

Discrepancies between climate velocity and dispersal capacity threaten subalpine forests in Northern Italy

Saman Ghasemian Sorboni

Department of Land, Environment, Agriculture and Forestry (TeSAF), University of Padova, Viale dell'Università,
16, 35020 Legnaro PD, Italy

Abstract

The acceleration of anthropogenic warming is fundamentally altering the climatic space available to foundational conifer species in European alpine environments. This study evaluates the potential impacts of future climate scenarios on the spatial distribution and elevational displacement of four key taxa (*Abies alba*, *Larix decidua*, *Picea abies*, and *Pinus sylvestris*) in the Italian Alps. We employed an ensemble modeling framework, integrating climatic and topographic predictors under two Shared Socioeconomic Pathways (SSP1-2.6 and SSP5-8.5) for mid- (2050) and late-century (2070) time horizons. The projections indicate a universal trajectory of habitat contraction and forced upslope migration across all modeled taxa, primarily driven by temperature and precipitation seasonality. While *A. alba* demonstrated relative spatial stability under moderate warming, *P. abies* exhibited the highest vulnerability, with a projected 87.8% reduction in climatically suitable area by 2070 under the high-emission scenario. Elevational analyses revealed that *A. alba*, *L. decidua*, and *P. sylvestris* would require sustained upslope migration velocities exceeding 70 meters per decade to track their optimal thermal niches. Conversely, the severe niche deterioration for *P. abies* under extreme warming resulted in a projected net downward shift, indicating a potential restriction to localized topographic micro-refugia rather than a biological migration. The required climate velocities substantially exceed the natural seed dispersal capacities of these long-lived conifers, introducing a pronounced migration lag. Consequently, relying solely

on natural regeneration may prove insufficient to maintain current distributions. Sustaining these alpine forests will likely require targeted climate-adaptive management, including the protection of micro-refugia and the evaluation of assisted migration.

Keywords: Upslope velocity; Migration lag; Range contraction; Alpine ecosystems; Ensemble species distribution modeling; Montane forests; European Silver Fir; Scots Pine; Norway Spruce; European Larch

1. Introduction

Climate change is a major driver of ecological transformation worldwide, reshaping the structure, functioning, and spatial distribution of species, with particularly pronounced effects in mountain environments (Albrich et al., 2020; Weiskopf et al., 2020; Nolan et al., 2018; Beniston, 2003). In recent decades, increasing global temperatures, altered precipitation regimes, and the rising frequency of extreme climatic events have prompted shifts in the geographic and ecological ranges of numerous plant taxa (Bradley et al., 2024; Kelly & Goulden, 2008; Jentsch et al., 2007; Ghasemian Sorboni et al., 2026). Mountain forests in the Alps are experiencing an acceleration in dynamics driven by climate warming, where elevation and topographic complexity modulate the rate of species composition and structural changes (Thom & Seidl, 2022; Albrich et al., 2020).

The Alpine region has experienced a temperature increase of approximately 2°C since the pre-industrial era, a trend that is accelerating forest dynamics and modifying vegetation composition, as evidenced by the upward migration of species and shifts in the altitudinal limits of tree species (Dumont et al., 2025; Chersich et al., 2015; Pauli et al., 2003). Under such conditions, many forest taxa exhibit a tendency to track suitable climatic niches by shifting their distribution ranges toward higher latitudes or elevations (Vitasse et al., 2021; Boisvert-Marsh et al., 2014; Lenoir & Svenning, 2014). This pattern is often described as an upslope shift, reflecting changes in the elevational distribution of species that can influence forest composition, species interactions, and stand structure.

Coniferous species are dominant components of many forests in the European Alps. Taxa such as *Abies alba*, *Picea abies*, *Pinus sylvestris*, and *Larix decidua* comprise a considerable proportion of the mountain woodlands in central and southern Europe, contributing substantially to biogeochemical cycling, carbon sequestration, and ecosystem stability (Piaszczyk et al., 2026;

Bledý et al., 2024; Walder et al., 2021; Moris et al., 2017; Knoke et al., 2007). However, due to their reliance on specific climatic conditions, these species exhibit vulnerabilities to rapid alterations in temperature and precipitation regimes (Izworska et al., 2025; Brichta et al., 2024; Rozenberg et al., 2020; Mamet et al., 2018; Langvall, 2011; Falk & Mellert, 2011; Rebetez & Dobbertin, 2004).

Although species' climatic niches may shift under climate change, the realization of these shifts often depends on species-specific dispersal capabilities. Dispersal limitations can impede species from migrating to newly suitable climatic zones at a sufficient pace, particularly within mountainous landscapes characterized by geographic barriers and abrupt environmental transitions (Zani et al., 2023; Siefert et al., 2015; Meier et al., 2011; Zhu et al., 2011). Consequently, evaluating both potential shifts in climatic ranges and the ability of species to track these changes is critical for projecting the future dynamics of mountain forests.

Focusing on the mountain forests of Northern Italy within the Italian Alps, the present research examines the potential shifts of four principal coniferous species: *A. alba*, *P. abies*, *P. sylvestris*, and *L. decidua*. Employing Species Distribution Modeling (SDM), the climatically suitable ranges for these taxa are projected under both current conditions and future climate scenarios. Furthermore, potential modifications in the altitudinal ranges of these species and their corresponding upslope velocities are evaluated to ascertain whether the potential dispersal capacity of these conifers can align with the velocity of regional climate change.

2. Material and Methods

2.1. Study Area and Species Occurrence Data

Geographically, this research is situated in northern Italy, spanning from 6.5° to 14° E longitude and 43.5° to 47° N latitude. The region features a distinct topographical transition from the

lowlands of the Po Valley to the high-elevation environments of the Italian Alps. These steep altitudinal gradients create significant environmental heterogeneity, supporting the extensive subalpine and alpine conifer forests that are vital to regional biodiversity and ecosystem stability. Primary occurrence data for the four target species were sourced from the Global Biodiversity Information Facility (GBIF). Because raw open-source biodiversity repositories often contain spatial artifacts, the downloaded records required quality control. Using the CoordinateCleaner package in R (Zizka et al., 2019), the dataset was filtered to exclude common spatial errors, including coordinate identical and zero coordinates. After cleaning and spatially restricting the occurrences to the target boundary, the finalized dataset retained 285 validated presences for *A. alba*, 1,673 for *L. decidua*, 834 for *P. sylvestris*, and 1,062 for *P. abies* (Fig. 1). To adequately parameterize the SDM, background points were generated following the framework established by Barbet-Massin et al, 2012. To optimize model calibration and mitigate spatial sampling bias, the number of randomly distributed background points was matched identically to the number of true presence records for each respective species across the study area.

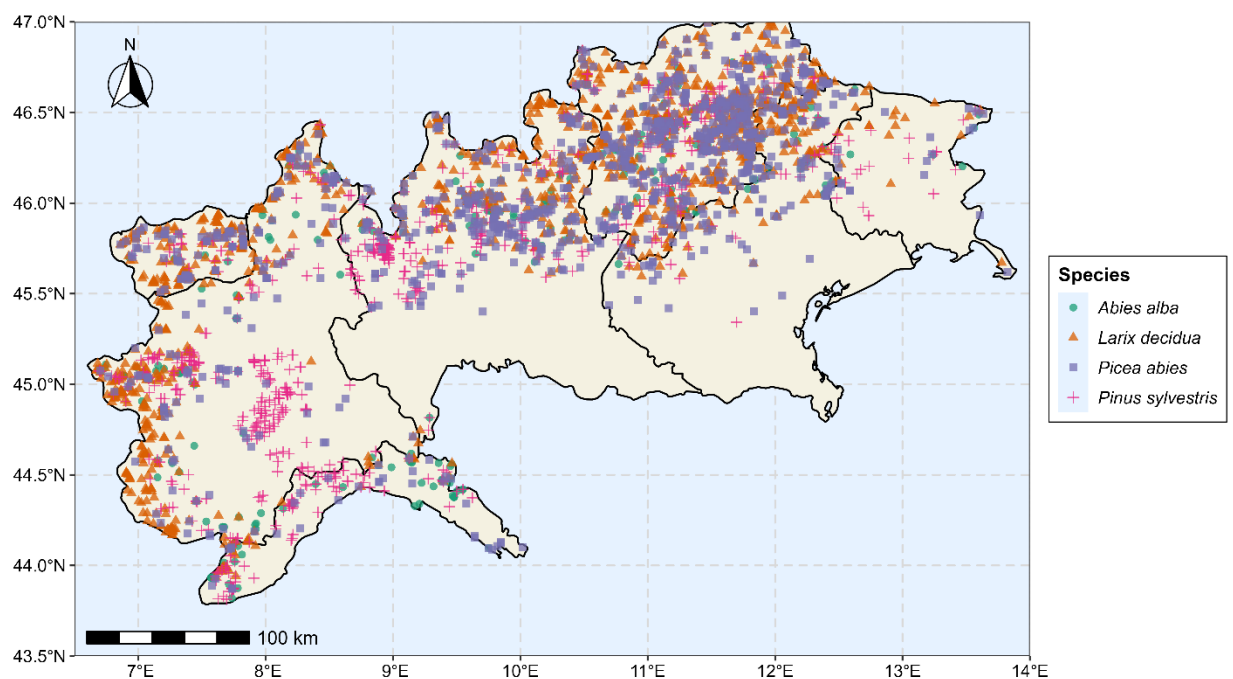


Figure 1. Geographical extent of the study area in northern Italy (6.5°–14° E, 43.5°–47° N), highlighting the distribution of the validated occurrence records for the four target conifer species (*A. alba*, *L. decidua*, *P. sylvestris*, and *P. abies*).

2.2. Environmental Predictors and Climate Scenarios

To characterize the ecological niches of the target conifer species, we compiled a set of environmental predictors including both climatic and topographic variables. Baseline climatic conditions were established using 19 standard bioclimatic metrics extracted from the WorldClim 2.1 database at a spatial resolution of 30 arc-seconds (Fick & Hijmans, 2017; Booth et al., 2013). Furthermore, to capture the pronounced topographic gradients that influence microclimatic conditions in alpine environments, a Digital Elevation Model (DEM) was incorporated into the analysis. Slope and aspect were subsequently derived from the DEM using spatial analysis tools. Future climate conditions were simulated in accordance with the Coupled Model Intercomparison Project Phase 6 (CMIP6). To mitigate the inherent uncertainties of individual climate models, an ensemble approach was implemented using five distinct General Circulation Models (GCMs): MRI-ESM2.0, EC-Earth3, CNRM-CM6-1, MIROC6, and MPI-ESM1.2. These models were projected across two Shared Socioeconomic Pathways (SSPs) to encapsulate a broad spectrum of future trajectories: SSP1-2.6 (a low-emission, sustainable development scenario) and SSP5-8.5 (a high-emission, fossil-fuel-dependent scenario). Projections were acquired for two future time horizons: mid-century (2041–2060) and late-century (2061–2080).

2.3. Collinearity Assessment and Variable Selection

Including highly correlated predictors can introduce multicollinearity, which severely compromises model calibration and the transferability of spatial projections (Brun et al., 2019; De Marco & Nóbrega, 2018). To address this, a systematic variable selection protocol was applied

using the *usdm* package in R (Naimi, 2012). The initial pool of environmental predictors, comprising the 19 bioclimatic variables alongside slope and aspect, was subjected to a stepwise Variance Inflation Factor (VIF) analysis. A conservative threshold of $VIF < 5$ was established to iteratively eliminate redundant predictors while preserving maximum independent environmental variance.

Following the stepwise elimination procedure, the final subset of non-collinear predictors varied slightly among the studied taxa (Table 1). The variable selection procedure retained nine independent predictors for each species, which were subsequently used for model calibration. All final selected variables demonstrated VIF values well below the predefined threshold of 5, ensuring strict statistical independence for the subsequent modeling phases.

Table 1. Final set of environmental predictors retained for each conifer species after multicollinearity assessment, alongside their respective Variance Inflation Factor (VIF) values.

Variable Code	Environmental Predictor	<i>P. abies</i>	<i>L. decidua</i>	<i>A. alba</i>	<i>P. sylvestris</i>
bio3	Isothermality	1.19	1.19	1.19	1.22
bio4	Temperature Seasonality	2.87	2.95	2.81	4.17
bio6	Minimum Temperature of the Coldest Month	3.61	3.76	3.60	-
bio8	Mean Temperature of the Wettest Quarter	-	-	-	3.87
bio9	Mean Temperature of the Driest Quarter	4.31	4.28	4.17	3.28
bio13	Precipitation of the Wettest Month	3.75	3.61	3.70	4.48
bio15	Precipitation Seasonality	1.23	1.20	1.19	1.69
bio18	Precipitation of the Warmest Quarter	3.99	4.12	4.14	4.76
slope	Slope	2.38	2.37	2.37	2.28

1

2 *2.4. Species Distribution Modeling and Ensemble Projection*

3 To estimate the climatically suitable areas, an ensemble modeling framework was implemented
4 utilizing the sdm package in the R statistical environment (Naimi & Araújo, 2016). Because relying
5 on a single algorithm can introduce considerable methodological bias (Li & Wang, 2013), four
6 distinct modeling techniques were employed to capture varying species-environment response
7 curves: Generalized Linear Models (GLM), Maximum Entropy (MaxEnt), Random Forest (RF),
8 and Boosted Regression Trees (BRT).

9 Model calibration and internal validation were executed through a five-fold cross-validation
10 procedure. During each iteration, the presence and background datasets were randomly partitioned,
11 with 70% of the data allocated for model calibration and the remaining 30% withheld for
12 independent evaluation.

13 Predictive performance was quantified using two standard discrimination metrics: the Area Under
14 the Receiver Operating Characteristic Curve (AUC) and the True Skill Statistic (TSS) (Shabani et
15 al., 2018). To minimize the propagation of errors from poorly fitted models and reduce overall
16 uncertainty, final spatial projections were derived via ensemble forecasting rather than relying on
17 individual model outputs (Grenouillet et al., 2011; Araujo & New, 2007). A strict pre-selection
18 criterion was applied prior to ensembling; only individual model runs achieving an $AUC > 0.70$
19 and $TSS > 0.50$ on the evaluation dataset were retained.

20 The final consensus projections were generated using a weighted averaging approach. The
21 contribution of each retained model to the final ensemble was weighted based on its evaluation
22 TSS score. To further refine the ensemble, these weights were squared, a procedure that
23 disproportionately increases the relative influence of highly accurate models while penalizing

those closer to the minimum performance threshold. Finally, for downstream spatial analyses, the continuous habitat suitability predictions were converted into binary presence-absence maps using the threshold that maximizes the sum of sensitivity and specificity (max SSS) (Liu et al., 2015).

2.5. Elevational Range Shifts and Upslope Velocity

To quantify projected shifts in the altitudinal distribution of the target species, the binary suitability projections were spatially intersected with the DEM. For each species across all modeled time horizons and SSPs, the underlying elevation values of all pixels classified as suitable habitat were extracted. The altitudinal boundaries of the climatic niche were subsequently characterized by computing the central tendency (mean) and variability (standard deviation) of these extracted elevation values.

Elevational displacement was quantified by calculating the difference in the mean suitable elevation between the baseline configuration and each respective future climate scenario. Based on these distributional shifts, the required upslope velocity was estimated to evaluate the theoretical migration rate necessary for these taxa to track their shifting climatic niches. This velocity was computed by dividing the projected altitudinal displacement by the temporal interval separating the baseline period and the future projection year. To standardize the metric for comparative analysis, the final upslope velocities were expressed as rates in both meters per year (m/year) and meters per decade (m/decade).

3. Results

3.1. Model Performance and Variables Contribution

The species distribution models demonstrated robust predictive accuracy across the target taxa. Evaluation metrics indicated that RF consistently outperformed the other algorithms, achieving the highest discrimination capacity for all four species (peak AUC > 0.84; TSS > 0.58). Conversely,

1 GLM generally exhibited the lowest predictive performance, notably falling below the predefined
2 ensemble inclusion thresholds ($AUC < 0.70$; $TSS < 0.50$) during specific runs for *P. sylvestris*.
3 Overall, the ensemble models for *L. decidua* yielded the highest evaluation scores (maximum AUC
4 = 0.88; TSS = 0.61 via RF), while *P. sylvestris* models displayed the widest variance in accuracy
5 across the tested algorithms (AUC: 0.69–0.87; TSS: 0.33–0.58) (Fig. 2).

6 The relative influence of the selected environmental predictors varied notably among the species,
7 though temperature and precipitation seasonality broadly dominated the model parameterizations
8 (Fig. 3). For *A. alba* and *L. decidua*, Temperature Seasonality (bio4) and Minimum Temperature
9 of the Coldest Month (bio6) emerged as the primary geographic constraints, contributing 30.0%
10 and 26.3% to their respective models. In contrast, precipitation metrics exerted a stronger influence
11 on *P. abies*, with Precipitation Seasonality (bio15) acting as the most influential predictor (18.3%),
12 followed by secondary contributions from bio6 (9.2%) and bio4 (6.4%). *P. sylvestris* exhibited a
13 distinct environmental response profile heavily driven by topography; slope was the predominant
14 predictor (19.9%), followed by Isothermality (bio3; 13.9%) and Mean Temperature of the Driest
15 Quarter (bio9; 10.1%). Across all species models, aspect consistently demonstrated a negligible
16 contribution to the spatial predictions.

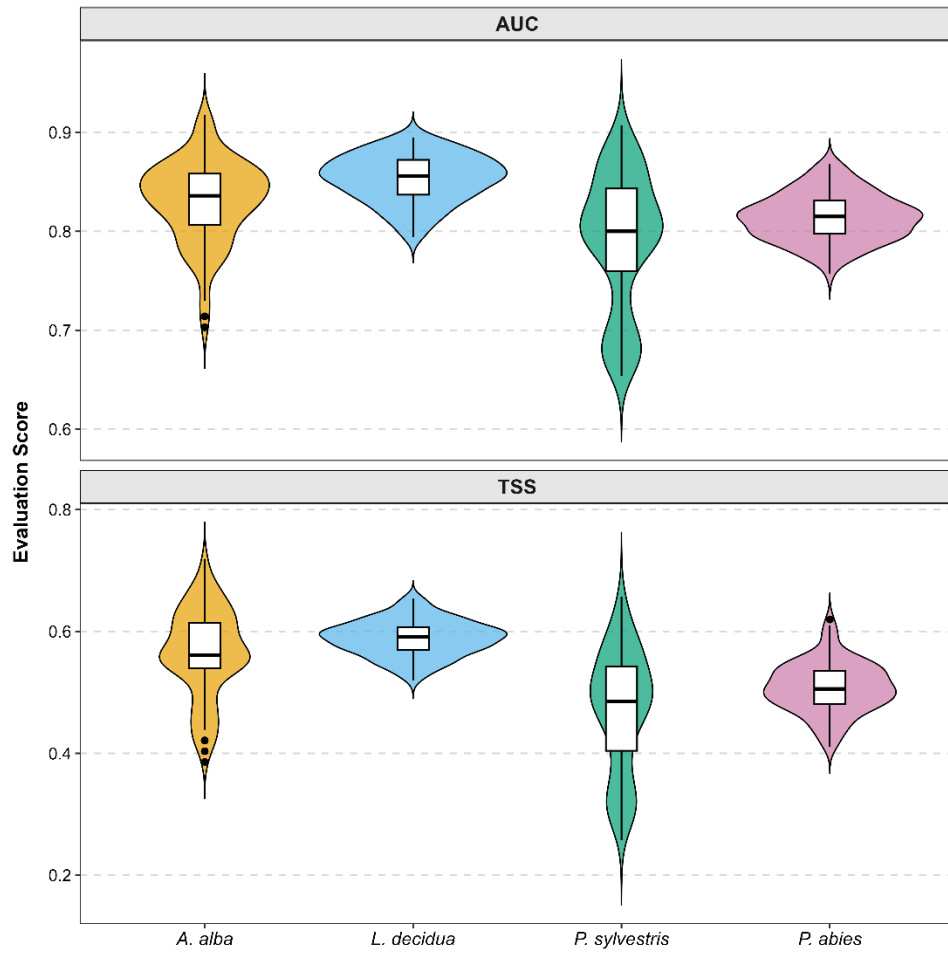


Figure 2. Predictive performance of the species distribution models for the four target conifer species (*A. alba*, *L. decidua*, *P. sylvestris*, and *P. abies*). Model accuracy is evaluated using AUC (top panel) and TSS (bottom panel).

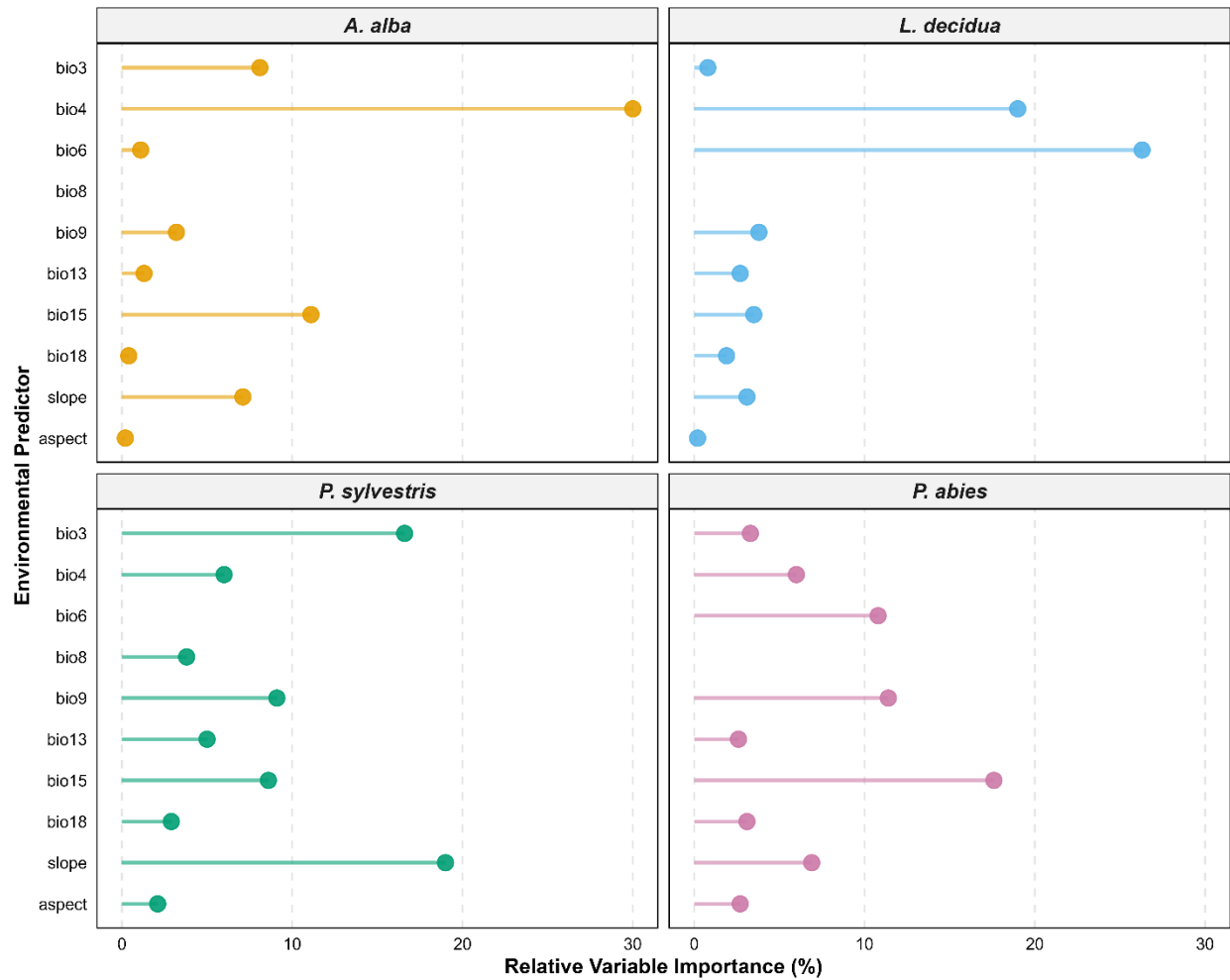


Figure 3. Relative environmental predictor importance for the four target conifer species (*A. alba*, *L. decidua*, *P. sylvestris*, and *P. abies*). The plots represent the mean contribution of climatic and topographic variables across the ensemble SDM iterations.

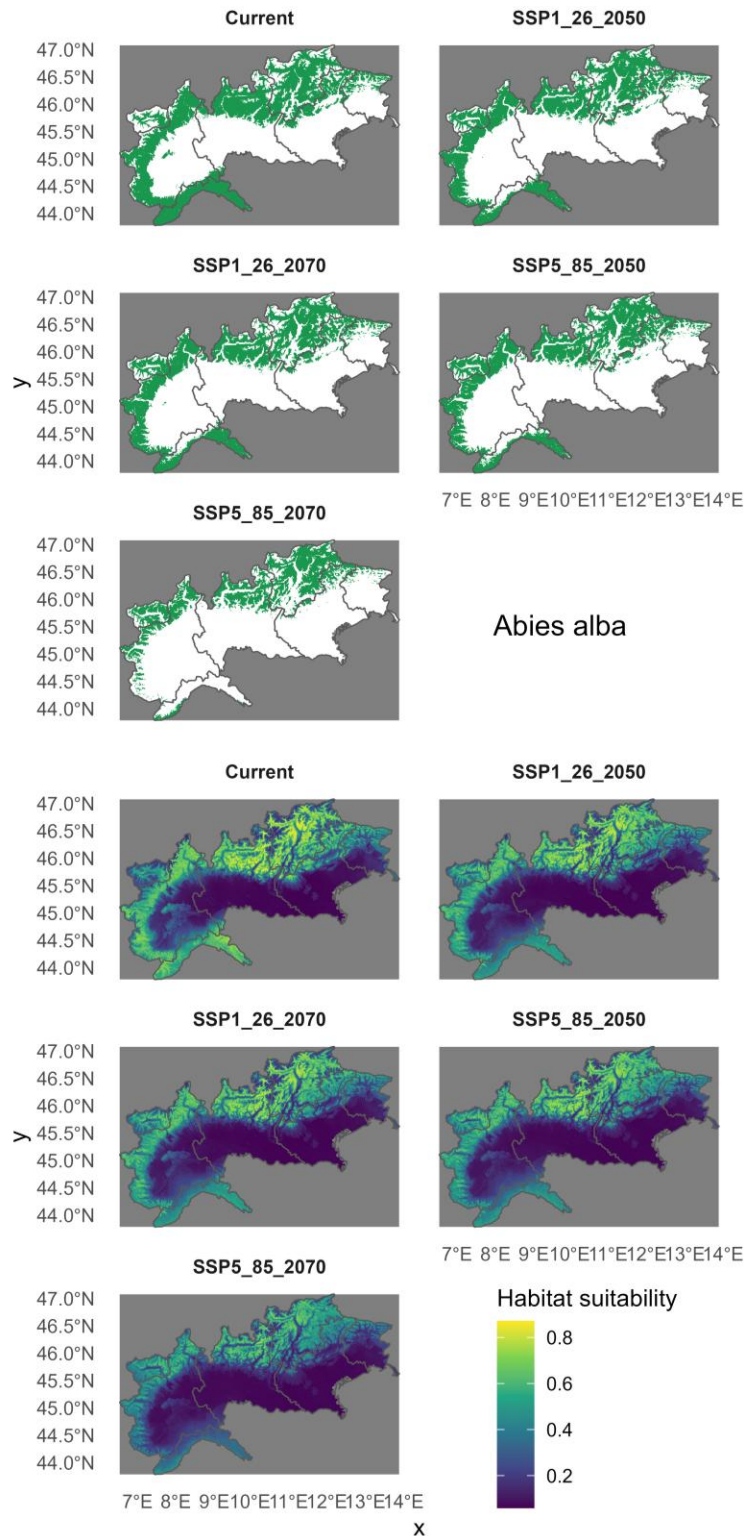
3.2. Current and Future Projections

Spatial projections of habitat suitability yielded distinct baseline extents for the four conifer species. Under current climatic conditions, *A. alba* exhibited the largest suitable area within the study region (38,474 km²), followed by *L. decidua* (30,157 km²). In contrast, *P. sylvestris* and *P. abies* occupied comparatively narrower climatic niches, with baseline suitable areas of 17,241 km² and 13,975 km², respectively.

1 Across all evaluated future climate scenarios and time horizons, the ensemble models projected a
2 universal trajectory of habitat contraction, though the magnitude of these shifts varied considerably
3 by taxon and emission severity. *A. alba* demonstrated the highest relative stability (Fig. 4). Under
4 the low emission SSP1-2.6 scenario, its suitable habitat was projected to decrease by 12.9% by
5 2050 and 15.0% by 2070. However, under the high-emission SSP5-8.5 scenario, range reductions
6 became more pronounced, culminating in a 44.1% net decline (21,349 km²) by 2070, driven by a
7 loss of over 54% of its baseline habitat against minimal anticipated gains.

8 *L. decidua* and *P. sylvestris* displayed more severe contraction patterns. For *L. decidua*, SSP1-2.6
9 resulted in a relatively stable mid-to-late century reduction of approximately 22.8%. Under SSP5-
10 8.5, this contraction accelerated, reaching a 62.0% net loss by 2070 as gross habitat loss (65.9%)
11 vastly outpaced potential expansion (3.9%) (Fig. 5). Similarly, *P. sylvestris* faced projected range
12 reductions of 26.5% by 2050 under SSP1-2.6. By 2070 under SSP5-8.5, its suitable area contracted
13 by 54.8% to 7,694 km²; although the models predicted moderate habitat gains of roughly 21% for
14 this species, these local expansions were insufficient to offset the projected widespread loss of its
15 current distribution (Fig. 6).

16 Among the modeled taxa, *P. abies* exhibited the sharpest decline in suitable climatic space. By
17 2050 under SSP1-2.6, its range contracted by 36.4% (to 8,885 km²), with negligible projected gains
18 (1.9%). This downward trajectory intensified significantly under the SSP5-8.5 scenario, where the
19 species lost 55.8% of its suitable area by mid-century. By 2070 under this high-emission pathway,
20 the models projected an 87.8% net reduction, leaving only 1,706 km² of suitable habitat as nearly
21 88% of its baseline distribution became climatically unsuitable (Fig. 7).



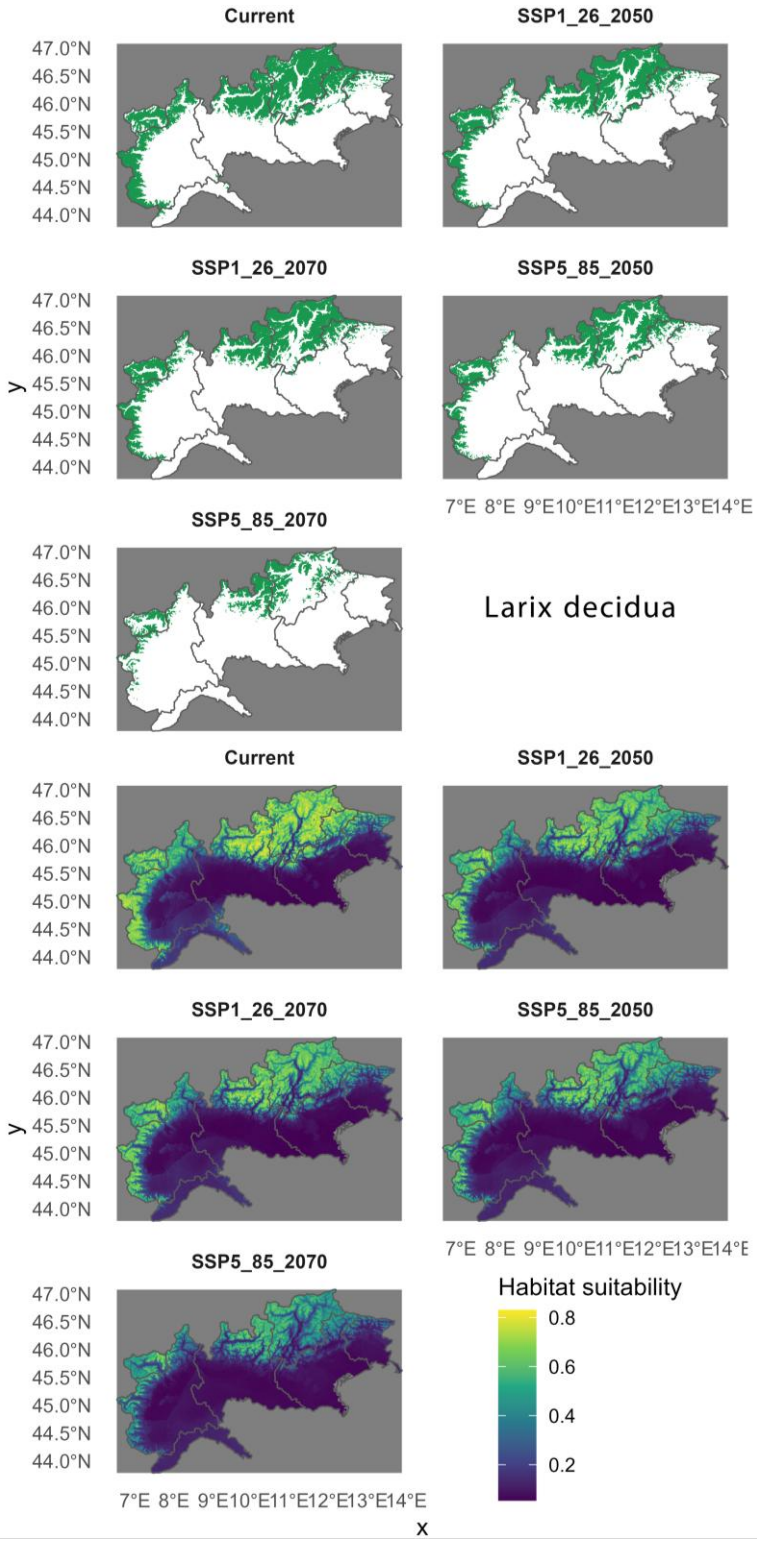
1

2

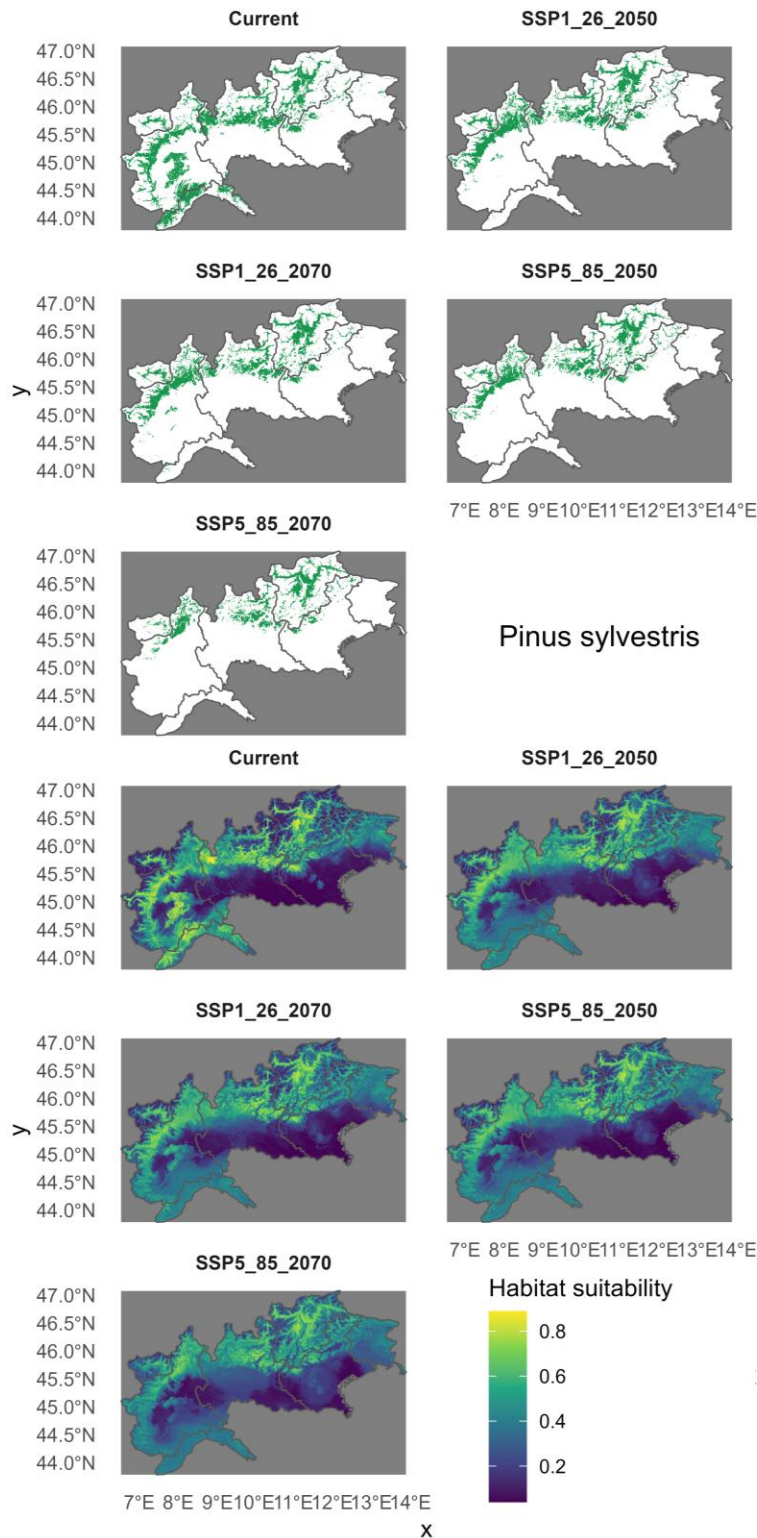
3

4

Figure 4. Spatial projections of *A. alba* under current climatic conditions and four future scenarios (SSP1-2.6 and SSP5-8.5 for 2050 and 2070). Panels include (A) binary projection, and (B) continuous suitability maps based on ensemble predictions.



1 **Figure 5.** Spatial projections of *L. decidua* under current climatic conditions and four future scenarios (SSP1-2.6 and
2 SSP5-8.5 for 2050 and 2070). Panels include (A) binary projection, and (B) continuous suitability maps based on
3 ensemble predictions.



1
2 **Figure 6.** Spatial projections of *P. sylvestris* under current climatic conditions and four future scenarios (SSP1-2.6 and
3 SSP5-8.5 for 2050 and 2070). Panels include (A) binary projection, and (B) continuous suitability maps based on
4 ensemble predictions.

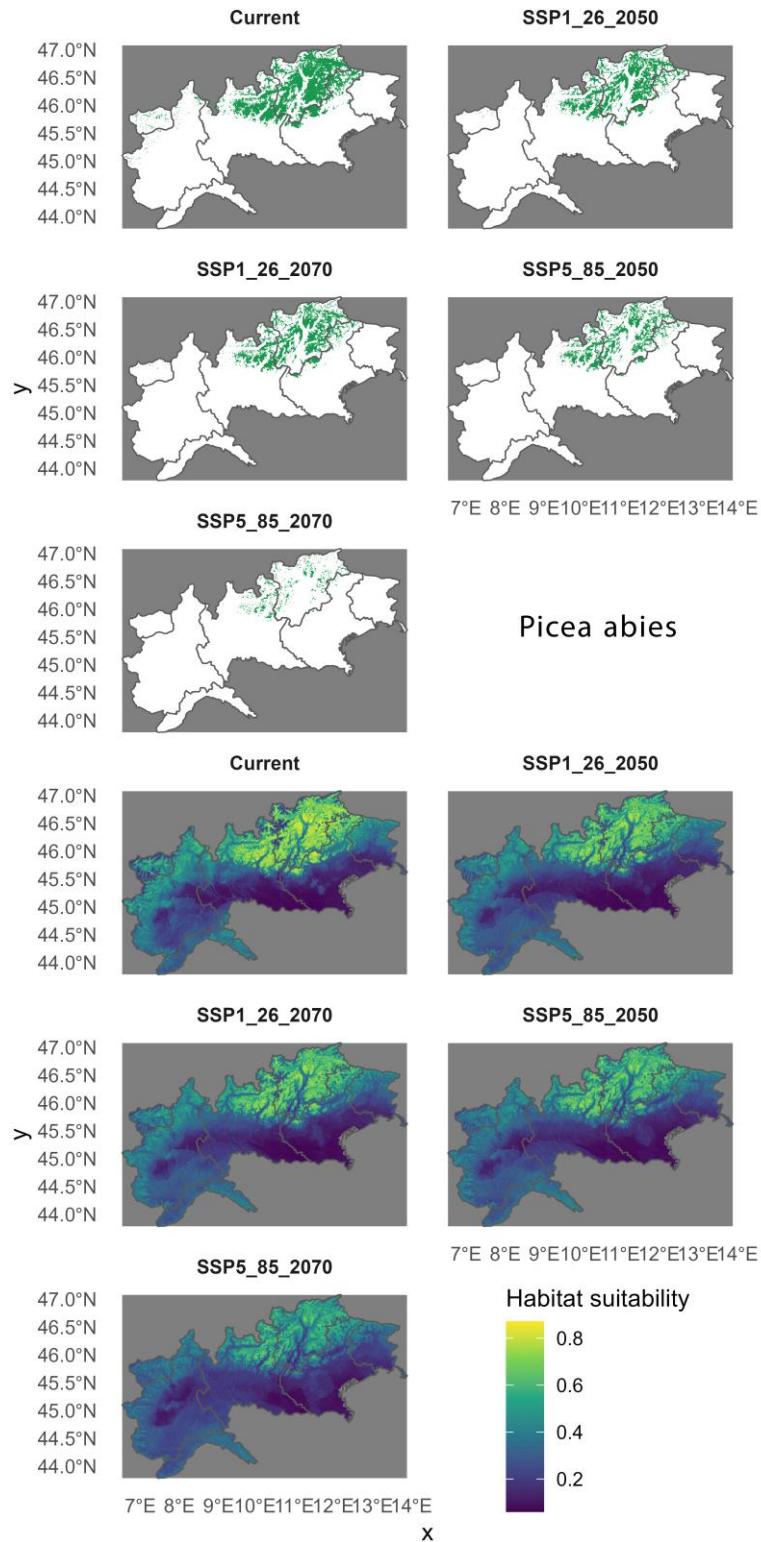


Figure 7. Spatial projections of *P. abies* under current climatic conditions and four future scenarios (SSP1-2.6 and SSP5-8.5 for 2050 and 2070). Panels include (A) binary projection, and (B) continuous suitability maps based on ensemble predictions.

1

2 3.3. Altitudinal Displacement and Upslope Velocity

3 The spatial intersection of suitable area projections with topographic data revealed a widespread
4 trend of altitudinal displacement across the modeled taxa. Under baseline climatic conditions, the
5 mean elevations of climatically suitable areas were localized at 785.0 m for *P. sylvestris*, 1193.4
6 m for *A. alba*, 1432.7 m for *P. abies*, and 1685.0 m for *L. decidua*. Under future climate scenarios,
7 three of the four species; *A. alba*, *L. decidua*, and *P. sylvestris*, exhibited consistent, pronounced
8 upward shifts in their optimal climatic niches (Table. 2).

9 For *A. alba*, *L. decidua*, and *P. sylvestris*, the magnitude of upslope displacement escalated with
10 both projection time and emission severity. By 2050 under the low SSP1-2.6 scenario, these
11 species showed mean elevational increases ranging from 191.4 m to 205.0 m, translating to upslope
12 velocities between 76.6 m and 82.0 m per decade. Under the high-emission SSP5-8.5 scenario by
13 2070, altitudinal shifts became substantially larger. *A. alba* projected the most extreme long-term
14 displacement, with a mean elevation increase of 438.7 m (97.5 m/decade). This was followed by
15 *P. sylvestris* with a shift of 389.8 m (86.6 m/decade) and *L. decidua* with an upward movement of
16 354.4 m (78.8 m/decade) under the same future conditions.

17 In contrast, *P. abies* demonstrated a distinct and comparatively restricted elevational response.
18 Under the SSP1-2.6 scenario, the species experienced a moderate upward shift of 85.6 m by 2050
19 (34.2 m/decade), which slightly receded to a net displacement of 75.9 m by 2070. Notably, under
20 the extreme SSP5-8.5 scenario by 2070, the mean elevation of climatically suitable areas for *P.*
21 *abies* declined to 1409.0 m. This represented a net downward displacement of 23.6 m relative to
22 baseline conditions, yielding a negative migration velocity of -5.3 m/decade (Fig. 8).

Table 2. Projected altitudinal displacement of the climatically optimal niche for the four target conifer species. Values indicate the mean elevation of suitable area under baseline conditions and future climate scenarios (SSP1-2.6 and SSP5-8.5) across the 2050- and 2070-time horizons, alongside the net elevational shift by the late century.

Species	Baseline	Scenario	2041-2060	2061-2080	Net Shift (to 2070)
<i>A. alba</i>	1193.4	SSP1-2.6	1394.3	1375.6	+182.2 m
		SSP5-8.5	1466.9	1632.1	+438.7 m
<i>L. decidua</i>	1685.0	SSP1-2.6	1890.0	1885.2	+200.2 m
		SSP5-8.5	1957.7	2039.4	+354.4 m
<i>P. sylvestris</i>	785.0	SSP1-2.6	976.3	975.7	+190.7 m
		SSP5-8.5	1050.6	1174.8	+389.8 m
<i>P. abies</i>	1432.7	SSP1-2.6	1518.3	1508.6	+75.9 m
		SSP5-8.5	1533.3	1409.0	-23.6 m

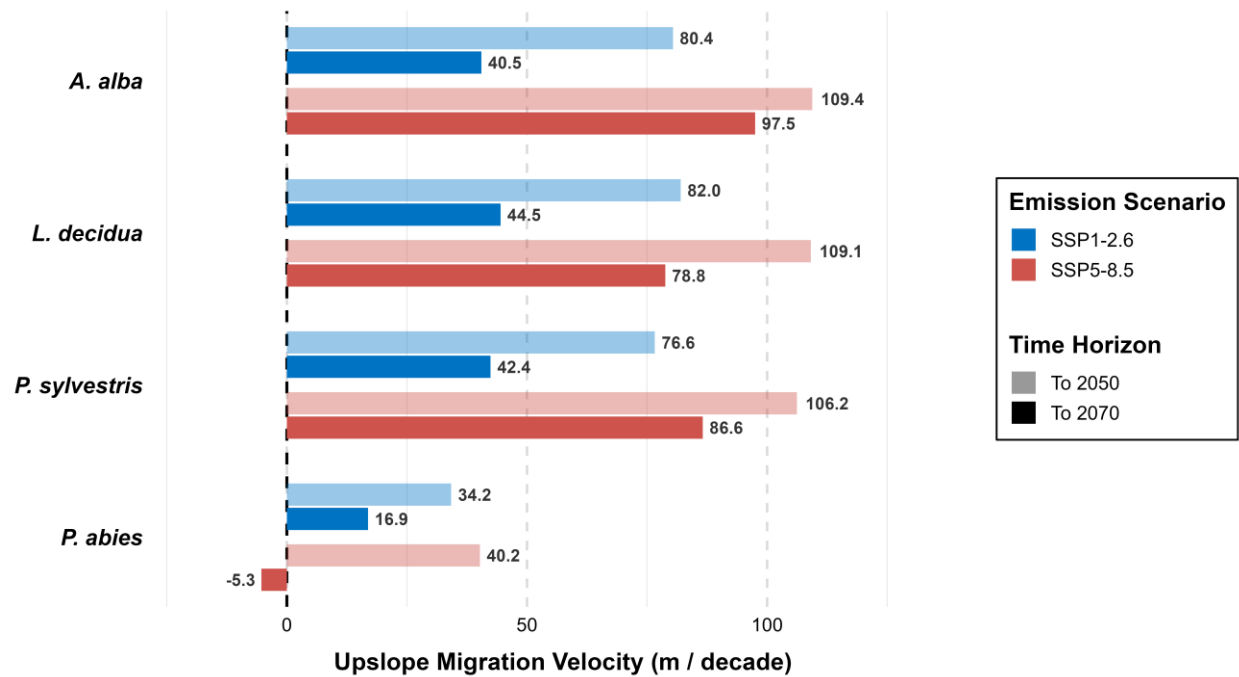


Figure 8. Estimated upslope migration velocities (m/decade) of climatically suitable area for the modeled conifer taxa. Velocities represent the rate of altitudinal displacement toward the 2050 and 2070 projection horizons under low-emission (SSP1-2.6) and high-emission (SSP5-8.5) scenarios.

4. Discussion

4.1. Divergent Responses of Alpine Conifers

Our projections suggest that the dominant conifer species of the Italian Alps are unlikely to respond to future climatic warming as cohesive ecological units, instead exhibiting highly species-specific spatial and elevational adjustments. The contrast between the relative persistence of suitable climatic conditions for *A. alba* and the pronounced contraction projected for *P. abies* indicates that subalpine forests may not undergo a simple upslope displacement while maintaining current community structure. Because co-occurring species differ substantially in climatic sensitivity and dispersal-mediated tracking capacity, their asynchronous responses are likely to progressively decouple existing assemblages (Alexander et al., 2016; Travis et al., 2013; Morin et al., 2008). Such individualistic redistribution may promote a reorganization of the subalpine belt, facilitating the emergence of novel species combinations and alter competitive interactions (Svenning & Sandel, 2013; Singer & Parmesan, 2010). Similar dynamics have been associated with the development of no-analog communities, where shifts in species overlap can substantially modify ecosystem functioning (Alexander et al., 2015; Le Roux & McGeoch, 2008).

4.2. Climatic and Topographic Constraints

The variable importance profiles indicate that the projected spatial dynamics of these alpine conifers are shaped by markedly different environmental constraints, providing a mechanistic basis for their divergent distributional responses. For *A. alba* and *L. decidua*, thermal regimes, particularly temperature seasonality (bio4) and minimum temperature of the coldest month (bio6), emerge as dominant predictors. Winter temperature minima are recognized as critical controls on high-elevation forest dynamics, influencing processes such as dormancy release, frost damage, and seedling establishment (Körner, 2021). The prominence of these variables in the models suggests

1 that projected warming may relax historical thermal limitations, thereby facilitating upward shifts
2 in climatically suitable conditions for these taxa, consistent with their relatively high modeled
3 upslope velocities.

4 In contrast, the distribution of *P. abies* appears to be more strongly constrained by moisture
5 availability, with precipitation seasonality (bio15) identified as the most influential predictor. This
6 pattern is consistent with the documented sensitivity of *P. abies* to drought stress and soil moisture
7 deficits, which can limit both growth and regeneration (Obladen et al., 2021; Lévesque et al., 2013;
8 Ditmarova et al., 2009). Under scenarios of intensified warming, the combination of reduced
9 climatic suitability and a modeled net-negative migration velocity suggests that altered
10 precipitation regimes and associated hydraulic constraints may hinder the species' capacity to track
11 shifting climatic envelopes, potentially increasing its vulnerability to secondary disturbances such
12 as bark beetles (Marini et al., 2017; McDowell et al., 2015; Parolo & Rossi, 2008).

13 Unlike the other taxa considered, the projected distribution of *P. sylvestris* is strongly mediated by
14 topographic conditions, with slope exerting a dominant influence. As a light-demanding, early-
15 successional species, *P. sylvestris* frequently occupies steep or edaphically marginal environments
16 where competitive pressure from shade-tolerant canopy species is reduced (Houston Durrant et al.,
17 2016). The importance of slope in the predictive models therefore suggests that its realized niche
18 in the Italian Alps is structured not only by macroclimatic gradients but also by topographically
19 mediated competitive interactions. Consequently, future distributional shifts of this species are
20 likely to depend on the spatial availability of suitable topographic refugia that allow it to maintain
21 a competitive advantage under changing climatic conditions.

22 4.3. Spatial Bottlenecks and Habitat Contraction

1 The ensemble projections indicate a consistent contraction of climatically suitable habitat across
2 the study region, with the most pronounced reductions occurring under the SSP5–8.5 scenario.
3 This pattern reflects, in part, the geometric constraints imposed by alpine landscapes, where the
4 spatial availability of suitable environments may decline with elevation as species track shifting
5 climatic conditions upslope (Dullinger et al., 2012; Colwell et al., 2008). Such topographically
6 mediated limitations are particularly evident in the projections for *P. abies*, which is expected to
7 experience an estimated 87.8% reduction in suitable area by 2070 under severe warming. This
8 contraction coincides with a modeled inability to maintain positive upslope migration rates,
9 suggesting that climatic displacement may outpace the species' capacity to track newly emerging
10 suitable conditions.

11 For taxa already confined to upper subalpine and alpine zones, continued altitudinal displacement
12 is likely to compress populations into progressively narrower elevational bands (Duan, 2026).
13 Rather than facilitating a simple upward redistribution of existing populations, these constraints
14 may promote increasing spatial fragmentation, potentially limiting the extent to which high-
15 elevation expansion can compensate for losses at lower elevations (Auld et al., 2022; Ettinger &
16 HilleRisLambers, 2017; Dirnböck et al., 2003). Such dynamics highlight the importance of
17 landscape configuration and connectivity in mediating the persistence of alpine forest species
18 under accelerating climate change.

19 *4.4. Climate Velocity and Dispersal Capacity*

20 A central implication of the modeled velocity estimates is the pronounced mismatch between the
21 rate of climatic niche displacement and the dispersal capacities of the studied taxa. Under the
22 SSP5–8.5 scenario, maintaining occupancy within climatically suitable environments would
23 require upward migration rates on the order of approximately 80–110 m per decade for species

1 such as *A. alba*, *L. decidua*, and *P. sylvestris*. However, recent trait-based classifications categorize
2 the natural seed dispersal of these taxa as highly localized, with mean distances typically restricted
3 to 40–150 m per dispersal event (Class 4; Lososová et al., 2023; Vittoz & Engler, 2007). When
4 compounding these restricted dispersal distances with the prolonged generation times required for
5 long-lived conifers to reach reproductive maturity, their realized decadal migration rates are
6 mathematically insufficient to pace with severe warming. This constraint is corroborated by
7 paleoecological reconstructions and contemporary observations, which consistently indicate that
8 historical migration rates are substantially slower than projected climate shifts (Bisbing et al.,
9 2020; Feurdean et al., 2013; Svenning & Skov, 2007). The discrepancy between required velocity
10 and biological capacity is therefore deeply rooted in fundamental dispersal limitations, delayed
11 population turnover, and the challenges associated with successful seedling establishment in newly
12 suitable environments.

13 This divergence suggests the likelihood of a pronounced migration lag, whereby the velocity of
14 regional climate change exceeds the capacity of populations to track shifting suitable conditions
15 through natural regeneration processes. Because spatial projections delineate potential climatic
16 suitability rather than realized colonization dynamics, such biological constraints imply that future
17 distributions may contract more strongly than indicated by the models alone. In particular,
18 populations at trailing, lower-elevation margins may undergo prolonged climatic stress and
19 localized decline, whereas leading-edge expansion typically occurs more slowly, creating an
20 imbalance between loss at the rear edge and gains at the advancing front (Vilà-Cabrera et al., 2019;
21 Gilbert et al., 2019; Rehm et al., 2015; Hampe & Petit, 2005).

22 4.5. Niche Collapse and Micro-Refugia in *P. abies*

1 A notable feature of the ensemble projections is the elevational response of *P. abies* under the high-
2 emission SSP5–8.5 scenario. By 2070, the models estimate a net downward shift in the mean
3 elevation of suitable habitat, resulting in a negative migration velocity (–5.3 m per decade). This
4 pattern does not imply an active downslope redistribution of the species; rather, it reflects a
5 pronounced contraction and fragmentation of its previously continuous high-elevation climatic
6 niche. As optimal thermal and hydrological conditions shift beyond the elevation range where
7 suitable environments currently occur, large portions of the upper subalpine zone are projected to
8 become climatically unsuitable.

9 Consequently, the remaining areas classified as suitable are disproportionately concentrated in
10 localized micro-refugia at lower elevations, leading to a downward shift in the statistical centroid
11 of suitable habitat (Dobrowski, 2011). These refugial environments, often associated with cold-air
12 pooling, north-facing slopes, or deeply incised valley systems, can partially decouple local
13 microclimates from broader regional warming trends (Pastore et al., 2022; Morelli et al., 2020;
14 Scherrer & Körner, 2010; Daly et al., 2009). Such topographically mediated buffering may
15 facilitate the short-term persistence of remnant populations, although long-term viability will
16 likely depend on the extent to which these fragmented habitats maintain demographic connectivity
17 and support successful regeneration under continued climatic change.

18 *4.6. Methodological Limitations*

19 While the ensemble SDM framework provides a spatially explicit reference for anticipating
20 potential climatic redistribution, its correlative structure entails well-recognized methodological
21 limitations. A primary assumption underlying the projections is the temporal stability of species–
22 environment relationships, effectively invoking climatic niche conservatism over the modeled
23 period (Peterson, 2011). This assumption does not explicitly account for the potential influence of

1 phenotypic plasticity or localized adaptive responses, which may partially mediate species
2 persistence under changing environmental conditions (A. Lee-Yaw et al., 2021; Morin et al., 2008).
3 Moreover, by emphasizing macroclimatic and broad topographic predictors, the models delineate
4 potential climatic suitability rather than realized distributional outcomes (Marcer et al., 2013).
5 Fine-scale processes likely to shape future range dynamics, including shifting competitive
6 interactions, edaphic heterogeneity, soil biotic feedbacks, and anthropogenic land-use change,
7 remain unresolved within this modeling framework (Maclean et al., 2023; Srivastava et al., 2019;
8 Lembrechts et al., 2018).

9 Importantly, both the spatial projections and the derived upslope velocity estimates operate under
10 an implicit assumption of unrestricted dispersal. Given the substantial migration rates required to
11 track projected climatic shifts, dispersal limitation and landscape fragmentation are likely to
12 constrain the capacity of these conifers to fully occupy emerging suitable habitats at higher
13 elevations (Feurdean et al., 2013; Meier et al., 2011). Consequently, the projected habitat
14 contractions should be interpreted as indicative of potential climatic exposure rather than definitive
15 forecasts of realized range change. To the extent that leading-edge expansion is limited by dispersal
16 while trailing-edge populations decline under deteriorating conditions, actual range reductions
17 may exceed those inferred from climatic suitability alone (Lenoir & Svenning, 2014; Zhu et al.,
18 2011).

19 *4.7. Conservation and Management Implications*

20 The pronounced dispersal lags indicated by our projections suggest that management strategies
21 relying solely on autonomous natural regeneration may be insufficient to track the rapid spatial
22 redistribution of subalpine conifer forests under severe climate warming. Because the migration
23 velocities required for *A. alba*, *L. decidua*, and *P. sylvestris* substantially exceed their documented

1 natural dispersal capacities, maintaining their functional presence within the regional forest
2 landscape may necessitate the consideration of targeted, climate-adaptive interventions. Given that
3 natural dispersal modes are insufficient to pace with these shifting envelopes, human-mediated
4 translocation (Class 7; Lososová et al., 2023), which represents the only dispersal mode capable
5 of spanning the required 500–5000 m geographic distances, has been proposed as a critical
6 mechanism to bridge this gap. While such assisted population migration could theoretically
7 overcome biological dispersal limitations, its ecological risks and long-term outcomes remain
8 subject to ongoing debate (Twardek et al., 2023; Palik et al., 2022; Williams & Dumroese, 2013;
9 McLachlan et al., 2007).

10 In contrast, the projected trajectory for *P. abies* suggests that conservation strategies should place
11 particular emphasis on the identification and strict protection of topographic micro-refugia. These
12 localized environments, characterized by buffered microclimatic conditions, may provide critical
13 short-term persistence zones for remnant populations where broader macroclimatic suitability
14 declines (Stark & Fridley, 2022; Suggitt et al., 2018; Patsiou et al., 2014). Safeguarding such
15 refugial habitats will be paramount to maintaining regional genetic diversity and preserving the
16 functional resilience of the alpine forest matrix during periods of rapid climatic transition.

17 **5. Conclusion**

18 This study employed an ensemble species distribution modeling framework to assess the projected
19 spatial and elevational dynamics of four dominant conifer species in the Italian Alps under future
20 climate scenarios. The results reveal a consistent pattern of habitat contraction accompanied by
21 species-specific upward redistribution of climatically suitable environments. While *A. alba*
22 displayed relative persistence under moderate warming, both *L. decidua* and *P. sylvestris* are
23 projected to experience substantial long-term reductions in suitable habitat. *P. abies* emerged as

1 the most climate-sensitive taxon, with projections indicating an estimated 87.8% decline in
2 suitable area by 2070 under the SSP5–8.5 scenario. For this species, the occurrence of negative
3 migration velocity reflects fragmentation and downslope displacement of the statistical centroid
4 of suitable habitat rather than an active redistribution, highlighting the potential confinement of
5 future populations to localized topographic micro-refugia.

6 Beyond spatial redistribution, the estimated upslope velocities underscore a critical mismatch
7 between the rate of climatic niche displacement and the dispersal capacities of long-lived conifers.

8 Under severe warming, maintaining occupancy within climatically suitable environments would
9 require migration rates frequently exceeding 80 m per decade, values that substantially exceed
10 empirically observed dispersal dynamics. This divergence suggests that realized future forest
11 distributions may contract more strongly than climatic suitability projections alone would indicate,
12 particularly where dispersal limitation and demographic inertia constrain leading-edge expansion.

13 Collectively, these findings emphasize that climate-driven forest reorganization in alpine regions
14 is likely to be governed not only by shifts in environmental suitability but also by the interaction
15 between topographic constraints, dispersal processes, and microclimatic buffering. In this context,
16 adaptive management approaches, such as the protection of climatic micro-refugia and the cautious
17 evaluation of assisted migration strategies, may play an important role in sustaining ecosystem
18 functioning and biodiversity in high-elevation forest systems under accelerating climate change.

20 **6. Data Availability Statement**

21 The datasets generated and analyzed during the current study are available from the corresponding
22 author on request.

23 **7. Funding**

This research received no external funding.

8. Conflicts of Interest

The authors declare no conflict of interest.

9. References

1. Albrich, K., Rammer, W., & Seidl, R. (2020). Climate change causes critical transitions and irreversible alterations of mountain forests. *Global Change Biology*, 26(7), 4013–4027. <https://doi.org/10.1111/gcb.15118>
2. Alexander, J. M., Diez, J. M., & Levine, J. M. (2015). Novel competitors shape species' responses to climate change. *Nature*, 525(7570), 515–518. <https://doi.org/10.1038/nature14952>
3. Alexander, J. M., Chalmandrier, L., Lenoir, J., Burgess, T. I., Essl, F., Haider, S., Kueffer, C., McDougall, K., Milbau, A., Nuñez, M. A., Pauchard, A., Rabitsch, W., Rew, L. J., Sanders, N. J., & Pellissier, L. (2017). Lags in the response of mountain plant communities to climate change. *Global Change Biology*, 24(2), 563–579. <https://doi.org/10.1111/gcb.13976>
4. Araujo, M., & New, M. (2007). Ensemble forecasting of species distributions. *Trends in Ecology & Evolution*, 22(1), 42–47. <https://doi.org/10.1016/j.tree.2006.09.010>
5. Auld, J., Everingham, S. E., Hemmings, F. A., & Moles, A. T. (2022). Alpine plants are on the move: Quantifying distribution shifts of Australian alpine plants through time. *Diversity and Distributions*, 28(5), 943–955. <https://doi.org/10.1111/ddi.13494>
6. Barbet-Massin, M., Jiguet, F., Albert, C. H., & Thuiller, W. (2012). Selecting pseudo-absences for species distribution models: how, where and how many? *Methods in Ecology and Evolution*, 3(2), 327–338. <https://doi.org/10.1111/j.2041-210x.2011.00172.x>

7. Beniston, M. (2003). Climatic Change in Mountain Regions: A Review of Possible Impacts. *Climatic Change*, 59(1–2), 5–31. <https://doi.org/10.1023/a:1024458411589>
8. Bisbing, S. M., Urza, A. K., Buma, B. J., Cooper, D. J., Matocq, M., & Angert, A. L. (2020). Can long-lived species keep pace with climate change? Evidence of local persistence potential in a widespread conifer. *Diversity and Distributions*, 27(2), 296–312. <https://doi.org/10.1111/ddi.13191>
9. Bledý, M., Vacek, S., Brabec, P., Vacek, Z., Cukor, J., Černý, J., Ševčík, R., & Brynychová, K. (2024). Silver Fir (*Abies alba* Mill.): Review of Ecological Insights, Forest Management Strategies, and Climate Change's Impact on European Forests. *Forests*, 15(6), 998. <https://doi.org/10.3390/f15060998>
10. Boisvert-Marsh, L., Périé, C., & de Blois, S. (2014). Shifting with climate? Evidence for recent changes in tree species distribution at high latitudes. *Ecosphere*, 5(7), 1–33. <https://doi.org/10.1890/es14-00111.1>
11. Booth, T. H., Nix, H. A., Busby, J. R., & Hutchinson, M. F. (2013). bioclim: the first species distribution modelling package, its early applications and relevance to most current MaxEnt studies. *Diversity and Distributions*, 20(1), 1–9. <https://doi.org/10.1111/ddi.12144>
12. Brichta, J., Šimůnek, V., Bílek, L., Vacek, Z., Gallo, J., Drozdowski, S., Bravo-Fernández, J. A., Mason, B., Roig Gomez, S., Hájek, V., Vacek, S., Štícha, V., Brabec, P., & Fuchs, Z. (2024). Effects of Climate Change on Scots Pine (*Pinus sylvestris* L.) Growth across Europe: Decrease of Tree-Ring Fluctuation and Amplification of Climate Stress. *Forests*, 15(1), 91. <https://doi.org/10.3390/f15010091>
13. Bradley, B. A., Beaury, E. M., Gallardo, B., Ibáñez, I., Jarnevich, C., Morelli, T. L., Sofaer, H. R., Sorte, C. J. B., & Vilà, M. (2024). Observed and Potential Range Shifts of Native

and Nonnative Species with Climate Change. *Annual Review of Ecology, Evolution, and Systematics*, 55(1), 23–40. <https://doi.org/10.1146/annurev-ecolsys-102722-013135>

14. Brun, P., Thuiller, W., Chauvier, Y., Pellissier, L., Wüest, R. O., Wang, Z., & Zimmermann, N. E. (2019). Model complexity affects species distribution projections under climate change. *Journal of Biogeography*, 47(1), 130–142. <https://doi.org/10.1111/jbi.13734>

15. Chersich, S., Rejšek, K., Vranová, V., Bordoni, M., & Meisina, C. (2015). Climate change impacts on the Alpine ecosystem: an overview with focus on the soil. *Journal of Forest Science*, 61(11), 496–514. <https://doi.org/10.17221/47/2015-jfs>

16. Colwell, R. K., Brehm, G., Cardelús, C. L., Gilman, A. C., & Longino, J. T. (2008). Global Warming, Elevational Range Shifts, and Lowland Biotic Attrition in the Wet Tropics. *Science*, 322(5899), 258–261. <https://doi.org/10.1126/science.1162547>

17. Daly, C., Conklin, D. R., & Unsworth, M. H. (2009). Local atmospheric decoupling in complex topography alters climate change impacts. *International Journal of Climatology*, 30(12), 1857–1864. <https://doi.org/10.1002/joc.2007>

18. De Marco, P., & Nóbrega, C. C. (2018). Evaluating collinearity effects on species distribution models: An approach based on virtual species simulation. *PLOS ONE*, 13(9), e0202403. <https://doi.org/10.1371/journal.pone.0202403>

19. Dirnböck, T., Dullinger, S., & Grabherr, G. (2003). A regional impact assessment of climate and land-use change on alpine vegetation. *Journal of Biogeography*, 30(3), 401–417. <https://doi.org/10.1046/j.1365-2699.2003.00839.x>

20. Ditmarova, L., Kurjak, D., Palmroth, S., Kmet, J., & Strelcova, K. (2009). Physiological responses of Norway spruce (*Picea abies*) seedlings to drought stress. *Tree Physiology*, 30(2), 205–213. <https://doi.org/10.1093/treephys/tpp116>

21. Dobrowski, S. Z. (2011). A climatic basis for microrefugia: the influence of terrain on climate. *Global Change Biology*, 17(2), 1022–1035. <https://doi.org/10.1111/j.1365-2486.2010.02263.x>
22. Duan, X. (2026). Climate-driven habitat shifts of *Abies fargesii* var. *faxoniana* using the MaxEnt model. *Journal of Water and Climate Change*, 17(2), 282–298. <https://doi.org/10.2166/wcc.2025.226>
23. Dullinger, S., Gatttringer, A., Thuiller, W., Moser, D., Zimmermann, N. E., Guisan, A., Willner, W., Plutzer, C., Leitner, M., Mang, T., Caccianiga, M., Dirnböck, T., Ertl, S., Fischer, A., Lenoir, J., Svenning, J.-C., Psomas, A., Schmatz, D. R., Silc, U., ... Hülber, K. (2012). Extinction debt of high-mountain plants under twenty-first-century climate change. *Nature Climate Change*, 2(8), 619–622. <https://doi.org/10.1038/nclimate1514>
24. Dumont, M., Monteiro, D., Filhol, S., Gascoin, S., Marty, C., Hagenmuller, P., Morin, S., Choler, P., & Thuiller, W. (2025). The European Alps in a changing climate: physical trends and impacts. *Comptes Rendus. Géoscience*, 357(G1), 25–42. <https://doi.org/10.5802/crgeos.288>
25. Ettinger, A., & HilleRisLambers, J. (2017). Competition and facilitation may lead to asymmetric range shift dynamics with climate change. *Global Change Biology*, 23(9), 3921–3933. <https://doi.org/10.1111/gcb.13649>
26. Falk, W., & Mellert, K. H. (2011). Species distribution models as a tool for forest management planning under climate change: risk evaluation of *Abies alba* in Bavaria. *Journal of Vegetation Science*, 22(4), 621–634. <https://doi.org/10.1111/j.1654-1103.2011.01294.x>

27. Feurdean, A., Bhagwat, S. A., Willis, K. J., Birks, H. J. B., Lischke, H., & Hickler, T. (2013). Tree Migration-Rates: Narrowing the Gap between Inferred Post-Glacial Rates and Projected Rates. *PLoS ONE*, 8(8), e71797. <https://doi.org/10.1371/journal.pone.0071797>
28. Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37(12), 4302–4315. <https://doi.org/10.1002/joc.5086>
29. Ghasemian Sorboni, S., Ghahremaninejad, F., Hadipour, M., & Carrer, M. (2027). Projecting future climatic refugia for *Fagus orientalis* in the Hyrcanian ecoregion. *Journal for Nature Conservation*, 95, 127444. <https://doi.org/10.1016/j.jnc.2026.127444>
30. Gilbert, S. L., Broadley, K., Doran-Myers, D., Droghini, A., Haines, J. A., Hämäläinen, A., Lamb, C. T., Neilson, E. W., & Boutin, S. (2019). Conservation triage at the trailing edge of climate envelopes. *Conservation Biology*, 34(1), 289–292. <https://doi.org/10.1111/cobi.13401>
31. Grenouillet, G., Buisson, L., Casajus, N., & Lek, S. (2011). Ensemble modelling of species distribution: the effects of geographical and environmental ranges. *Ecography*, 34(1), 9–17. <https://doi.org/10.1111/j.1600-0587.2010.06152.x>
32. Hampe, A., & Petit, R. J. (2005). Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters*, 8(5), 461–467. <https://doi.org/10.1111/j.1461-0248.2005.00739.x>
33. Houston Durrant, T., de Rigo, D., & Caudullo, G. (2016). *Pinus sylvestris* in Europe: Distribution, habitat, usage and threats. In J. San-Miguel-Ayanz, D. de Rigo, G. Caudullo, T. Houston Durrant, & A. Mauri (Eds.), *European Atlas of Forest Tree Species* (pp. e016b94+). Publications Office of the European

1 Union.[https://www.researchgate.net/profile/Giovanni-](https://www.researchgate.net/profile/Giovanni-Caudullo/publication/299470777_Pinus_sylvestris_in_Europe_distribution_habitat_usage_and_threats/links/61ee73a8dafcdb25fd4a0b70/Pinus-sylvestris-in-Europe-distribution-habitat-usage-and-threats.pdf)
2 [Caudullo/publication/299470777 Pinus sylvestris in Europe distribution habitat usage](https://www.researchgate.net/profile/Giovanni-Caudullo/publication/299470777_Pinus_sylvestris_in_Europe_distribution_habitat_usage_and_threats/links/61ee73a8dafcdb25fd4a0b70/Pinus-sylvestris-in-Europe-distribution-habitat-usage-and-threats.pdf)
3 [_and_threats/links/61ee73a8dafcdb25fd4a0b70/Pinus-sylvestris-in-Europe-distribution-](https://www.researchgate.net/profile/Giovanni-Caudullo/publication/299470777_Pinus_sylvestris_in_Europe_distribution_habitat_usage_and_threats/links/61ee73a8dafcdb25fd4a0b70/Pinus-sylvestris-in-Europe-distribution-habitat-usage-and-threats.pdf)
4 [habitat-usage-and-threats.pdf](https://www.researchgate.net/profile/Giovanni-Caudullo/publication/299470777_Pinus_sylvestris_in_Europe_distribution_habitat_usage_and_threats/links/61ee73a8dafcdb25fd4a0b70/Pinus-sylvestris-in-Europe-distribution-habitat-usage-and-threats.pdf)

5 34. Izworska, K., Zielonka, T., & Muter, E. (2025). Changes in climate–growth relationships
6 in *Larix decidua* revealed by daily climatic data in the Tatra Mountains. *Forest Ecosystems*,
7 14, 100363. <https://doi.org/10.1016/j.fecs.2025.100363>

8 35. Jentsch, A., Kreyling, J., & Beierkuhnlein, C. (2007). A new generation of climate-change
9 experiments: events, not trends. *Frontiers in Ecology and the Environment*, 5(7), 365–374.
10 [https://doi.org/10.1890/1540-9295\(2007\)5\[365:angoce\]2.0.co;2](https://doi.org/10.1890/1540-9295(2007)5[365:angoce]2.0.co;2)

11 36. Langvall, O. (2011). Impact of climate change, seedling type and provenance on the risk
12 of damage to Norway spruce (*Picea abies* (L.) Karst.) seedlings in Sweden due to early
13 summer frosts. *Scandinavian Journal of Forest Research*, 26(S11), 56–63.
14 <https://doi.org/10.1080/02827581.2011.564399>

15 37. A. Lee-Yaw, J., L. McCune, J., Pironon, S., & N. Sheth, S. (2021). Species distribution
16 models rarely predict the biology of real populations. *Ecography*, 2022(6).
17 <https://doi.org/10.1111/ecog.05877>

18 38. Lembrechts, J. J., Nijs, I., & Lenoir, J. (2018). Incorporating microclimate into species
19 distribution models. *Ecography*, 42(7), 1267–1279. <https://doi.org/10.1111/ecog.03947>

20 39. Lenoir, J., & Svenning, J. -C. (2014). Climate-related range shifts – a global
21 multidimensional synthesis and new research directions. *Ecography*, 38(1), 15–28.
22 <https://doi.org/10.1111/ecog.00967>

40. Le ROUX, P. C., & McGEACH, M. A. (2008). Rapid range expansion and community reorganization in response to warming. *Global Change Biology*, 14(12), 2950–2962. <https://doi.org/10.1111/j.1365-2486.2008.01687.x>
41. Lévesque, M., Saurer, M., Siegwolf, R., Eilmann, B., Brang, P., Bugmann, H., & Rigling, A. (2013). Drought response of five conifer species under contrasting water availability suggests high vulnerability of Norway spruce and European larch. *Global Change Biology*, 19(10), 3184–3199. <https://doi.org/10.1111/gcb.12268>
42. Liu, C., Newell, G., & White, M. (2015). On the selection of thresholds for predicting species occurrence with presence-only data. *Ecology and Evolution*, 6(1), 337–348. <https://doi.org/10.1002/ece3.1878>
43. Lososová, Z., Axmanová, I., Chytrý, M., Midolo, G., Abdulhak, S., Karger, D. N., Renaud, J., Van Es, J., Vittoz, P., & Thuiller, W. (2023). Seed dispersal distance classes and dispersal modes for the European flora. *Global Ecology and Biogeography*, 32(9), 1485–1494. <https://doi.org/10.1111/geb.13712>
44. Kelly, A. E., & Goulden, M. L. (2008). Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences*, 105(33), 11823–11826. <https://doi.org/10.1073/pnas.0802891105>
45. Knoke, T., Ammer, C., Stimm, B., & Mosandl, R. (2007). Admixing broadleaved to coniferous tree species: a review on yield, ecological stability and economics. *European Journal of Forest Research*, 127(2), 89–101. <https://doi.org/10.1007/s10342-007-0186-2>
46. Körner, C. (2021). The cold range limit of trees. *Trends in Ecology & Evolution*, 36(11), 979–989. <https://doi.org/10.1016/j.tree.2021.06.011>

- 1 47. Maclean, I. M. D., & Early, R. (2023). Macroclimate data overestimate range shifts of
2 plants in response to climate change. *Nature Climate Change*, 13(5), 484–490.
3 <https://doi.org/10.1038/s41558-023-01650-3>
- 4 48. Mamet, S. D., Brown, C. D., Trant, A. J., & Laroque, C. P. (2018). Shifting global *Larix*
5 distributions: Northern expansion and southern retraction as species respond to changing
6 climate. *Journal of Biogeography*, 46(1), 30–44. <https://doi.org/10.1111/jbi.13465>
- 7 49. Marcer, A., Sáez, L., Molowny-Horas, R., Pons, X., & Pino, J. (2013). Using species
8 distribution modelling to disentangle realised versus potential distributions for rare species
9 conservation. *Biological Conservation*, 166, 221–230.
10 <https://doi.org/10.1016/j.biocon.2013.07.001>
- 11 50. Marini, L., Økland, B., Jönsson, A. M., Bentz, B., Carroll, A., Forster, B., Grégoire, J.,
12 Hurling, R., Nageleisen, L. M., Netherer, S., Ravn, H. P., Weed, A., & Schroeder, M.
13 (2017). Climate drivers of bark beetle outbreak dynamics in Norway spruce forests.
14 *Ecography*, 40(12), 1426–1435. <https://doi.org/10.1111/ecog.02769>
- 15 51. McDowell, N. G., Williams, A. P., Xu, C., Pockman, W. T., Dickman, L. T., Sevanto, S.,
16 Pangle, R., Limousin, J., Plaut, J., Mackay, D. S., Ogee, J., Domec, J. C., Allen, C. D.,
17 Fisher, R. A., Jiang, X., Muss, J. D., Breshears, D. D., Rauscher, S. A., & Koven, C. (2015).
18 Multi-scale predictions of massive conifer mortality due to chronic temperature rise.
19 *Nature Climate Change*, 6(3), 295–300. <https://doi.org/10.1038/nclimate2873>
- 20 52. McLachlan, J. S., Hellmann, J. J., & Schwartz, M. W. (2007). A Framework for Debate of
21 Assisted Migration in an Era of Climate Change. *Conservation Biology*, 21(2), 297–302.
22 <https://doi.org/10.1111/j.1523-1739.2007.00676.x>

53. Meier, E. S., Lischke, H., Schmatz, D. R., & Zimmermann, N. E. (2011). Climate, competition and connectivity affect future migration and ranges of European trees. *Global Ecology and Biogeography*, 21(2), 164–178. <https://doi.org/10.1111/j.1466-8238.2011.00669.x>
54. Morelli, T. L., Barrows, C. W., Ramirez, A. R., Cartwright, J. M., Ackerly, D. D., Eaves, T. D., Ebersole, J. L., Krawchuk, M. A., Letcher, B. H., Mahalovich, M. F., Meigs, G. W., Michalak, J. L., Millar, C. I., Quiñones, R. M., Stralberg, D., & Thorne, J. H. (2020). Climate-change refugia: biodiversity in the slow lane. *Frontiers in Ecology and the Environment*, 18(5), 228–234. <https://doi.org/10.1002/fee.2189>
55. Morin, X., Viner, D., & Chuine, I. (2008). Tree species range shifts at a continental scale: new predictive insights from a process-based model. *Journal of Ecology*, 96(4), 784–794. <https://doi.org/10.1111/j.1365-2745.2008.01369.x>
56. Moris, J. V., Vacchiano, G., Ascoli, D., & Motta, R. (2017). Alternative stable states in mountain forest ecosystems: the case of European larch (*Larix decidua*) forests in the western Alps. *Journal of Mountain Science*, 14(5), 811–822. <https://doi.org/10.1007/s11629-016-4328-1>
57. Naimi, B. (2012). usdm: Uncertainty Analysis for Species Distribution Models (Version 2.1-7) [R package]. The Comprehensive R Archive Network. <https://cran.r-project.org/web/packages/usdm>
58. Naimi, B., & Araújo, M. B. (2016). sdm: a reproducible and extensible R platform for species distribution modelling. *Ecography*, 39(4), 368–375. <https://doi.org/10.1111/ecog.01881>

59. Nolan, C., Overpeck, J. T., Allen, J. R. M., Anderson, P. M., Betancourt, J. L., Binney, H. A., Brewer, S., Bush, M. B., Chase, B. M., Cheddadi, R., Djamali, M., Dodson, J., Edwards, M. E., Gosling, W. D., Haberle, S., Hotchkiss, S. C., Huntley, B., Ivory, S. J., Kershaw, A. P., ... Jackson, S. T. (2018). Past and future global transformation of terrestrial ecosystems under climate change. *Science*, 361(6405), 920–923.
<https://doi.org/10.1126/science.aan5360>
60. Obladen, N., Dechering, P., Skiadaresis, G., Tegel, W., Keßler, J., Höllerl, S., Kaps, S., Hertel, M., Dulamsuren, C., Seifert, T., Hirsch, M., & Seim, A. (2021). Tree mortality of European beech and Norway spruce induced by 2018-2019 hot droughts in central Germany. *Agricultural and Forest Meteorology*, 307, 108482.
<https://doi.org/10.1016/j.agrformet.2021.108482>
61. Palik, B. J., Clark, P. W., D’Amato, A. W., Swanston, C., & Nagel, L. (2022). Operationalizing forest-assisted migration in the context of climate change adaptation: Examples from the eastern <sc>USA</sc>. *Ecosphere*, 13(10).
<https://doi.org/10.1002/ecs2.4260>
62. Pauli, H., Gottfried, M., & Grabherr, G. (2003). Effects of climate change on the alpine and nival vegetation of the Alps. *Journal of Mountain Ecology*, 7(Suppl.), 9–12.
https://www.pngp.it/sites/default/files/documenti/Pubblicazioni/ibex_journal_mountain_ecology/134-491-1-PB.pdf
63. Patsiou, T. S., Conti, E., Zimmermann, N. E., Theodoridis, S., & Randin, C. F. (2014). Topo-climatic microrefugia explain the persistence of a rare endemic plant in the Alps during the last 21 millennia. *Global Change Biology*, 20(7), 2286–2300.
<https://doi.org/10.1111/gcb.12515>

64. Peterson, A. T. (2011). Ecological niche conservatism: a time-structured review of evidence. *Journal of Biogeography*, 38(5), 817–827. <https://doi.org/10.1111/j.1365-2699.2010.02456.x>
65. Piaszczyk, W., Szlachta, A., Łyszczarz, S., Szymański, N., Jasik, M., Żelazny, M., Małek, S., Lasota, J., & Błońska, E. (2026). Stoichiometry of peatlands and plants: Mutual interactions in biogeochemical cycles. *Geoderma*, 466, 117687. <https://doi.org/10.1016/j.geoderma.2026.117687>
66. Parolo, G., & Rossi, G. (2008). Upward migration of vascular plants following a climate warming trend in the Alps. *Basic and Applied Ecology*, 9(2), 100–107. <https://doi.org/10.1016/j.baae.2007.01.005>
67. Pastore, M. A., Classen, A. T., D’Amato, A. W., Foster, J. R., & Adair, E. C. (2022). Cold-air pools as microrefugia for ecosystem functions in the face of climate change. *Ecology*, 103(8). <https://doi.org/10.1002/ecy.3717>
68. Rebetez, M., & Dobbertin, M. (2004). Climate change may already threaten Scots pine stands in the Swiss Alps. *Theoretical and Applied Climatology*, 79(1–2), 1–9. <https://doi.org/10.1007/s00704-004-0058-3>
69. Rehm, E. M., Olivas, P., Stroud, J., & Feeley, K. J. (2015). Losing your edge: climate change and the conservation value of range-edge populations. *Ecology and Evolution*, 5(19), 4315–4326. <https://doi.org/10.1002/ece3.1645>
70. Rozenberg, P., Chauvin, T., Escobar-Sandoval, M., Huard, F., Shishov, V., Charpentier, J.-P., Sergent, A.-S., Vargas-Hernandez, J. J., Martinez-Meier, A., & Pâques, L. (2020). Climate warming differently affects *Larix decidua* ring formation at each end of a French

Alps elevational gradient. *Annals of Forest Science*, 77(2). <https://doi.org/10.1007/s13595-020-00958-w>

71. Scherrer, D., & Körner, C. (2010). Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *Journal of Biogeography*, 38(2), 406–416. <https://doi.org/10.1111/j.1365-2699.2010.02407.x>

72. Shabani, F., Kumar, L., & Ahmadi, M. (2018). Assessing accuracy methods of species distribution models: AUC, specificity, sensitivity and the true skill statistic. *Global Journal of Human-Social Science: B Geography, Geo-Sciences, Environmental Science & Disaster Management*, 18(1)

73. Siefert, A., Lesser, M. R., & Fridley, J. D. (2015). How do climate and dispersal traits limit ranges of tree species along latitudinal and elevational gradients? *Global Ecology and Biogeography*, 24(5), 581–593. <https://doi.org/10.1111/geb.12287>

74. Singer, M. C., & Parmesan, C. (2010). Phenological asynchrony between herbivorous insects and their hosts: signal of climate change or pre-existing adaptive strategy? *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1555), 3161–3176. <https://doi.org/10.1098/rstb.2010.0144>

75. Srivastava, V., Lafond, V., & Griess, V. C. (2019). Species distribution models (SDM): applications, benefits and challenges in invasive species management. *CABI Reviews*, 1–13. <https://doi.org/10.1079/pavsnnr201914020>

76. Stark, J. R., & Fridley, J. D. (2022). Microclimate-based species distribution models in complex forested terrain indicate widespread cryptic refugia under climate change. *Global Ecology and Biogeography*, 31(3), 562–575. <https://doi.org/10.1111/geb.13447>

- 1 77. Suggitt, A. J., Wilson, R. J., Isaac, N. J. B., Beale, C. M., Auffret, A. G., August, T., Bennie,
2 J. J., Crick, H. Q. P., Duffield, S., Fox, R., Hopkins, J. J., Macgregor, N. A., Morecroft, M.
3 D., Walker, K. J., & Maclean, I. M. D. (2018). Extinction risk from climate change is
4 reduced by microclimatic buffering. *Nature Climate Change*, 8(8), 713–717.
5 <https://doi.org/10.1038/s41558-018-0231-9>
- 6 78. Svenning, J., & Sandel, B. (2013). Disequilibrium vegetation dynamics under future
7 climate change. *American Journal of Botany*, 100(7), 1266–1286.
8 <https://doi.org/10.3732/ajb.1200469>
- 9 79. Svenning, J., & Skov, F. (2007). Could the tree diversity pattern in Europe be generated by
10 postglacial dispersal limitation? *Ecology Letters*, 10(6), 453–460.
11 <https://doi.org/10.1111/j.1461-0248.2007.01038.x>
- 12 80. Thom, D., & Seidl, R. (2021). Accelerating Mountain Forest Dynamics in the Alps.
13 *Ecosystems*, 25(3), 603–617. <https://doi.org/10.1007/s10021-021-00674-0>
- 14 81. Travis, J. M. J., Delgado, M., Bocedi, G., Baguette, M., Bartoń, K., Bonte, D., Boulangeat,
15 I., Hodgson, J. A., Kubisch, A., Penteriani, V., Saastamoinen, M., Stevens, V. M., &
16 Bullock, J. M. (2013). Dispersal and species' responses to climate change. *Oikos*, 122(11),
17 1532–1540. <https://doi.org/10.1111/j.1600-0706.2013.00399.x>
- 18 82. Twardek, W. M., Taylor, J. J., Rytwinski, T., Aitken, S. N., MacDonald, A. L., Van Bogaert,
19 R., & Cooke, S. J. (2023). The application of assisted migration as a climate change
20 adaptation tactic: An evidence map and synthesis. *Biological Conservation*, 280, 109932.
21 <https://doi.org/10.1016/j.biocon.2023.109932>

83. Vilà-Cabrera, A., Premoli, A. C., & Jump, A. S. (2019). Refining predictions of population decline at species' rear edges. *Global Change Biology*, 25(5), 1549–1560. <https://doi.org/10.1111/gcb.14597>
84. Vitasse, Y., Ursenbacher, S., Klein, G., Bohnenstengel, T., Chittaro, Y., Delestrade, A., Monnerat, C., Rebetez, M., Rixen, C., Strebel, N., Schmidt, B. R., Wipf, S., Wohlgemuth, T., Yoccoz, N. G., & Lenoir, J. (2021). Phenological and elevational shifts of plants, animals and fungi under climate change in the European Alps. *Biological Reviews*, 96(5), 1816–1835. <https://doi.org/10.1111/brv.12727>
85. Vittoz, P., & Engler, R. (2007). Seed dispersal distances: a typology based on dispersal modes and plant traits. *Botanica Helvetica*, 117(2), 109–124. <https://doi.org/10.1007/s00035-007-0797-8>
86. Walder, D., Krebs, P., Bugmann, H., Manetti, M. C., Pollastrini, M., Anzillotti, S., & Conedera, M. (2021). Silver fir (*Abies alba* Mill.) is able to thrive and prosper under meso-Mediterranean conditions. *Forest Ecology and Management*, 498, 119537. <https://doi.org/10.1016/j.foreco.2021.119537>
87. Weiskopf, S. R., Rubenstein, M. A., Crozier, L. G., Gaichas, S., Griffis, R., Halofsky, J. E., Hyde, K. J. W., Morelli, T. L., Morissette, J. T., Muñoz, R. C., Pershing, A. J., Peterson, D. L., Poudel, R., Staudinger, M. D., Sutton-Grier, A. E., Thompson, L., Vose, J., Weltzin, J. F., & Whyte, K. P. (2020). Climate change effects on biodiversity, ecosystems, ecosystem services, and natural resource management in the United States. *Science of The Total Environment*, 733, 137782. <https://doi.org/10.1016/j.scitotenv.2020.137782>

- 1 88. Williams, M. I., & Dumroese, R. K. (2013). Preparing for Climate Change: Forestry and
2 Assisted Migration. *Journal of Forestry*, 111(4), 287–297. <https://doi.org/10.5849/jof.13->
3 016
- 4 89. Zani, D., Lischke, H., & Lehsten, V. (2023). Climate and dispersal limitation drive tree
5 species range shifts in post-glacial Europe: results from dynamic simulations. *Frontiers in*
6 *Ecology and Evolution*, 11. <https://doi.org/10.3389/fevo.2023.1321104>
- 7 90. Zizka, A., Silvestro, D., Andermann, T., Azevedo, J., Duarte Ritter, C., Edler, D., Farooq,
8 H., Herdean, A., Ariza, M., Scharn, R., Svantesson, S., Wengström, N., Zizka, V., &
9 Antonelli, A. (2019). CoordinateCleaner: Standardized cleaning of occurrence records
10 from biological collection databases. *Methods in Ecology and Evolution*, 10(5), 744–751.
11 <https://doi.org/10.1111/2041-210x.13152>
- 12 91. Zhu, K., Woodall, C. W., & Clark, J. S. (2011). Failure to migrate: lack of tree range
13 expansion in response to climate change. *Global Change Biology*, 18(3), 1042–1052.
14 <https://doi.org/10.1111/j.1365-2486.2011.02571.x>