, 29 species are projected to shift upslope (Figure 3b), with the centroid of their climatically suitable areas moving upward by +2.03 % to +194.22 % (mean: 53.65 %). In contrast, only four species are

projected to shift downslope (Figure 3b), with centroid elevations decreasing by −35.38 % to −4.17 % (mean: −20.98 %). Longitudinally, suitability centroids shifted predominantly westward, with 25 species shifting on average by −83.1 km (range: −222.3 to −0.1 km), whereas eight species shifted eastward on average by +14.8 km (range: +4.2 to +25.6 km). Latitudinally, suitability centroids shifted mainly northward, with 23 species shifting on average by +20.2 km (range: +3.1 to +56 km), while 10 species shifted southward on average by −11.8 km (range: −34.7 to 0 km) (Figure 3a).

Spatial overlap between current and future suitable areas declined steadily as emission levels increased (Figure 3c). Under the most optimistic scenario (SSP126), sixteen species maintained near to complete (>75 %) overlap with their current climatic range. This number decreased sharply under intermediate scenarios (e.g., only nine species under SSP245 and six under SSP370). Under the most pessimistic scenario (SSP585), overlap collapsed: six species showed no overlap with their present climatic niche, twenty retained only 0–25 % overlap, and only five maintained near to complete overlap. Low overlap reflected either the disappearance of present climatic conditions (1 case under SSP245 and SSP370, two cases for SSP585) or a strong spatial displacement of suitable areas relative to the current range (1 case under SSP245, 2 cases for SSP370 and 4 cases for SSP585).

Rising invasion risk in montane belts with limited overlap with endemic hotspots

Hotspot analysis, defined as areas where several species simultaneously retain suitable conditions, revealed marked changes across time (Figure 4). Current hotspots reached a maximum suitability of 0.73, which declined to 0.59 by the 2081–2100 period, and showed upward displacement that became increasingly marked as climate scenarios became pessimistic. The most persistent hotspot was concentrated in the Atlantic sector of the Pyrenees, consistent with westward shifts in species centroids of bioclimatic suitability. No hotspot extended above 2 000 m in any scenario, and the low-elevation plains south of the range became increasingly unsuitable, contributing to the overall decline in hotspot maximum suitability.

Spatial overlap between invasive and endemic bioclimatic hotspots was limited under current climatic conditions and declined sharply under future scenarios (Figure 5). Under current conditions, hotspot overlap represented 2 750 km², corresponding to 16.6 % of endemic hotspot area and 10.1 % of invasive hotspot area (Jaccard index = 0.07). By the 2081-2100 period, overlap decreased markedly across all scenarios, falling to 878 km² under SSP126 (8.4 % of endemic and 2.9 % of invasive hotspots; Jaccard index = 0.02), and becoming nearly negligible under SSP245 (< 3.16 km²; Jaccard index ≈ 0). No spatial overlap was detected under the most pessimistic scenarios (SSP370 and SSP585).

Climatic winners currently incur lower costs but may drive future economic impacts

Across all species, economic costs were analyzed over the 1999–2020 period based on 940 cost estimates. Within this dataset, differences emerged between projected climatic losers and winners among the 19 invasive species for which economic costs could be assessed. Species classified as climatic losers (n = 13) were associated with substantially higher economic costs, with a mean annual cost of 4.47 × 10□ USD and a median annual cost of 3.93 × 10□ USD. In contrast, climatic winners (n = 6) exhibited much lower costs, with a mean annual cost of 3.41 × 10□ USD and a median of 2.04 × 10□ USD. This contrast reflected strong interspecific heterogeneity, with *Ambrosia artemisiifolia* (climatic loser) showing the highest average annual cost (5.74 × 10□ USD), whereas *Araujia sericifera* (climatic winner) displayed the lowest (2.55 × 10^2 USD). Economic cost projections for 2050 were available for 12 species. For most taxa, wide confidence intervals encompassing current annual cost values prevented the detection of clear temporal trends. However, three species exhibited unambiguous trajectories. Climatic winner species (*Egeria densa* and *Opuntia stricta*) showed declining projected costs, whereas the climatic loser *Reynoutria japonica* exhibited a marked increase in projected costs. No consistent trends could be identified for the remaining species (Supporting information).

Discussion

Our study provides a range-wide, spatially explicit assessment of invasion risks in a major European mountain system and reveals that climate change will not systematically promote invasive plant expansion in mountain landscapes. Although invasive plant species are generally perceived, and often reported, as most winners under climate change (GOURY *ET AL.*, 2025), we found that 80% will be likely rather losers (and only found 7 species as putative winners). Our results thus stand out from the ones of comparable studies available in the literature and incite to reconsider the actual status of these invasive species and better adjust the strategies to control them.

Climate change will not promote invasive plant expansion in mountain landscapes

Our results challenge the expectation that invasive species are generally beneficiaries of global change. Most of the assessed taxa (80% of the 35 species) are projected to lose suitable bioclimatic areas by 2081–2100 period under at least one emission scenario, on average by −9.12% under SSP126 to −82.59% under SSP585. Two species even lose all suitable bioclimatic areas, *Paspalum dilatatum* and *Heracleum mantegazzianum*, under pessimistic scenarios after 2041–2060 period. This demonstrates that even invasive species, often assumed to tolerate broad environmental conditions (EYSTER & WOLKOVICH, 2021 ; GODOY *ET*

AL., 2011 ; HIGGINS & RICHARDSON, 2014) and to gain a relative advantage over native species under changing climate change (DESLIPPE & VEENENDAAL, 2025 ; LIU *ET AL.*, 2017 ; YANG *ET AL.*, 2022), can experience sharp declines as climatic stress intensifies. Conversely, a smaller subset of species displayed an expansion potential, with seven species increasing their bioclimatic suitable area on average by +191.42% under SSP126 and up to +380.83% under SSP585. Among these, *Araujia sericifera* and *Opuntia stricta* showed particularly pronounced gains, exceeding 800%. In addition, several taxa that initially appeared to benefit under moderate warming ultimately shifted to net losses under more extreme scenarios, indicating that apparent climatic "winners" can quickly become "losers" once tolerance thresholds are exceeded. Together, these findings reinforce emerging global evidence that alien species do not uniformly benefit from warming, a conclusion already suggested by early global assessments showing that climate change does not systematically advantage exotic species (BELLARD *ET AL.*, 2013 ; THUILLER *ET AL.*, 2007). Moreover, the literature consistently shows that invasion success is context-specific, shaped by interactions between species characteristics (BUCKLEY & CSERGŐ, 2017) and recipient ecosystem properties (CATFORD *ET AL.*, 2022 ; GIORIA *ET AL.*, 2023 ; KAUSHIK *ET AL.*, 2022 ; NOVOA *ET AL.*, 2020 ; PYSEK *ET AL.*, 2020a).

While these results illustrate how bioclimatic projections can be used to explore potential climate-driven shifts in invasion risk, their interpretation requires careful consideration of their scope and limitations (COLLETTE *ET AL.*, 2025a). By design, bioclimatic SDMs focus on climate–suitability relationships and therefore capture only one component of the invasion process, overlooking key drivers of establishment and spread, such as land-use change, propagule pressure, dispersal constraints, microclimatic buffering, edaphic and hydrological conditions, and biotic interactions (GALLIEN *ET AL.*, 2015 ; SRIVASTAVA *ET AL.*, 2019). Although incorporating these additional dimensions can refine spatial prioritization and management decisions, such approaches often rely on extensive, high-quality datasets, which may limit their applicability in data-poor contexts (FENOLLOSA *ET AL.*, 2025) such as mountain systems. Thus, projected gains or losses in climatic suitability do not directly predict future abundance or realized spread but instead provide a partial baseline for identifying conditions that may facilitate the establishment of non-native species, which must be integrated with broader ecological and socio-environmental processes.

Climate change reshapes invasion risk toward mountain belts

For invasive species, climate change is expected to drive pronounced spatial redistribution of suitable bioclimatic conditions, reshaping potential invasion pathways. Spatial overlap between current and future suitable areas declines sharply with increasing emission scenarios, indicating a growing mismatch between present-day distributions and future climatic conditions. This reflects two complementary processes: the loss

of currently suitable climates for some taxa, and the spatial displacement of suitability for others. Both point to pronounced distributional turnover and increasing constraints on species' ability to track suitable conditions under high-emission trajectories (CHAN *ET AL.*, 2024 ; VITASSE *ET AL.*, 2021), with consequences for invasion risk assessment. Among taxa that retain suitable conditions across all climate scenarios by 2081-2100 period, our results show that the centroid of bioclimatic suitable areas is projected to shift upward by an average of +161 m, northward by 10.5 km and westward by 59.4 km. In the Pyrenees, these shifts are consistent with projected increases in mean annual temperature (+2.2 °C under SSP126 to +6.1 °C under SSP585) and declining precipitation (−3.6 mm under SSP126 to −132.4 mm under SSP585) (COLLETTE *ET AL.*, 2025b), suggesting an upslope tracking of suitable climates as foothill environments become increasingly restrictive. The westward and northward shifts align with the climatic contrast across the range, as Atlantic sectors in the western Pyrenees are wetter than the Mediterranean-influenced eastern side, and warmer climatic conditions prevail on the Spanish side south of the Pyrenees. These patterns are also consistent with the widespread altitudinal and latitudinal shifts in plant distributions documented in the literature over recent decades (ISELI *ET AL.*, 2023 ; LENOIR *ET AL.*, 2008 ; RUBENSTEIN *ET AL.*, 2023). Despite these upslope shifts, no invasion hotspots, defined as areas where the highest number of species could simultaneously find suitable conditions, are projected to occur above 2 000 m, highlighting the persistent environmental constraints of alpine environments throughout the century. This pattern is consistent with the well-documented decline in species richness with elevation (ALEXANDER *ET AL.*, 2016 ; DI MUSCIANO *ET AL.*, 2021), with only a limited number of species occurring in the alpine zone (BECKER *ET AL.*, 2005). However, the persistence and intensification of hotspots within the montane belt indicate increasing invasion pressure at higher elevations. In contrast, hotspots in the southwestern foothills and adjacent lowlands show marked losses of climatic suitability, suggesting a progressive retreat of invasive plants from areas projected to become excessively warm or dry. Together, these patterns indicate that invasive species may increasingly concentrate at intermediate elevations, consistent with the recurrent mid-elevation peak in plant species richness along elevational gradients (MCCAIN & GRYTNES, 2010), as limited suitability in both lowland and alpine zones constrains further downslope or upslope expansion. In this context, the Pyrenees may function as a climatic trap, temporarily retaining invasive populations within a narrowing elevational band.

At the regional scale, these projections are supported by empirical evidence from a mountain system located south of the Pyrenees, where vegetation belts have already shifted upslope, characterized by the expansion of Mediterranean formations and the regression of montane and subalpine communities, driven by rising temperatures and land-use changes, particularly the abandonment of agro-pastoral practices (PENUELAS &

BOADA, 2003). In the Pyrenees themselves, invasion patterns already reflect strong biogeographical and anthropogenic structuring. On the Mediterranean side, coastal areas host the highest richness of established alien species, some of which have spread into the Pyrenean foothills and subalpine zones. In central areas such as Andorra, most introductions are recent, mainly after the 1980s, coinciding with the rise of mountain tourism and the ornamental plant trade (SOTO *ET AL.*, 2025). In the south of the Pyrenees, these introductions are predominantly of Palearctic origin, reflecting intra-continental "neo-naturalization" rather than tropical exotic invasion. These trends are consistent with biogeographical patterns, with alien species with a wide distribution largely associated with Mediterranean and temperate climates and rarely linked to boreal–alpine environments. As a result, they are mainly concentrated at low to mid-elevations, where such habitats are available (NINOT *ET AL.*, 2007). In line with these observations, several species in our dataset already persist within the montane and, in some cases, alpine belts, suggesting that more clement future climates could promote the expansion of these early colonizers and facilitate the establishment of additional taxa at higher elevations. This upward recruitment is likely to be further reinforced by anthropogenic dispersal processes. Roads and valley corridors act as efficient conduits for upslope spread (ISELI *ET AL.*, 2023 ; VORSTENBOSCH *ET AL.*, 2020), as reflected by the clustering of current occurrence records along the valleys for the studied species, influenced by a large lowland urban center (>250 000 inhabitants) and the proximity of the Mediterranean coast. In addition, recreational and agro-pastoral activities can inadvertently transport propagules into otherwise isolated high-elevation habitats and facilitate their establishment by disturbing natural habitats (BARROS *ET AL.*, 2025 ; HEMP, 2008 ; KOYAMA *ET AL.*, 2024 ; LIEDTKE *ET AL.*, 2020 ; MONTAGNANI *ET AL.*, 2022). Together, these mechanisms highlight mountain valleys and adjacent elevational gradients as key areas for early detection, rapid response and coordinated transboundary management.

Spotlights on trajectories of famous climatic winners, conditional winners and consistent losers

Species-specific climatic trajectories reveal heterogeneity in how invasive taxa may respond to future warming. To illustrate these contrasts, we focus on several representative species from our dataset. Among the most consistent climatic winners, *Opuntia stricta* shows continuous increases in projected suitability across all scenarios. This perennial succulent is highly tolerant to heat, drought and climatic seasonality, with evidence of persistence beyond arid systems (GAYE *ET AL.*, 2025 ; SONG *ET AL.*, 2025). It preferentially establishes in open, disturbed habitats associated with human activities (MISURI *ET AL.*, 2025 ; SHACKLETON *ET AL.*, 2017). Under future warming, its bioclimatic suitable conditions are projected to expand mainly at mid elevations, where reduced frost frequency may facilitate its upslope expansion into open grasslands and pastoral systems in the Pyrenees. Given its status among the world's most problematic invasive species

(SIMBERLOFF & REJMANEK, 2019) targeted monitoring is needed where future climatic suitability overlaps with human activities. Similar patterns observed in other mountain systems suggest that climatic winners under warming often combine thermophile, ruderal strategies and high colonization capacity, traits overrepresented among invasive taxa (GOURY *ET AL.*, 2025), as exemplified by *Opuntia stricta*, calling for heightened vigilance in the Pyrenees.

In contrast, *Senecio inaequidens,* a well-known invasive species in grasslands, and *Datura stramonium*, a toxic invasive herb posing risks to livestock and agricultural systems, emerge as conditional winners. They displayed increases in suitability under moderate warming (SSP126–245) followed by declines under high-emission scenarios (SSP370–585) after 2041–2060. Although *S. inaequidens* already recruits at high elevations in the Pyrenees and other mountain systems and has not fully occupied its current climatic niche (VACCHIANO *ET AL.*, 2013), projected declines under severe warming indicate emerging climatic constraints. Its capacity for rapid local adaptation (MONTY & MAHY, 2009), tolerance to cold winters (LACHMUTH *ET AL.*, 2010), and early establishment in species-poor communities (DELORY *ET AL.*, 2019), may nonetheless allow persistence despite declining suitability. *D. stramonium* displays a comparable non-linear response: gains under intermediate scenarios likely reflect its broad climatic niche (CHEN *ET AL.*, 2025) and warming-driven growth advantages, whereas subsequent declines may result from increasing drought stress at lower elevations (CHADHA *ET AL.*, 2020). But once again, this result must be interpreted with caution, as this species can maintain high seed production under moderate drought and may, therefore, remain invasive despite climatic constraints. Together, these cases illustrate that early climatic gains do not necessarily translate into sustained expansion once key physiological thresholds are exceeded.

A third set of species, including *Buddleja davidii*, a fast-growing invasive shrub that disrupts native pollination networks, and *Reynoutria japonica*, a highly invasive clonal plant forming dense monospecific strands, emerges as consistent climatic losers, with projected contractions of suitable areas under all scenarios. In both cases, the hypothesis is that range losses are primarily driven by upward shifts of lower elevational limits rather than successful colonization at higher elevations, resulting in net range contraction (ZU *ET AL.*, 2021). This pattern is consistent with evidence from the Alps, where successful upslope colonization by invasive plants is largely restricted to cold-tolerant taxa (PETITPIERRE *ET AL.*, 2016), and with global analysis showing that local extinctions disproportionately affect populations at warm range margins as annual maximum temperatures increase (ROMÁN-PALACIOS & WIENS, 2020). Despite their broad ecological and altitudinal tolerance in their native ranges (B. davidii, up to 3500 m across temperate to subtropical climates (TALLENT & WATT, 2009); R. japonica, up to 3 800 m (BEERLING *ET AL.*, 1994 ; NEGREA *ET AL.*, 2022))

associated with riparian and disturbed habitats (BARNEY *ET AL.*, 2006)) projected declines in the Pyrenees are best interpreted as an altitudinal squeeze. Increasing summer heat, moisture limitation and water stress reduce suitability at lower elevations (KADLECOVÁ *ET AL.*, 2024 ; MIROSHNYK *ET AL.*, 2025), while upward expansion remains constrained by persistent cold conditions, temperature variability and minimum growing-season temperatures (MIROSHNYK *ET AL.*, 2025 ; WITTIG, 2012). For both species, reliance on phenotypic and ecological plasticity rather than local adaptation (B. davidii: EBELING *ET AL.*, 2011, R. japonica: MARTIN *ET AL.*, 2020) may limit their ability to overcome these upper-elevation constraints.

Together, these examples illustrate a continuum of invasion trajectories shaped by species-specific combinations of climatic tolerance, habitat dependence and sensitivity to climatic thresholds. While identifying traits associated with persistent expansion can inform risk assessment (but see EARLE *ET AL.*, 2023 ; MOLES *ET AL.*, 2012) invasion outcomes remain strongly context-dependent.

Climate could constrain direct competition between invasive and endemic plants in the Pyrenees

The decline in hotspot intensity and their upward displacement resulted in a contraction of spatial overlap between invasive and endemic plants hotspots, declining from 16.6 % under current conditions to nearly zero in the future. This pattern suggests that ongoing warming will substantially reduce the area simultaneously suitable for both invasive and endemic taxa, thereby limiting the spatial scope for direct biotic interactions. Such upward invasion pressure raises management concerns, as alpine and subalpine communities may, in some cases, be particularly vulnerable to replacement by taxa that track warming climates more efficiently (BRADLEY *ET AL.*, 2024 ; DAINESE *ET AL.*, 2017 ; GEPPERT *ET AL.*, 2023). However, our results indicate that climatic constraints may also restrict the long-term co-occurrence of invasive and endemic plants. Insights from a comparable analysis of Pyrenean endemic plant species (Collette et al., 2025b) show that suitability hotspots for endemics are projected to remain largely confined above 2 000 m, whereas our results show that invasive species hotspots predominantly occur below this elevation. This consistent elevational segregation suggests that climate change may act as an environmental filter, allowing endemic taxa to persist in high-elevation climatic refugia while limiting the upward expansion of most invasive species. Even where invasive and endemic species may locally co-occur at high elevations, the impacts of non-native plants on alpine ecosystems are not systematic and have so far been documented as limited (ALEXANDER *ET AL.*, 2016). Under our scenarios, invasive and endemic plants would increasingly occupy distinct climatic niches, reducing the likelihood of widespread direct competition along the mountain chain, even if endemic species face substantial constraints in tracking suitable conditions.

Rethinking invasive risks under climate change: should invaders be "allowed" to persist for the sake of species conservation?

The divergent trajectories observed among taxa call for a reassessment of how invasion risk is defined in the context of rapid global change. Our results reveal contrasting situations in which the same mountain system may either facilitate or constrain the persistence of non-native species. *Carpobrotus edulis*, illustrates this complexity in our analysis. In the Pyrenees, this species is a climatic winner, projected to expand its suitable area under future warming. Yet, model-based extinction-risk assessments suggest that it may become threatened in parts of its native range (BACHMAN *ET AL.*, 2024). Here, mountain systems may act as climatic refugia, providing to a non-native taxa one of the last environments matching its fundamental climatic niche. Conversely, climatic losers such as *Ambrosia artemisiifolia* illustrate the opposite trajectory. This species currently represents a major management concern due to its severe health impacts (SCHAFFNER *ET AL.*, 2020) and generates the highest economic costs within our dataset. Our projections further suggest that its long-term persistence in the Pyrenees may become increasingly unlikely, with potentially positive implications for human health in the region. Here, mountain systems may instead act as climatic barriers, or even as traps, limiting future establishment and spread. Together, these contrasting outcomes raise a fundamental question: should global invasive species be managed uniformly when their climatic vulnerability and persistence differ across regions? (BAQUERO *ET AL.*, 2023). Beyond this dichotomy, our framework also allows for a third outcome, in which species could potentially face extinction risks in both their native and invaded regions, as illustrated in our study by *Impatiens balfourii*. Such cases exemplify the conservation–invasion paradox, whereby invasive species may simultaneously pose ecological threats in some regions while raising conservation concerns in others (HONG *ET AL.*, 2025 ; STAUDE *ET AL.*, 2025), calling for more nuanced, context-dependent management strategies.

In mountainous systems where most endemic species are threatened by climate change regardless of invasive species (COLLETTE *ET AL.*, 2025b), the future composition of the flora becomes a central issue. But the role of non-native and invasive species in this composition is unclear. In the Pyrenees, our results indicate only marginal spatial overlap between endemic and invasive plants, suggesting that invasive species may contribute to future floristic reorganization without constituting a primary threat to endemic persistence. Beyond species redistribution, further investigation is needed into whether invasive species may also shape future flora through the generation of evolutionary novelty. This may occur through rapid adaptation (CLEMENTS & JONES, 2021 ; MORAN & ALEXANDER, 2014) or through hybridization with native taxa or among non-native lineages, potentially leading to the emergence of new evolutionary lineages

(ELLSTRAND, 2009 ; ELLSTRAND & SCHIERENBECK, 2000) and thus generate novel evolutionary outcomes (MEYERSON *ET AL.*, 2010 ; MOONEY & CLELAND, 2001) and diversity when colonizing new environments (VELLEND *ET AL.*, 2007). However, although evolutionary change can occur over short timescales, its magnitude is frequently insufficient to keep pace with the rate of projected climate change (JEZKOVA & WIENS, 2016).

Using projection of bioclimatic niche modeling to reallocate management investment

Species-specific climatic futures become particularly informative when interpreted alongside economic projections. Across all species, economic costs estimated over the 1999–2020 period reveal a strong asymmetry between climatic losers and winners: taxa projected to lose climatic suitability are currently associated with substantially higher economic costs than climatic winners. This contrast is largely driven by a concentration of economic costs in a few highly impactful species, such as *Ambrosia artemisiifolia*, which accounts for a substantial share of current cost burdens, whereas climatic winners are fewer in number and remain weakly documented in terms of economic impacts to date (858 vs. 182 studies). When focusing on species showing clear climatic and economic trajectories, an unexpected inverse relationship emerges between future climatic suitability and projected management costs. Costs tend to decrease for climatic winners (e.g. *Egeria densa*, *Opuntia stricta*), while increasing for climatic losers (e.g. *Reynoutria japonica*), suggesting that current economic impacts do not necessarily anticipate future invasion risks. Species projected to gain climatic suitability may exert increasing impacts despite currently low management costs. This result emphasizes that management priorities should anticipate emerging risks rather than mirror current cost allocations, reallocating efforts toward species projected to expand or exert increasing impacts, while reprioritizing those expected to decline. In practice, while climatic losers may justify a gradual reallocation of management resources, complete disengagement is rarely warranted. Taxa may persist long after climatic conditions become unsuitable, a process described as extinction debt (KUUSSAARI *ET AL.*, 2009). Even after population decline or local eradication, invasive species may continue to exert ecological and economic impacts through persistent legacies on soils, biotic interactions and ecosystem processes, thereby affecting vulnerable communities well beyond their expansion phase (AHMAD *ET AL.*, 2021 ; CORBIN & D'ANTONIO, 2012 ; ESSL *ET AL.*, 2015 ; PRIOR *ET AL.*, 2018).

Although invasive species are increasingly recognized as an emerging threat in mountain systems, the Pyrenees still lack a harmonized transnational framework to identify priority areas for surveillance and to

coordinate management across administrative boundaries. Focusing monitoring efforts on areas projected to become climatically suitable could substantially improve efficiency, as early detection and rapid response are consistently more cost-effective and ecologically sustainable than reactive control following establishment (AHMED *ET AL.*, 2022 ; HANLEY & ROBERTS, 2019 ; VENETTE *ET AL.*, 2021). This is particularly critical in mountain landscapes, where rugged and inaccessible terrain constrains mechanized control and increases reliance on labor-intensive interventions, thereby amplifying both financial and human costs (MCDOUGALL *ET AL.*, 2011).

Overall, our findings highlight a growing mismatch between climatic opportunities, economic impacts and conventional invasion risk assessments, underscoring the need to reassess how non-native species are evaluated and prioritized under ongoing climate change. Climate change increasingly blurs the boundary between natural range shifts and biological invasions, challenging traditional invasion categories and complicates the terminology and frameworks traditionally used in invasion ecology (FUSCO *ET AL.*, 2024 ; WALTHER *ET AL.*, 2009). These dynamics call for more flexible, context-dependent management frameworks, commonly referred to as climate-smart approaches (COLBERG *ET AL.*, 2024), which highlight the importance of considering climate-driven shifts in species distributions and persistence, as well as their implications for management feasibility and effectiveness. Our results further indicate that mountain systems such as the Pyrenees may simultaneously act as climatic barriers and as refugia, or potential traps, for non-native taxa. A central challenge therefore lies in distinguishing species that are likely to lose climatic suitability and ecological relevance from those that may benefit from warming, in evaluating the magnitude of their future impacts, and in anticipating which taxa could increasingly contribute to the future emblematic flora of the Pyrenees as suitable conditions disappear elsewhere. Integrating genetic, ecological and environmental data across invasion stages provides a powerful framework for anticipating invasion dynamics under global change, and supports the development of flexible, climate-informed management strategies that explicitly account for evolutionary and demographic processes (SHERPA & DESPRÉS, 2021).

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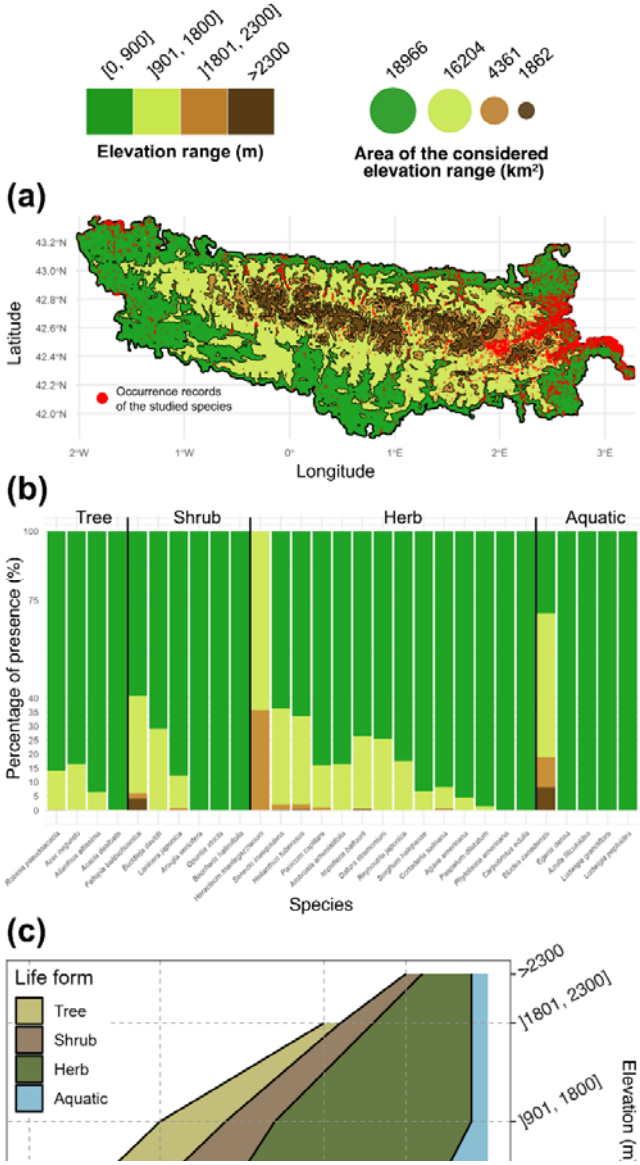

Figures for:

Climbing invasions or climatic refugees: how many and to which extent non-native plant species could reach the Pyrenees mountains under climate change?

Figure 1. Spatial, elevational and life-form distribution of 35 invasive plant species in the Pyrenees. (a) Spatial distribution of all occurrence records across the main vegetation belts of the Pyrenees: foothills and lower montane (0–900 m), montane (901–1 800 m), subalpine (1 801–2 300 m), and alpine (> 2 300

m). **(b)** Percentage of occurrences per species across the four vegetation belts and their life-form categories (tree, shrub, herb and aquatic). **(c)** Species richness across elevation for each life-form category.

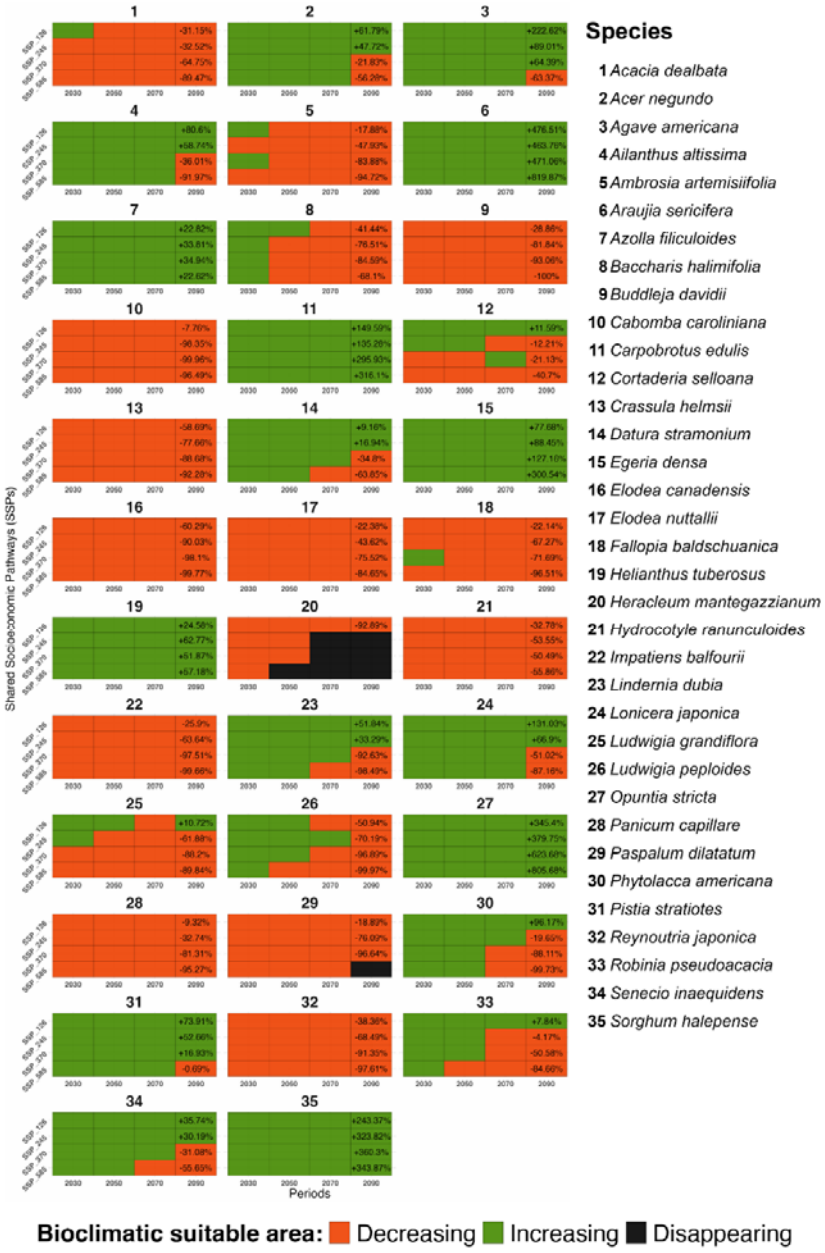

Figure 2. Projected extent changes in bioclimatic suitability for invasive plant species in the Pyrenees. Extent changes in suitable areas over the 2021-2100 period under Shared Socioeconomic Pathways (SSP) SSP126, SSP245, SSP370, SSP585, relative to the baseline period (1970-2000) for 35 invasive plant species. Each box represents the extent change in suitable areas, 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.

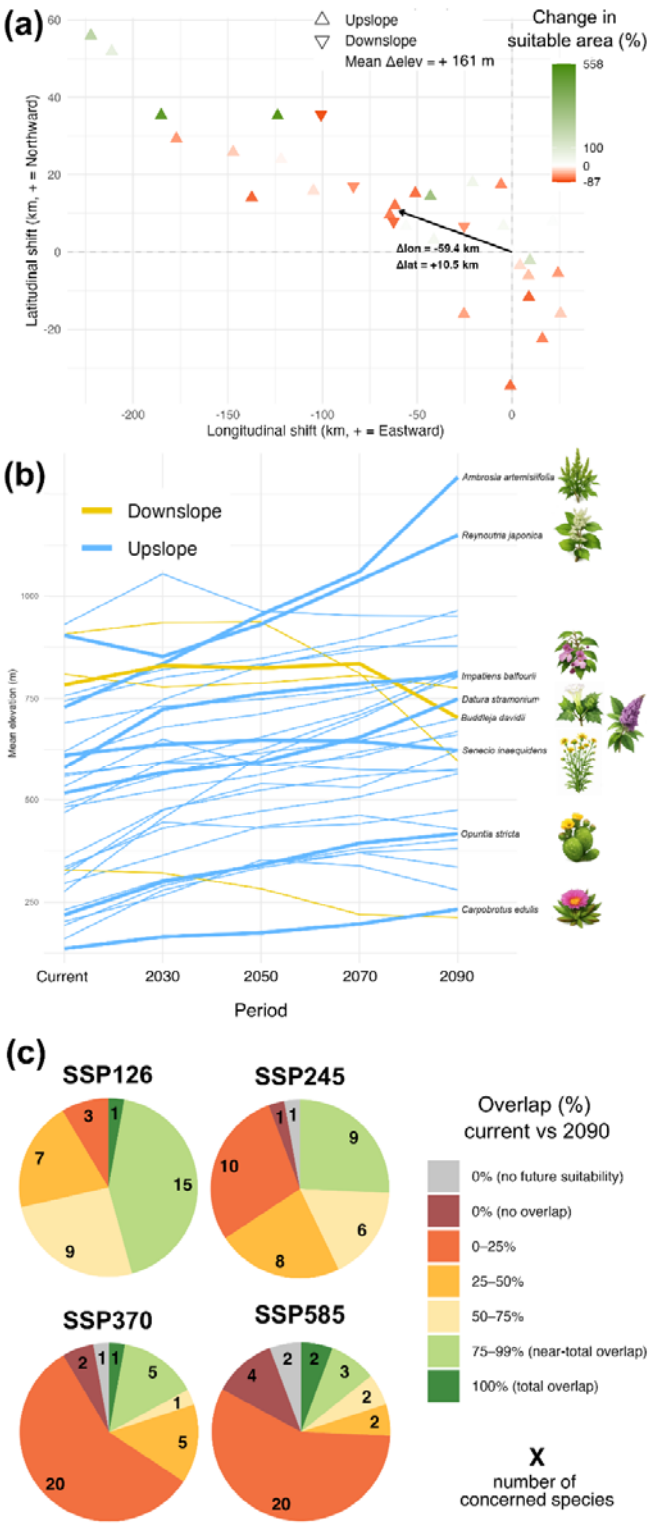

Figure 3. Projected distribution changes in bioclimatic suitability for invasive plant species between the current (1970-2000) and 2081-2100 periods in the Pyrenees. (a) Projected latitudinal, longitudinal and elevational shifts of the centroids of bioclimatic suitability for the 2081–2100 period, averaged across SSPs.

Each triangle represents one of the 33 species retaining suitable areas under all SSPs. Triangle color reflects changes in suitable areas (green = gain; red = loss). Triangle orientation indicates elevational shifts: upward-pointing triangles denote upslope shifts, and downward-pointing triangles denote downslope shifts. The black arrow indicates the overall centroid mean displacement in latitude (△ lat) and longitude (△ lon) across species. **(b)** Projected elevational shifts of the centroids of bioclimatic suitability of invasive plant species, averaged across SSPs. Yellow lines indicate downslope shifts and blue lines upslope shifts relative to the current period. Highlighted species are further discussed in the Discussion section. **(c)** Spatial overlap (%) between current and future (2081–2100) bioclimatic suitable areas for invasive plant species under SSPs. Each pie chart displays the number of species considered and their distribution among overlap classes, ranging from total overlap (100%) to no overlap (0%). 2021-2040, 2041-2060, 2061-2080, 2081-2100 periods designated as 2030, 2050, 2070, 2090.

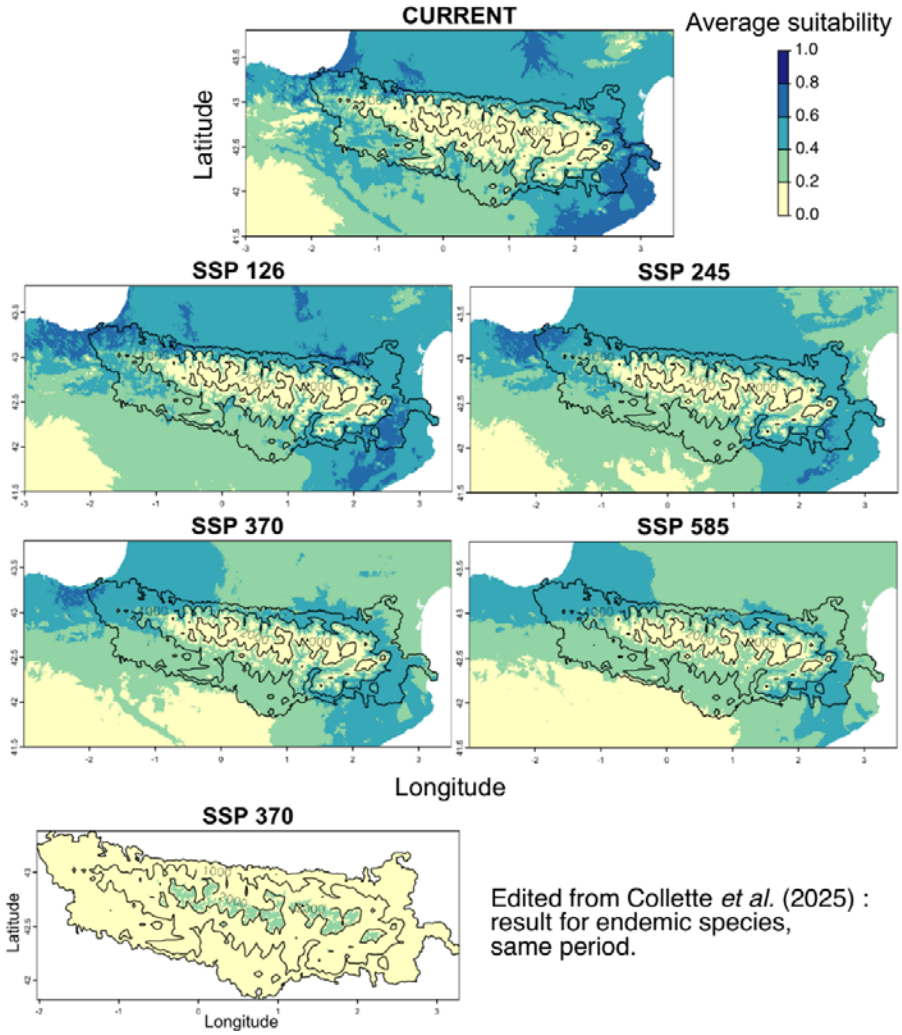

Figure 4. Current and future bioclimatic hotspots for invasive plant species in the Pyrenees. Current and projected (2081-2100) bioclimatic hotspots, i.e. areas where the highest number of species could find suitable bioclimatic conditions, under Shared Socioeconomic Pathways (SSPs). Darker colors indicate higher bioclimatic suitability. Contour lines mark the 1000- and 2000-meter elevation topography. The inset reproduces a portion of a figure from Collette et al. (2025), illustrating results for endemic Pyrenean species over the same period under SSP370, for comparison purposes.

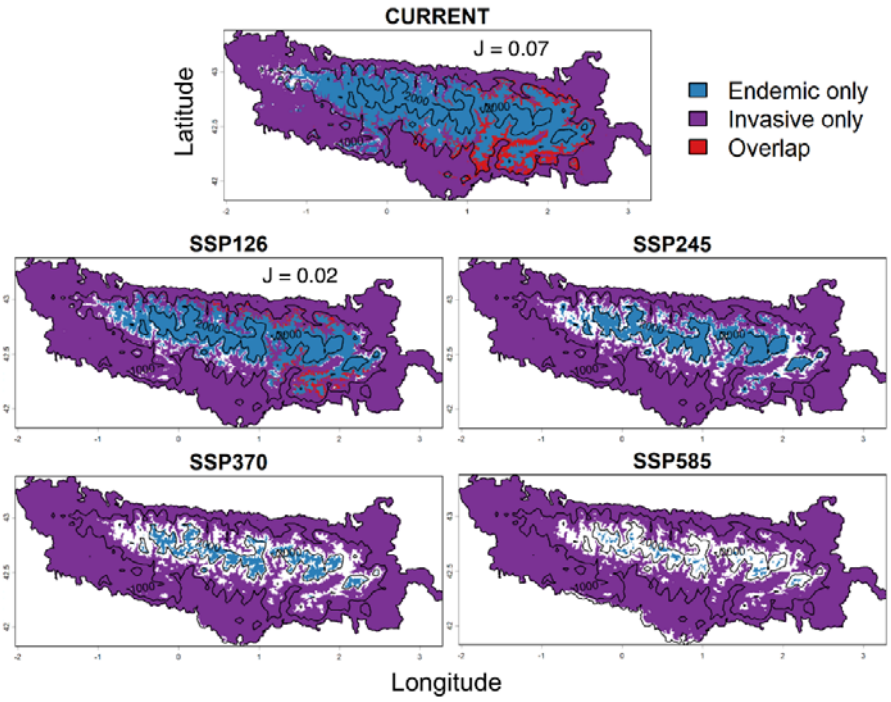

Figure 5. Spatial overlap between invasive and endemic bioclimatic hotspots in the Pyrenees. Current and projected (2081–2100) bioclimatic hotspots for invasive and endemic plant species under SSPs, binarized using a threshold of 0.2 to retain all areas showing any hotspot signal and facilitate the assessment of spatial overlap. Areas exclusive to endemic species (blue), invasive species (purple), and their overlap (red) are shown. Spatial overlap is quantified using the Jaccard index (J; shown when > 0). Contours denote the 1,000 and 2,000 m elevation isolines.