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Ecological Niche Modelling of Forest Tree Species in the Alpine Space: a Stacked SDM Approach at Regional Scale

**Modellizzazione della nicchia ecologica delle specie arboree forestali in
territorio alpino: un approccio stacked SDM a scala regionale**

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ABSTRACT

Climate change is deeply altering the structure and composition of forest ecosystems, particularly in mountain landscapes. Ecological Niche Modelling (ENM) provides a valuable tool to estimate the potential distribution of species under current and future climate scenarios. Although many studies have assessed tree-species distributions at continental or national extents with coarse spatial resolution, few have addressed regional, high-resolution modelling – despite its clear relevance for local forest planning and conservation. Key challenges for fine-scale modelling include limited field data availability and high computational and methodological complexity.

This thesis implements Ecological Niche Modelling at 50-m resolution to estimate the potential distribution of 23 dominant forest tree species in the Autonomous Province of Trento (Italian Alps). The modelling was performed using the R package SSDM which combines an ensemble of statistical and machine-learning algorithms to produce individual species models and community-level outputs via Stacked Species Distribution Modelling (SSDM). Models were calibrated using downscaled, high-resolution climate projections (ECLIPS2.0), terrain metrics from a Digital Terrain Model (DTM), and detailed occurrence data from local forest inventories, remote sensing, and a citizen-science platform.

Model performance was evaluated using metrics including Area Under the receiver-operating-characteristic Curve (AUC), Cohen’s Kappa, sensitivity, and specificity. Species richness maps were produced using the SSDM framework, providing a replicable protocol for modelling both individual species distributions and community composition. Additionally, future projections for the 23 species under two IPCC emission scenarios (RCP4.5 and RCP8.5) were generated to assess potential vegetation shifts across three time periods (2041–2060, 2061–2080, and 2081–2100). The analysis also included the assessment of feature importance and modelling uncertainty, which improves the interpretability and robustness of the projections.

Species were classified according to projected changes in their distributional ranges. Taxa such as *Fagus sylvatica* L., *Fraxinus ornus* L. and *Quercus ilex* L. are predicted to exhibit range expansion (“gainers”), whereas *Picea abies* (L.) H.Karst., *Pinus cembra* L. and *Fraxinus excelsior* L. are anticipated to contract (“losers”). Other taxa, including *Betula pendula* Roth, *Larix decidua* Mill., and *Populus tremula* L., display non-linear temporal trend, with initial gains followed by subsequent losses of suitable areas. All the studied species will experience an upward elevation shift of their climate optimum.

Species richness is projected to remain largely stable under the RCP4.5 scenario, whereas a decline is expected under RCP8.5.

Results can support adaptive forest planning and biodiversity conservation in the Alpine contexts. The approach adopted in this study contributes to bridging the gap between broad-scale modelling and local forest management needs. The work provides spatial insights into biodiversity patterns and could help to identify areas of high ecological significance or conservation concern.

KEYWORDS: Niche Modelling; Stacked SDMs; Species richness; Occurrence mapping; Fine-scale modelling.

RIASSUNTO

Il cambiamento climatico sta modificando sostanzialmente la struttura e la composizione degli ecosistemi forestali, con effetti particolarmente rilevanti nelle aree montane. La modellizzazione della nicchia ecologica (*Ecological Niche Modelling*, ENM) rappresenta uno strumento utile per stimare la distribuzione potenziale delle specie in scenari climatici presenti e futuri. Sebbene numerosi studi abbiano analizzato la distribuzione delle specie arboree su scale continentali o nazionali utilizzando dati a bassa risoluzione spaziale, poche ricerche hanno affrontato la modellizzazione regionale ad alta risoluzione, nonostante la sua evidente rilevanza per la pianificazione forestale locale e le politiche di conservazione. Le principali sfide per la modellizzazione ad alta risoluzione comprendono la limitata disponibilità di dati di campo e l'elevata complessità computazionale e metodologica.

La presente tesi applica l'ENM a una risoluzione di 50 m per stimare la distribuzione potenziale di 23 specie arboree dominanti nella Provincia Autonoma di Trento (Alpi italiane). La modellizzazione è stata eseguita con il pacchetto R SSDM, che integra un insieme *ensemble* di algoritmi statistici e di machine learning per produrre modelli di specie individuali e output a livello di comunità mediante l'approccio di *Stacked Species Distribution Modelling* (SSDM). I modelli sono stati calibrati utilizzando proiezioni climatiche ottenute tramite *downscaling* ad alta risoluzione (ECLIPS2.0), metriche topografiche derivate dal Modello Digitale del Terreno (DTM) e dati di presenza dettagliati provenienti da inventari forestali locali, telerilevamento e una piattaforma di *citizen science*.

La validazione dei modelli è stata effettuata mediante l'uso di diverse metriche di valutazione, tra cui l'area sotto la curva ROC (AUC), il coefficiente Kappa di Cohen, la sensibilità e la specificità. Sono state inoltre prodotte mappe di ricchezza specifica tramite l'approccio SSDM, fornendo un protocollo replicabile per la modellizzazione sia delle singole specie sia della composizione comunitaria. Le proiezioni future sono state generate per tre orizzonti temporali (2041–2060, 2061–2080, 2081–2100) e per due scenari di emissione dell'IPCC (RCP4.5 e RCP8.5). L'analisi include infine una valutazione dell'incertezza modellistica, volta a migliorare l'interpretabilità e la robustezza delle proiezioni.

Le specie sono state classificate in base alle proiezioni di variazione dei rispettivi areali di distribuzione. Specie come *Fagus sylvatica* L., *Fraxinus ornus* L. e *Quercus ilex* L. sono

previste in espansione del loro areale («gainers»), mentre *Picea abies* (L.) H.Karst., *Pinus cembra* L. e *Fraxinus excelsior* L. sono attese in contrazione («losers»). Altre specie, tra cui *Betula pendula* Roth, *Larix decidua* Mill. e *Populus tremula* L., mostrano andamenti temporali non lineari, con guadagni iniziali seguiti da successive perdite dell'areale ottimale.

La ricchezza specifica è prevista rimanere sostanzialmente stabile nello scenario RCP4.5, mentre ci si aspetta una diminuzione nello scenario RCP8.5.

I risultati possono supportare la pianificazione forestale adattiva e la conservazione della biodiversità in contesti alpini. L'approccio adottato contribuisce a colmare il divario tra modellizzazioni su larga scala e le esigenze gestionali locali, offrendo informazioni spaziali dettagliate sui pattern di biodiversità e strumenti utili per l'individuazione di aree di elevato valore ecologico o di interesse conservazionistico.

PAROLE CHIAVE: Modellizzazione della nicchia ecologica (ENM); Modelli aggregati di distribuzione delle specie (SSDM); ricchezza specifica; mappatura delle presenze; modellizzazione ad alta risoluzione.

1 INTRODUCTION

Terrestrial ecosystems currently face an unprecedented challenge in both scale and pace: climate change (Parmesan et al., 2022). Anthropogenic greenhouse-gas emissions have elevated atmospheric CO₂ concentrations above 420 ppm – levels unmatched during the past 800,000 years (Lüthi et al., 2008) and by some estimates not seen for up to 14 million years (Hönisch et al., 2023). Global mean surface temperature has risen by approximately 0.9–1.2 °C relative to the 1850–1900 baseline (Eyring et al., 2021). Some regions experience larger changes; for instance, the Alpine region has warmed by about 1.8 °C since 1880 (Kotlarski et al., 2023). Anthropogenic forcing has also increased the magnitude, frequency, and spatiotemporal variability of extreme weather events (Seneviratne et al., 2021).

Environmental changes have consistently shaped Earth's history, influencing the evolution and distribution of both plant and animal species (Huntley, 1991; Pitelka & Group, 1997). Over millions of years, habitats, including forest ecosystems, have maintained a dynamic equilibrium with environmental conditions, while species individually and gradually tracked their ecological niches in response to glacial and interglacial cycles (Davis & Shaw, 2001). Migration has thus emerged as a natural strategy for survival, alongside adaptation and genetic evolution. However, such processes typically occur over longer temporal scales and can entail significant costs and constraints, such as the loss of genetic variability or collateral effects on other adaptive traits (De Meester et al., 2018). Nevertheless, the current pace of climate transformation represents a historical anomaly. According to Hansen et al. (2023), the rate of global warming is exceeding 0.27° per decade, 10 times faster than an average postglacial era. This acceleration is pushing species beyond the limits of their spatial and temporal response capacities, contributing to the collapse of ecosystems that were historically considered stable (Canadell & Jackson, 2021). Forests, in particular, are proving to be highly vulnerable to these changes, primarily due to the longevity and relatively slow response times of tree species (Forzieri et al., 2021; Lindner et al., 2010; Vacek et al., 2023). Under stable conditions, forest ecosystems are known for their resilience and plasticity, enabling them to respond to environmental variations through local acclimation processes or by migrating toward more climatically favourable regions. However, the effectiveness of these strategies is increasingly compromised by the rapid advance of climate change, to the extent that, in the absence of a viable response, the risk of local extinction becomes tangible (Aitken et al., 2008; Loreto

& Atzori, 2024). Unlike animals, plants require significantly more time to migrate, often on the order of centuries and across multiple generations (Loreto & Atzori, 2024). To track current rates of climate change, species would need to migrate at speeds exceeding $\sim 1 \text{ km yr}^{-1}$ in a latitudinal direction, yet the majority do not attain this rate (Corlett & Westcott, 2013; Loreto & Atzori, 2024). Altitudinal shifts are well documented: globally, 67% of alpine treelines exhibit upslope movement, with 88.8% of undisturbed sites in the Northern Hemisphere showing the same trend (Adler et al., 2022). In the Alps, Parolo & Rossi (2008) documented an average upward shift of 34.2 ± 26.7 meters per decade among 52 species of vascular plants. Consequently, the impacts of climate change will continue to alter areas that have historically provided optimal conditions for the majority of forest plant species, raising fundamental questions about ecosystem sustainability and the adaptive capacity of biological communities (Mauri et al., 2022).

Although the progressive elimination of fossil fuel use remains the foremost priority for global climate stability, it is now evident that climate change cannot be halted, but rather managed in terms of its impacts (Brooks, 2013; IPCC, 2023). In this context, human intervention can play a critical role in facilitating species dispersal, accelerating the colonization of more favourable areas and enabling the dynamic tracking of their ecological niches (Williams & Dumroese, 2013). Assisted migration, defined as the intentional relocation of species and populations to promote the natural expansion of their range, may serve as an effective tool for directly responding to climate change, particularly for species that are unable to acclimate or in cases where environments are highly fragmented or isolated (De Meester et al., 2018; Williams & Dumroese, 2013).

Properly guiding forest policy and silvicultural decision-making is critically important, particularly concerning the identification and promotion of species best suited for current and future optimal growth conditions. **Ecological Niche Models** (ENMs) offer valuable support for such decisions by predicting the potential current and future distribution of species based on their ecological preferences. Therefore, the next section describes the state of the art regarding Ecological Niche Models, to facilitate understanding of their application in forest management and in shaping adaptive strategies in response to climate change.

1.1 What Are Ecological Niche Models?

Ecological Niche Models (ENMs) – also referred to as Species Distribution Models (SDMs), bioclimatic envelope models, habitat suitability models, resource selection functions (RSFs), or range maps – are statistical/numerical techniques (correlative methods) used to characterize the ecology of a species by relating distribution or abundance data to environmental, climatic and spatial characteristics of the study area (Elith & Leathwick, 2009; Guisan & Thuiller, 2005; Marchi & Ducci, 2018; Miller, 2010; Pecchi et al., 2019). In other words, ENMs are statistical algorithms that link the spatial distribution of species to environmental factors to define their ecological requirements (Pecchi et al., 2020). Ecological niche models use species presence data to identify the environmental characteristics of the locations where the species occur, to predict which other geographic areas exhibit ecological conditions suitable for their survival (GBIF, 2022).

Correlative ENMs are generally developed in four main phases (Beery et al., 2021):

1. Data collection: acquisition of georeferenced data related to the presence (and absence) of the target species;
2. Association of predictive variables: integration of presence data with corresponding values of selected environmental variables (features), extracted at the recorded geographic points;
3. Model calibration: application and calibration of statistical/machine learning algorithms to define the relationships between predictive variables and species distribution;
4. Spatio-temporal prediction: projection of the calibrated model to estimate the potential distribution of the species within the geographic area and time frame of interest.

ENMs are employed for a wide range of purposes, including the conservation, planning, protection and study of species of interest (Guisan et al., 2006); predicting the impacts of climate change on biodiversity and populations (Guisan & Zimmermann, 2000); supporting forest management (Marchi & Ducci, 2018); identifying priority areas for ecological restoration (Elith & Leathwick, 2009); facilitating assisted migration interventions (Hällfors et al., 2016); monitoring the spread of animal and plant diseases and pathogens (Escobar & Craft, 2016) as well as invasive species (Jiménez-Valverde et al., 2011). ENM studies are not limited to terrestrial species but also extend to marine ecosystems (Melo-Merino et al., 2020). In addition to current and future distributions,

models can also reconstruct past distributions (Guillory & Brown, 2021), and they are applicable to virtually all living organisms: animals, plants, fungi, bacteria, and viruses.

Future modelling techniques should be interpreted not as deterministic predictions of species distribution, but rather as projections of ecological suitability based on scenarios involving changes in environmental covariates. These models represent hypotheses about how species suitability or potential distribution could be configured if the projected climatic scenarios were to happen (Parmesan et al., 2022).

In recent years, ENMs have evolved to predict species richness and composition within a given geographic area by assembling multiple individual ENMs through a technique known as **Stacked Species Distribution Modelling** (SSDM) (Benito et al., 2013). This approach enables assessments of biodiversity trends in specific areas, including the identification of species richness (Schmitt et al., 2017). The focus thus shifted from individual models to a community-level model (Ferrier & Guisan, 2006; see Section 1.4). However, this shift in scale and complexity – from species-level predictions to community-level inferences – also amplifies the propagation of modelling errors and uncertainties arising from data quality, algorithmic complexity, and environmental variability. The main sources of error and uncertainty in ENMs include (Pecchi et al., 2020):

- Uncertainty in the parameters used (e.g., inaccurate presence data);
- Uncertainty within the models (inherent to the complex algorithms involved);
- Uncertainty in climatic data (e.g., projections of future climate conditions).

Although the uncertainty stemming from climate source selection depends on the dataset itself, the first two points remain manageable through strategies such as selecting appropriate occurrence datasets and testing different features and algorithms, with the goal of finding the best accuracy.

Ecological Niche Models and Species Distribution Models are closely tied to the concept of the ecological niche, which is described in the following section (Pecchi et al., 2019).

1.1.1 Ecological Niche Concept

Species are distributed across both geographic and environmental space, making it essential to use appropriate terminology for each dimension. Geographic space is represented through maps with two-dimensional coordinates or three-dimensional digital elevation models, whereas environmental space is defined by a multidimensional set of

environmental variables, including topographic, geo-pedological, climatic, and management/disturbance-related factors (Elith & Leathwick, 2009).

In the last century, the definition of the ecological niche evolved through four main steps (Escobar & Craft, 2016) as shown in Figure 1.1:

- Grinnellian Niche (1917): defined as the area where a species encounters optimal abiotic conditions for survival and reproduction, without requiring external inputs;
- Eltonian Niche (1927): emphasizes the role of the species within an ecosystem, including its biotic interactions such as competition, predation, and other ecological relationships;
- Hutchinsonian Niche (1957): distinguishes between the *fundamental niche*, the theoretical set of environmental conditions – represented as a multidimensional hypervolume – in which a species could potentially survive in the absence of interspecific interactions, and the *realized niche*, which accounts for the actual conditions under which the species exists, including both positive and negative interactions with other organisms;
- Soberón & Peterson's Niche (2005) further expands upon Hutchinson's realized niche by incorporating the *dispersal ability* of the species. Within this framework, the ecological niche is understood as the set of environmental conditions that allow a species to sustain stable populations over time without relying on external immigration.

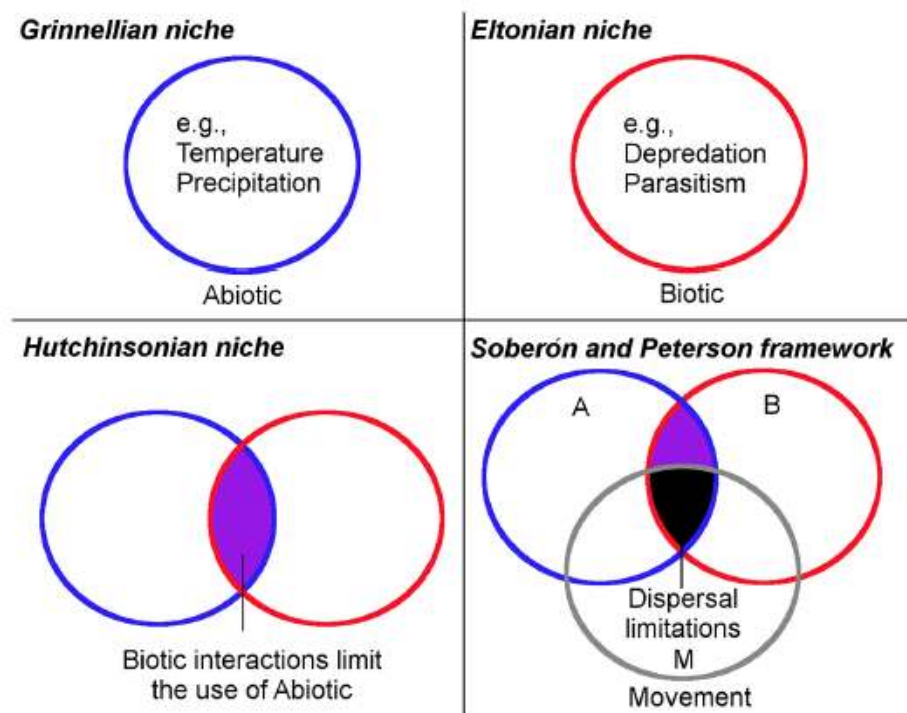


Figure 1.1. The blue circle (A) represents abiotic limits, the red circle (B) denotes biotic constraints and the grey circle (M) illustrates movement and dispersal limitations. Together they form the “BAM framework”. According to Peterson & Soberón (2012), ENMs model species distributions based on the Grinnellian niche, whereas SDMs should refer to the modelling of the realized niche as described by Soberón and Peterson (2005).

Source: Escobar & Craft (2016).

1.1.2 Ecological Niche Models vs. Species Distribution Models

Although the terms *Ecological Niche Models* (ENMs) and *Species Distribution Models* (SDMs) have often been mistakenly used interchangeably, there is now broad consensus on the need to distinguish between the two concepts, which should be applied in different contexts depending on the objectives of the study (Melo-Merino et al., 2020; Peterson & Soberón, 2012).

Ecological niche models aim to estimate the potential geographic distribution of a species, particularly in response to changes in environmental, topographic, and climatic conditions (i.e., future projections). These models focus on the concept of the *fundamental ecological niche* (Grinnellian niche, as discussed in Section 1.1.1 and illustrated in Figure 1.1). Thus, ENMs do not seek to reconstruct current distributions, but rather to delineate the species’ environmental potential (Peterson & Soberón, 2012). It is important to note that ENMs are strongly influenced by human activities, particularly by the type of forest management practices adopted. The preferential treatment of certain species over others (Seim et al., 2022) – for example, the favouring of Norway spruce and European larch over

European beech in the Alpine region – introduces bias into the presence data used as input. As a result, the models may overestimate habitat suitability for favoured species and underestimate it for those disadvantaged by forest management (Anselmetto et al., 2025). Incorporating complex biotic interactions and the dispersal capacity of a species into these models is inherently challenging, given that such processes require detailed knowledge of historical distributional dynamics. For this reason, correlative ENMs are generally simpler and faster to implement, as they consider only the abiotic constraints on species distributions (Melo-Merino et al., 2020).

The term **Species Distribution Models**, on the other hand, refers to studies that aim to estimate the current distribution of one or more species integrating other factors beyond only abiotic ones, such as dispersal capacity and biotic interactions (Soberón & Peterson, 2005). SDMs allow for modelling distribution without necessarily invoking the ecological niche concept or relying exclusively on environmental variables. Their goal is to translate the estimated potential range into the area of actual occupation. Consequently, SDMs focus specifically on reconstructing the *realized niche* (Peterson & Soberón, 2012). Elith & Leathwick (2009) consider the term SDM to be more generic and neutral compared to other terms often used as synonyms.

In light of this distinction, the most accurate term to describe the present study is *Ecological Niche Modelling*, as it considers only environmental abiotic factors, specifically climatic, topographic, soil-related and disturbance-related variables. These include temperature- and precipitation-related indices as well as terrain-derived metrics, which are detailed in Sections 2.3.2 – 2.3.5. Throughout this thesis, the term SSDM is used to refer specifically to the Stacked Species Distribution Modelling methodology described in Section 1.4, and not as a synonym for ENM. Understanding the origins and evolution of these models is crucial for contextualizing their historical development and for analysing the methodological integration of machine learning models that have broadened their applicability in ecosystem management and conservation.

1.2 A Brief History of Ecological Niche Modelling

The earliest attempts to model species distributions date back to the early 1900s, when researchers began to qualitatively correlate biological patterns with geographic and/or environmental variables (Elith & Leathwick, 2009). Among the first examples, Grinnell (1904) studied the distribution of the chestnut-backed chickadee in North America (cited

in Beery et al., 2021) and Johnston (1924) studied the spread of invasive cactus species in Australia (cited in Guisan & Thuiller, 2005). By the 1950s, studies demonstrated that species respond individually to environmental changes, suggesting that modelling individual species is more appropriate than modelling entire communities (Elith & Leathwick, 2009). In 1963, Hintikka was among the first researchers to evaluate the distribution of various European species based on climatic variables (cited in Pearson & Dawson, 2003). Between the 1970s and 1980s, the first computer-based studies emerged (Guisan & Thuiller, 2005). Subsequently, more robust statistical models were developed, such as the Generalized Linear Models (GLMs), marking the beginning of regression-based SDMs. These models introduced a new level of quantitative sophistication and realism, and are still widely used today (Elith & Leathwick, 2009). The advent and evolution of machine learning models has led to significant advancements in species distribution modelling. Machine learning models are adaptive algorithms capable of learning and self-modifying based on performance assessment criteria (Gobeyn et al., 2019; Figure 1.2),

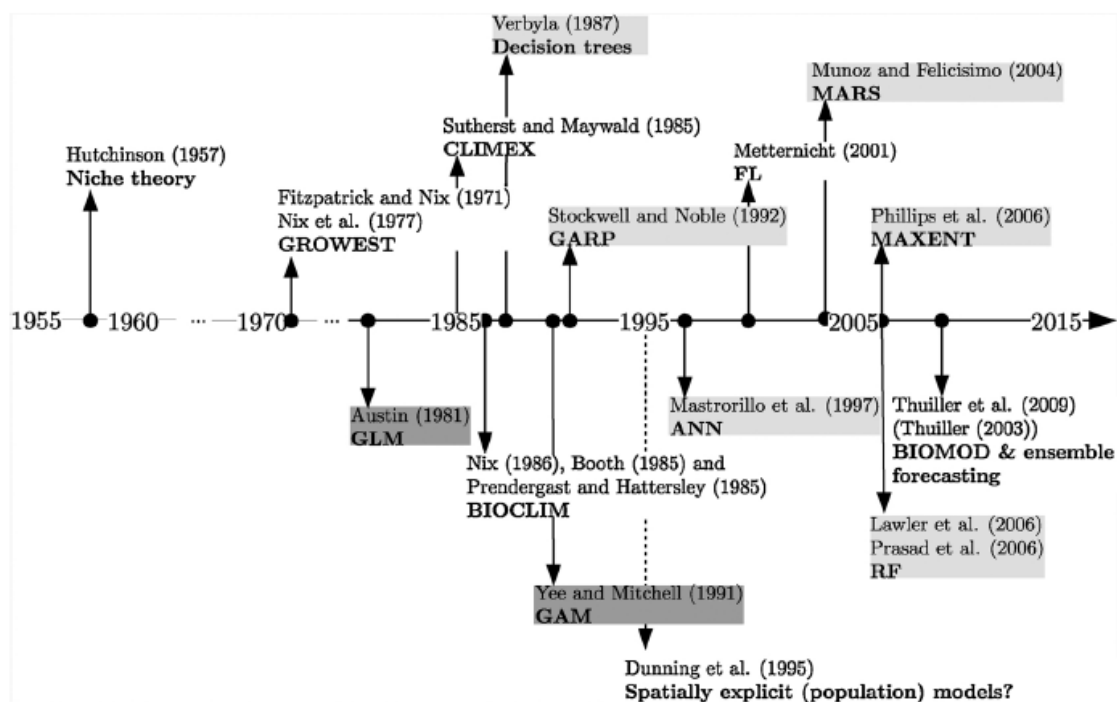


Figure 1.2. Chronological overview of the development of key statistical and machine learning methods used in Species Distribution Modelling.
Source: Gobeyn et al., 2019

A significant advancement occurred in the late 1990s with the release of various high-resolution global climate databases, including WorldClim – a global dataset of gridded environmental variables – which substantially enhanced the accuracy of species distribution predictions (Pecchi et al., 2019). Simultaneously, during the 2000s, the technology for collecting and digitizing geographic, topographic, and climatic data improved significantly. The development of Geographic Information Systems (GIS) enabled more effective handling of both presence data and environmental variables (Elith & Leathwick, 2009; Kearney & Porter, 2009). Driven by the exponential growth in computational power, current research is increasingly focused on the development of deep learning tools capable of providing more accurate information on species distributions through the use of machine learning algorithms (Bonannella et al., 2022). These algorithms can process large volumes of increasingly accessible field and environmental datasets and are better equipped to capture the interacting and non-linear relationships between species and their environments (Beery et al., 2021). Further advancements are also taking place in the field of meteorology, with the development of increasingly high-resolution maps for predicting climate evolution.

Despite these advancements, the majority of studies have been conducted at broad spatial scales and low resolution (e.g. 1 to 50 km), which are not well-suited for practical forest management (Anselmetto et al., 2025). Maps with resolutions finer than 100 meters are more useful for policymakers, even at the expense of reduced prediction accuracy (Bonannella et al., 2022). Although data resolution has recently improved, the challenge remains to generate operational data at the local scale. This is largely due to the lack of high-resolution climate projections and the scarcity of accurate, well-georeferenced presence datasets, particularly in more remote areas.

Limited progress has also been made at the regional scale regarding species richness.

In managed forests, which constitute the majority of Europe's forested areas, biological limitations such as competition and dispersal tend to be less significant, as these factors are largely governed by human intervention, whereby abiotic factors gain more importance in driving the species spatial distribution (Thurm et al., 2018). In this context, Ecological Niche Models, which are based on predicting the distribution solely on abiotic factors, can become particularly effective tools for silvicultural planning.

1.3 Practical Applications of Ecological Niche Models

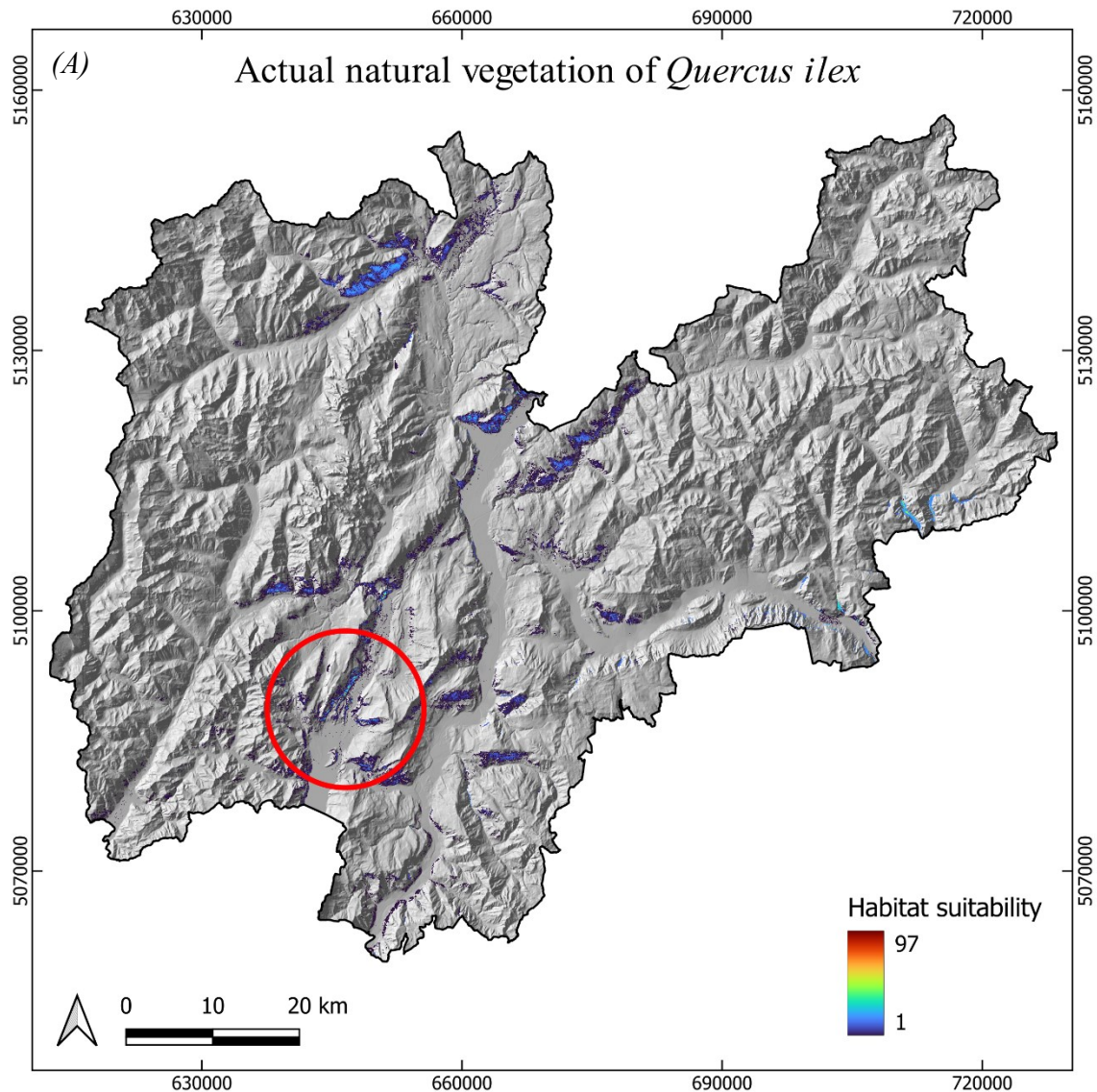
The forestry literature on Environmental Niche Modelling (or Species Distribution Modelling) is extensive. Numerous studies have been conducted on modelling the niches of species of major economic, ecological, social, and environmental importance across Europe. However, this non-exhaustive review of the available literature reveals a clear gap: a lack of local-scale studies that could provide concrete support for silvicultural planning. Studies conducted over large areas at continental or national scales are certainly valuable for understanding macro-trends in species distribution dynamics, but they are not suitable for forest management, which requires decision-making based on sub-compartment level information, typically at a spatial resolution of tens to hundreds of meters (Anselmetto et al., 2025). Furthermore, the use of local presence datasets, as opposed to more generalized or global ones, is considered to enhance the accuracy of predictions, as these datasets are less prone to collection biases and errors, but are subject to the niche truncation bias (Anselmetto et al., 2025).

A brief review of the literature on species richness modelling is also provided. This synthesis highlights that few studies have applied Stacked species distribution models (SSDMs) to investigate these community-level parameters specifically within the forest sector.

Starting with the single-species models, examples of continental-scale applications include Bonannella et al. (2022) for Europe, Henderson et al. (2014) for North America and Pérez Chaves et al. (2018) for South America. In these studies, the authors modelled potential current species distributions (at a high resolution of 30 meters) without projecting them in the future.

The study by Bonannella et al. (2022), focusing on modelling both the Actual Natural Vegetation (ANV) and Potential Natural Vegetation (PNV) distribution of 16 of the most widespread forest species in Europe, currently represents one of the most comprehensive contributions in the field of SDM. The presence data used were sourced from heterogeneous databases including GBIF and national forest inventories. They cover the entire European continent and were subjected to spatial and qualitative filtering. Furthermore, the spatial resolution of the model is remarkably high (30 m), making this study particularly advanced from a methodological perspective. However, despite the overall high quality of the modelling framework, some limitations remain regarding its applicability at the local scale, especially in mountainous areas with complex morphology

such as the Autonomous Province of Trento (PAT). Specifically, for species with a limited or marginal distribution in the Alpine context, such as *Quercus ilex* L. (holm oak), the model demonstrates reduced predictive capacity. As shown in Figure 1.3, this species is not accurately modelled in areas where it is known to be stably present, such as the Val dei Laghi. This discrepancy is particularly evident in the case of potential distribution (Figure 1.3, A), suggesting that the model's effectiveness may be lower in biogeographically peripheral areas relative to the species' core range. Figure 1.4 illustrates that the distribution of holm oak presence points used to train the model is heavily concentrated in the Mediterranean area, with limited representation in Alpine regions such as Trentino. This imbalance may have constrained the model's ability to accurately detect the species in marginal areas of its range.



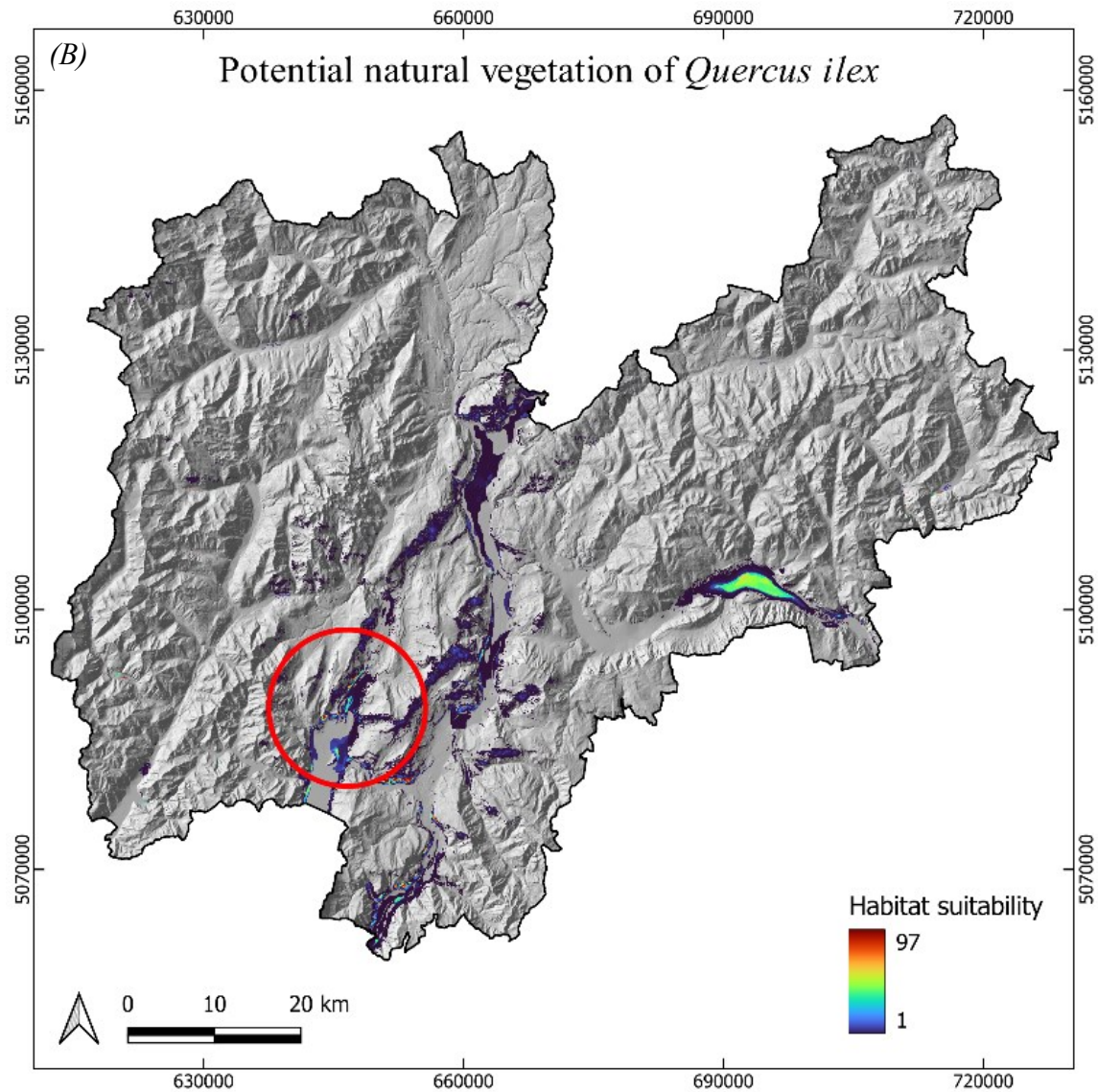


Figure 1.3. Maps of the actual distribution, Actual Natural Vegetation (ANV), (A) and potential distribution, Potential Natural Vegetation (PNV), (B) of *Quercus ilex* (holm oak), clipped for the Province of Trento. The spatial resolution is high, at 30 meters. It is evident that certain areas—such as Val dei Laghi (circled), where the species is endemic—were not accurately predicted by the study, particularly in the case of the actual vegetation map (A).

Source: Bonannella et al. (2022, supplementary material), processed with QGIS.

Quercus ilex

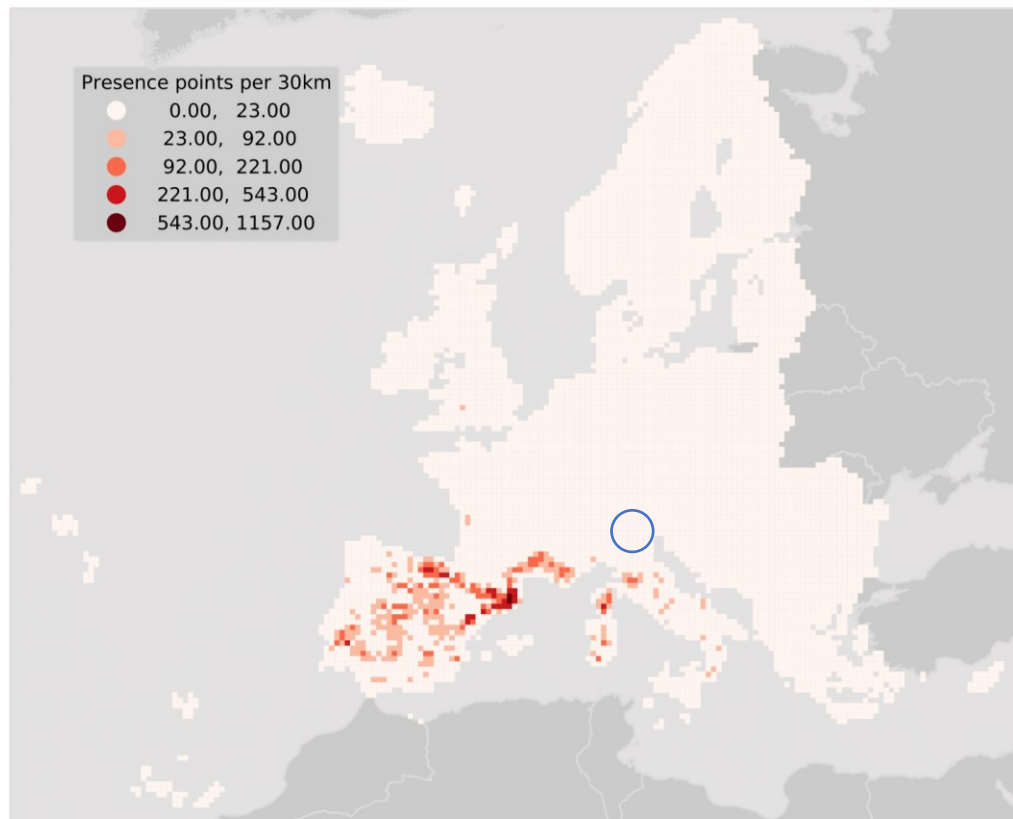


Figure 1.4. Distribution of presence points of holm oak used to train the models. The vast majority of the occurrence points are in the mediterranean area, thus the peripheral zones, as in the case of the Autonomous Province of Trento, are excluded (blue circle). This led to discrepancies in local-scale distribution studies.

Source: Bonannella et al. (2022, supplementary material).

One of the most significant and recent contributions in Ecological Niche Modelling at the European level is that of Mauri et al. (2022), which examines the distribution of 67 major plant species, projecting their future distributions across three time horizons (2035, 2065, and 2095) under two emission scenarios from the IPCC AR5 (RCP 4.5 and 8.5; Figure 1.5). The spatial resolution used is 5 arc-minutes (approximately 9 km). The study employs six different algorithms implemented using the Biomod2 platform in R, and incorporates a natural dispersal model (MigClim).

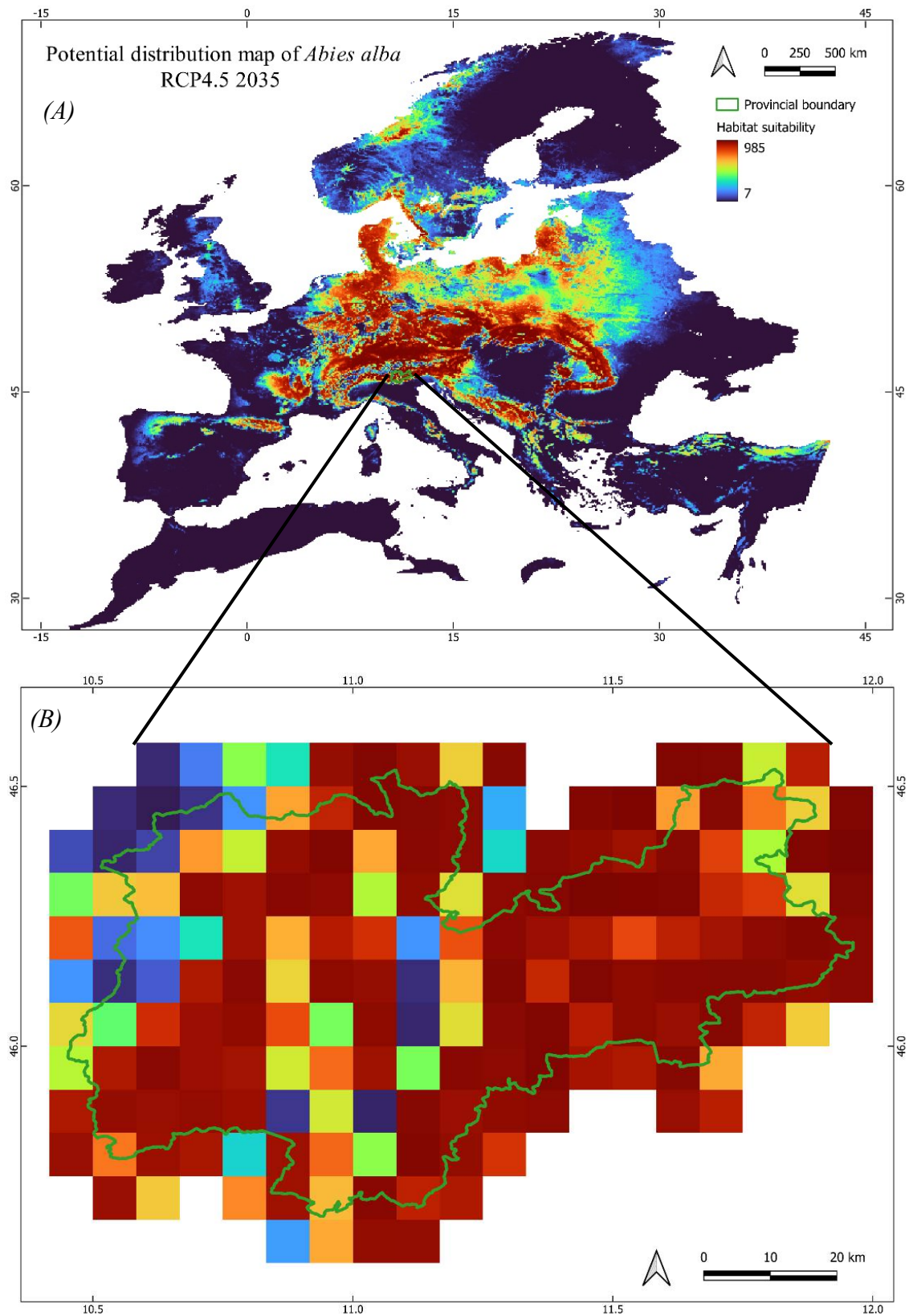


Figure 1.5. (A) Map of the potential distribution of silver fir (*Abies alba* Mill.) in Europe, under climate scenario RCP4.5 in 2035. (B) The same map clipped for the Autonomous Province of Trento. The resolution (5 arc-minutes) is not suitable for local-scale management. The full dataset, including raster files for all 67 species projected under the considered climate scenarios, is available in the study's repository.

Source: Mauri et al. (2022, supplementary material), processed with QGIS.

Among the first European studies to model both the current and future distribution of up to 1,350 European plant species is that of Thuiller et al. (2005). The predictions in this study were generated using four algorithms and four climate scenarios (Third Assessment Report IPCC) for the period 2051–2080, with a spatial resolution of 50 km.

Zimmermann et al. (2013) focused on more than 50 tree species in the Alps, projecting their distribution across four time periods (present, 1991–2020, 2021–2050, and 2051–2080). They employed six Regional Climate Models (RCMs) from the IPCC Fifth Assessment Report (AR5) and six of the most commonly used statistical models. Although the spatial resolution is not explicitly stated, the authors specified that a 100 m Digital Terrain Model (DTM) was used, which is relatively high compared to the previous studies. The models were combined using the ensemble SDM approach to produce habitat suitability maps, as illustrated in Figure 1.6.

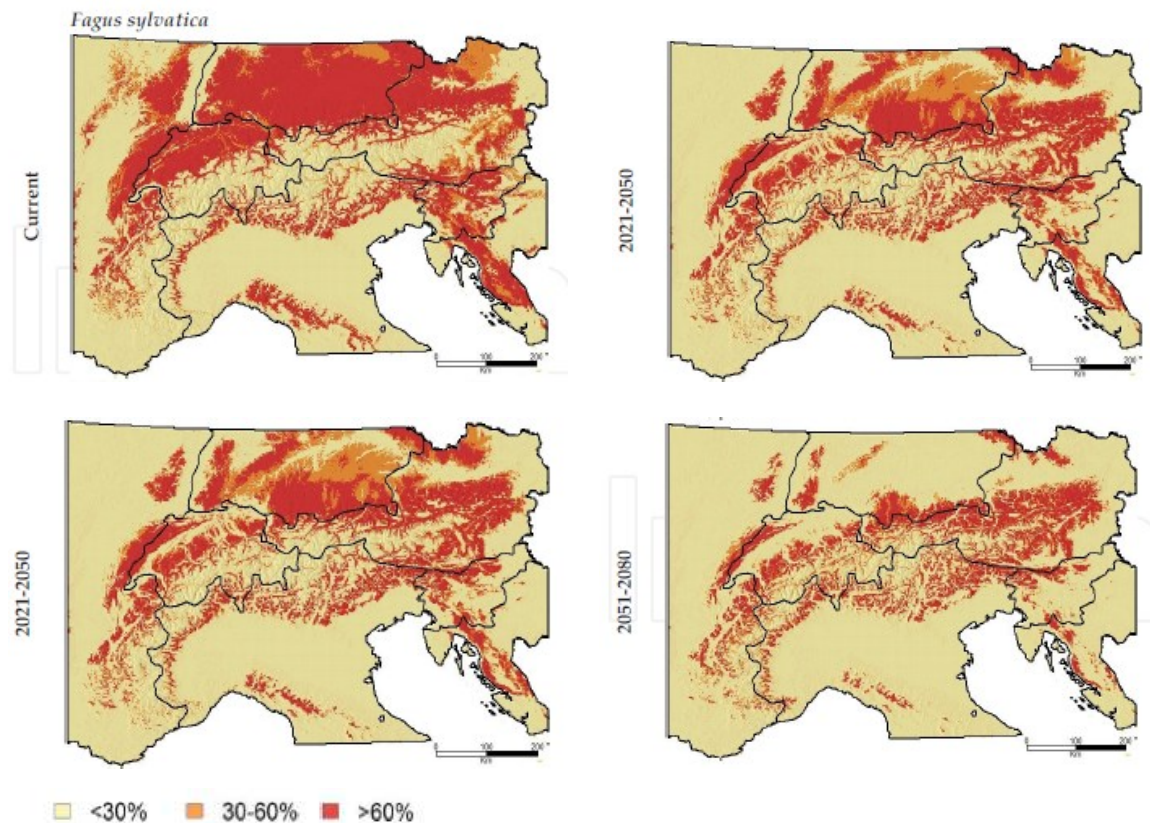


Figure 1.6: Habitat suitability maps for European beech (*Fagus sylvatica* L.) across four time periods: one current and three future projections. Red indicates a high level of confidence in habitat suitability, with more than 60% of models predicting species presence in those areas, whereas orange reflects uncertainty, with only 30–60% of models simulating species occurrence. The spatial resolution of 100 m may be particularly valuable for regional management purposes.

Source: Zimmermann et al. (2013).

An important study at the European continental scale is that of Takolander et al. (2019), which models the current and future distribution of 14 of the most representative forest species. The study considers four emission scenarios (SRES) across two future time periods (2021–2050 and 2071–2100), using a spatial resolution of 10 arc-minutes. Eight algorithms are employed within the Biomod2 R platform, alongside a Dynamic Vegetation Model (LPJ-GUESS), which simulates tree population dynamics, competition, and biogeochemical cycles.

Another European study, conducted by Buras & Menzel (2019), modelled the distribution of the 26 most abundant tree species, projecting them across three climate scenarios: a historical baseline (1961–1990) and two future projections, RCP4.5 and RCP8.5 (2061–2090; Figure 1.7). This study used a lower resolution (30 arc-minutes, approximately 55 km).

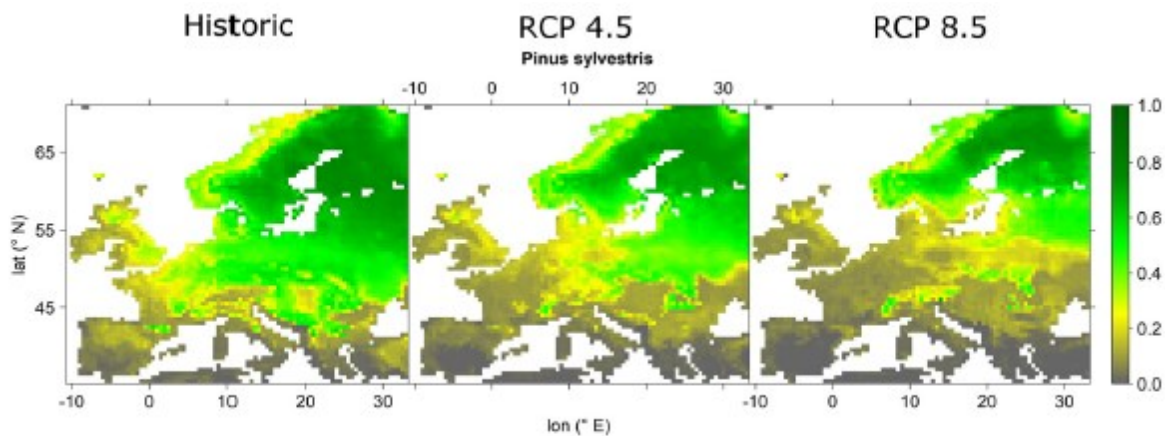


Figure 1.7. Historical (1961–1990) and future (2061–2090) projections of the distribution of Scots pine (*Pinus sylvestris* L.) in Europe under two climate scenarios (RCP4.5 and RCP8.5). The spatial resolution is very low (approximately 55 km), allowing for analysis only at the continental scale.

Source: Buras & Menzel (2019).

Thurm et al. (2018) analysed the European distribution of 12 thermophilous tree species, along with Norway spruce and European beech as reference species, to assess whether these species could effectively replace those currently most widespread and utilized, but increasingly threatened by climate change (Figure 1.8). For their statistical analyses, the authors employed Generalized Additive Models (GAM) and Linear Regression Models (LM). The study considered two climate scenarios (RCP4.5 and RCP8.5) and two time periods (present and 2061–2080), at a spatial resolution of 1 km. The analysis was based on 7 climatic variables and 13 geological variables.

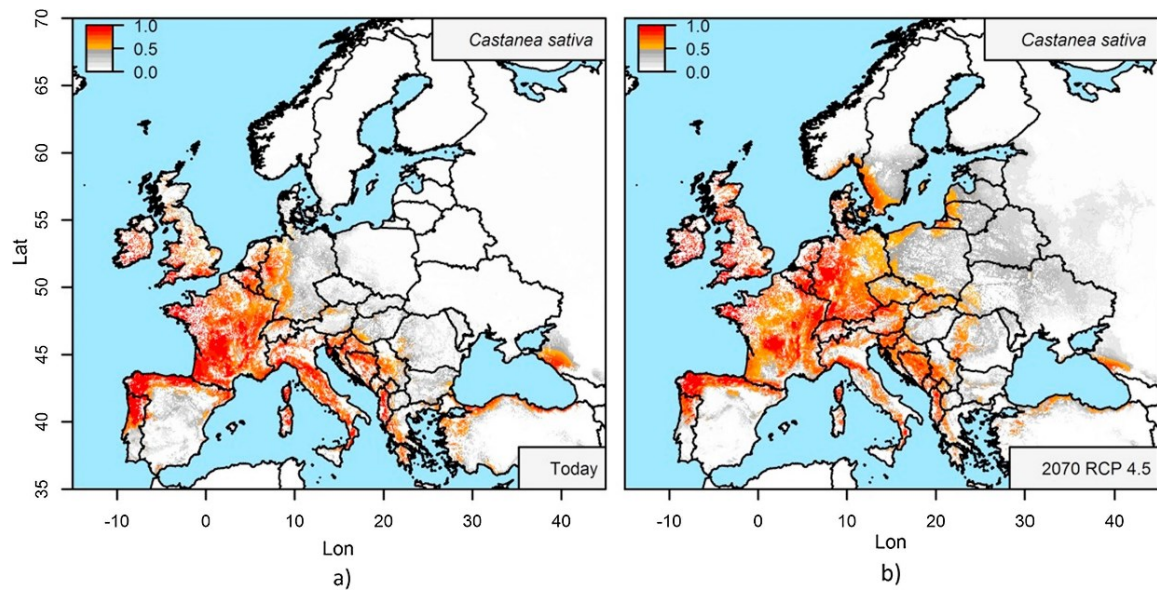


Figure 1.8: (a) Current distribution of sweet chestnut (*Castanea sativa* Mill.) in Europe. (b) Chestnut distribution in 2070 under climate scenario RCP4.5. A general northward expansion of the species' distribution can be observed (probability > 0.5, colour scale from orange to red). However, the 1 km resolution does not allow for regional-scale analysis.

Source: Thurm et al. (2018).

Other ENM studies notable in Europe are: Chakraborty, Móricz, et al. (2021), Dyderski et al. (2018, 2025), and Noce et al. (2017). At the Italian scale, the work of Noce et al. (2023) is particularly noteworthy. All these works modelled the future distribution of tree species using multiple algorithms at a spatial resolution greater than 1 km.

For a thorough and up-to-date review of the literature on ENM applied to forest species, refer to Xu et al. (2025).

In terms of estimating community parameters as species richness, explained in the following Section 1.4, fewer examples are found in the literature. Among a few others, Bedair et al. (2023) conducted a community-level study along the northwestern coastal strip of Egypt, an area known for high biodiversity and the presence of Mediterranean endemic species. The work employed the *Stacked Species Distribution Modelling* (SSDM) approach to model *species richness* using a spatial resolution of 30 arc-seconds (approximately 1 km). Predictions were generated using an ensemble modelling framework combining Random Forest and MaxEnt algorithms. The result is presented in Figure 1.9.

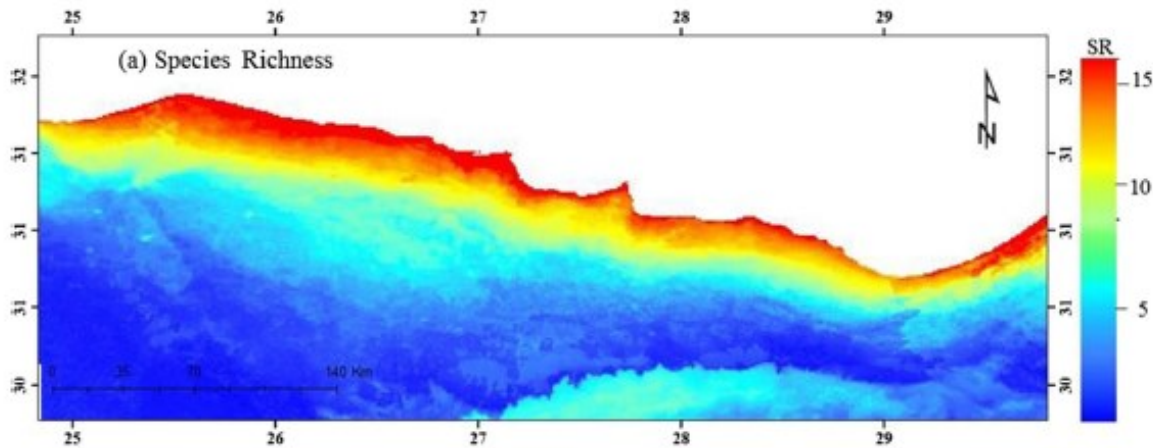


Figure 1.9. Spatial maps of species richness along the northwestern Mediterranean coast of Egypt. Estimates were obtained using the Stacked Species Distribution Modelling (SSDM) technique with a spatial resolution of 30 arc-seconds (~1 km).
Source: Bedair et al. (2023).

Other studies from various regions have applied the SSDM approach to estimate species richness, including those by Benito et al. (2013); Melin et al. (2024); Pottier et al. (2013); Thakur et al. (2022), and Chung & Lee (2024).

The following section defines and contextualizes the concept of species richness.

1.4 Species Richness

The most recently developed ENM approaches allow not only for the modelling of individual species distributions but also for an understanding of how species behave collectively at the community level, enabling predictions of species richness trends within a given area (Schmitt et al., 2017).

Species richness is a metric that reflects the floristic composition of a biological community (Dubuis et al., 2011). It is simply the number of unique species that are present in a defined area (Sanjit & Bhatt, 2005). Within the ENM field, it is often used as a proxy to estimate the potential number of species present in each spatial unit. Through the Stacked Species Distribution Modelling (SSDM) approach (Section 2.4.2), the results of individual distribution models (SDM or ESDM) can be aggregated to produce predictive maps of local species richness (Schmitt et al., 2017). These maps enable the identification of areas with high potential biodiversity, thus providing scientific support for conservation planning and forest resource management (Schmitt et al., 2017). Species richness must be clearly distinguished from the concept of *species diversity*, as the latter is a more complex and comprehensive measure: it accounts not only the number of species present, but also for

the relative abundance, or evenness, with which individuals are distributed among those species and it can be calculated using various formulas (Beery et al., 2021; Sanjit & Bhatt, 2005).

1.5 Knowledge Gap and Objectives

Currently available maps, typically characterized by low spatial resolution and developed at the continental scale, do not meet the practical and operational needs of silvicultural management, which is carried out at regional and sub-regional scales and requires data at compartmental or sub-compartmental resolution. This shortcoming is partly due to the technical complexity involved in high-resolution species distribution modelling in mountainous terrain: the use of machine learning algorithms combined with large volumes of presence data imposes significant computational demands. This study aims to bridge this gap by producing high-resolution species distribution maps based on locally collected ground data.

The specific objectives of this thesis are as follows:

- 1) Estimating the current and future potential distribution of the 23 dominant forest tree species in the Autonomous Province of Trento using Ecological Niche Models (ENMs) at a relevant management scale. Generating species richness maps using Stacked Species Distribution Models (SSDMs);
- 2) Evaluating model performance (predictive accuracy), variable importance and computational time using different modelling setups for the individual and community models.

2 MATERIALS AND METHODS

2.1 Study Area

The Autonomous Province of Trento is located in northeastern Italy, between 10° 30' and 11° 50' E longitude and 45° 40' and 46° 30' N latitude (Figure 2.1). It spans an area of 6,207 km², approximately 70% of which lies at elevations above 1,000 m a.s.l.

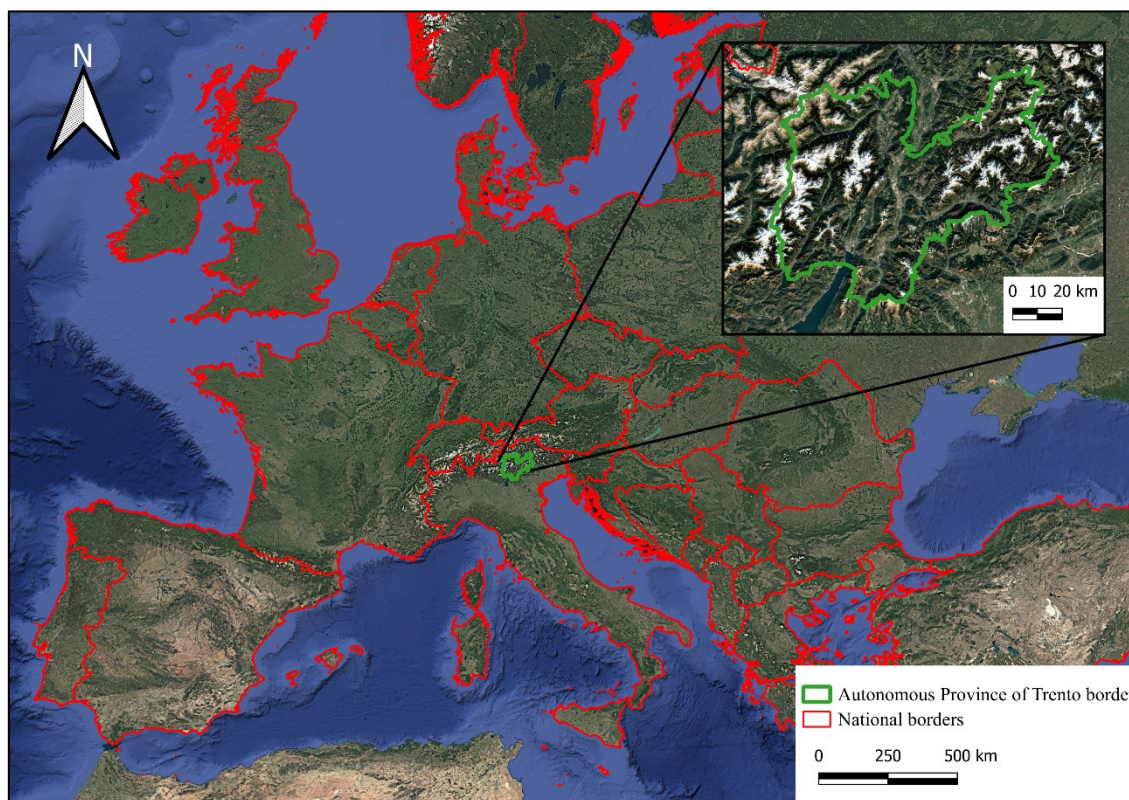


Figure 2.1. Geographical position of the Autonomous Province of Trento within Europe.

Trentino's territory is extremely heterogeneous due to its climatic and morphological characteristics. Its complex terrain, which ranges from 65 m a.s.l. to 3,764 m a.s.l., results in significant microclimatic variability. Broadly speaking, Trentino can be divided into three distinct climatic macrozones, each characterized by different types of vegetation (Odasso et al., 2018):

- Inner-Alpine/microthermal zone: Includes the highest mountain ranges, such as the Dolomites and other alpine massifs, where harsh, continental-alpine climates prevail and forest communities are dominated by boreal conifers (e.g., *Picea abies* (L.) H. Karst, *Larix decidua* Mill., *Pinus cembra* L.);

- Mid-Alpine/mesothermal zone: Encompasses mid-elevation ranges (around 1,000 m a.s.l.) and plateaus, with a cooler climate ranging from subcontinental to suboceanic. Forests in this zone are dominated by mesophilic species such as *Abies alba* Mill. and *Fagus sylvatica* L.;
- Outer-Alpine/macothermal zone: Extends along a north-south corridor that includes valleys such as the Valle dell'Adige, Val dei Laghi, and Val di Non, as well as other low-lying areas. These environments, all below 1,000 m a.s.l., exhibit sub-Mediterranean or steppe-like characteristics, with forests composed of thermophilous broadleaves (e.g., *Quercus ilex* L., *Ostrya carpinifolia* Scop., *Fraxinus ornus* L., *Quercus pubescens* Willd.).

Mean annual precipitation in valley bottoms typically exceeds 700–800 mm yr⁻¹, and in high-altitude or plains-exposed valleys it may exceed 1,500 mm yr⁻¹ (Michielin, 2003).

The region's geology is complex, featuring magmatic, sedimentary, and metamorphic rocks that produce a diverse mosaic of soils with varying pH levels.

Forests in Autonomous Province of Trento cover 3,904 km², equal to 63% of the territory (PAT, 2025a), making it an invaluable multifunctional resource.

Some species appear to be more vulnerable than others to ongoing climate change: although Norway spruce (*Picea abies*) has shown the most striking and rapid effects, especially after the Vaia storm and the bark-beetle outbreak (PAT, AA.VV., 2022), many other species are also struggling and require altitudinal migration to survive. Trentino's entire flora, not just forest species, is shifting to higher elevations in response to rising temperatures and changes in land use (Prosser et al., 2019). Adapting silviculture to these changes is crucial, and the present study may serve as a starting point for effective management planning. Bridging the gap between advanced ecological research and practical forest management requires the use of robust software tools and well-structured modelling frameworks.

The following section presents the methodological setups, including the R packages and supporting software used to conduct the analyses.

2.2 Methodological Framework: R Packages and Supporting Software

All analyses were performed using **R** statistical software (v. 4.4.2; R Core Team, 2024). The principal R packages used in this study include:

- **SSDM** (Schmitt et al., 2017): Core package for species distribution analysis, supporting both individual- and community-level modelling for present and future scenarios. Individual species models may be built with single or multiple algorithms (regression-based or machine-learning), producing: (i) continuous habitat-suitability maps, (ii) binary presence/absence maps, and (iii) uncertainty maps quantifying inter-algorithm discrepancies. It allows for choosing different modelling setups, enabling fine tuning of parameters and providing a flexible and complete tool for ecological niche modelling. Additionally, the package provides several evaluation metrics, including variable importance, algorithm accuracy, and inter-model correlations, which contribute to a complete assessment of the performance and reliability of the predictions (see Section 2.4.1).

At the community level, the package implements the Stacked Species Distribution Modelling approach, producing species richness and endemism maps. Endemism – defined as the degree to which a species is restricted to a particular geographic area – is not considered in this study because, since all focal species’ ranges exceed the study-area boundaries, this can lead to misleading and artefactual estimations of the metric. However, the species richness output offers a comprehensive view of the suitability across all species considered. Like individual models, community-level workflows are fully configurable, and SSDM computes additional evaluation metrics to facilitate model interpretability (Section 2.4.2).

SSDM also offers a graphical user interface via the R package **Shiny** (Chang et al., 2024), enabling interactive exploration of model outputs.

- **rinat** (Barve & Hart, 2022): Used to retrieve presence records from the iNaturalist database (Section 2.3.1).
- **GeoThinner** (Mestre-Tomás, 2024): Used to spatially thin georeferenced occurrence data, reducing sampling-density bias and computational time while retaining spatial information (Section 2.3.1).
- **ggplot2** (Wickham, 2017): One of the most comprehensive and widely used R packages for data visualization and statistical graphics. It offers an intuitive syntax based on the grammar of graphics, allowing users to easily create sophisticated and customizable visualizations.
- **raster** (Hijmans, 2025a): A package designed for managing and processing spatial geographic data in raster format.
- **terra** (Hijmans, 2025b): Evolution of the raster package.

- **ggspatial** (Dunnington, 2023): Used to plot the habitat suitability maps.

Throughout this work, QGIS (v. 3.32.3-Lima; QGIS.org, 2025) was employed to refine and display model outputs, while GitHub (2025) served as the platform for retrieving open-source code. Two distinct computational environments, provided by the CIRGEO department at the University of Padova, were used: a Windows computer equipped with 32 cores and 137 GB of RAM, and a High-Performance Computing (HPC) machine featuring 384 cores and 811 GB of RAM.

Assistance with coding and technical writing was supported in part by OpenAI's ChatGPT version 3.5 and Google's Gemini version 2.5 Pro.

Additional materials included the results, the computational workflow and the codes are uploaded in Zenodo EU platform (link in Supplementary Material).

2.3 Species Occurrence and Environmental Predictor Datasets

In this Ecological Niche Modelling study, local presence data for the 23 target species were collected, along with climatic data from the ECLIPS2.0 dataset (Chakraborty, Dobor, et al., 2021), topographic data derived from the Digital Terrain Model (DTM), soil-related features from the provincial Geological Map, and disturbance layers from the provincial Hazards Map.

2.3.1 Species Occurrence

The main presence dataset used was derived from the **Forest Unit (UFor)** map, which represents the basic units for describing and interpreting the landscape and consists of homogeneous forest stand segments (PAT, 2016). The UFor polygons contain information on the percentage presence of the main forest species within each area. The complete file, provided by the Trentino Forest Service (*Servizio Foreste della PAT*) in shapefile format, includes all digitized polygons based on the local Forest Management Plans of nearly all managed forest properties in Trentino. For each species, the analysis selected UFor polygons in which the species accounted for at least 10% of the cover. Subsequently, a high-resolution (10 m) map of the current distribution of species and formations was created, using Sentinel-2 imagery, digital terrain models (DTMs), forest canopy height data obtained from LiDAR scans, and climatic information. The mapping included five types of vegetation. The UFor polygons were then overlaid onto the current vegetation map. This map was subdivided into 18 raster layers at a spatial resolution of 50 meters, each

containing presence and absence data for the respective species (absence data were not used in the study). If a polygon did not match the species indicated on the map, it was discarded; if a match was found, only the portion of the polygon corresponding to the species' presence was retained. Finally, a grid with 50 m × 50 m cells was generated, and grid nodes falling within the polygons of each species were extracted. The data were saved in CSV format, including the species name and X (easting) and Y (northing) coordinates in the EPSG:25832 reference system – ETRS89 / UTM zone 32N. For species with more than 6,000 points (n = 13), **spatial thinning** was applied using the *thin_points* function from the R package GeoThinnerR. The process was carried out in three stages:

- **Preliminary reduction:** points were reduced using the “brute force” method.
- **Block-wise thinning:** the dataset was divided into chunks to optimize RAM usage and additional thinning was applied to each chunk.
- **Final aggregation:** the thinned chunks were merged into a single spatial dataset.

The parameters *chunk_size* and *thin_dist* were set manually, with various configurations tested to obtain a final number of points between 4,200 and 5,800 (Table 2.1) which were considered optimal to ensure accurate spatial predictions.

The thinning step was essential for reducing the severe computational load in training the models, especially with over 6,000 occurrence points. Notably, even with access to a high-performance computing (HPC) infrastructure, the ensemble species distribution modelling phase (Section 2.4.1) remained highly time-consuming. This was largely due to the combination of fine spatial resolution, the relatively large extent of the study area, and the high number of target species, all of which imposed substantial computational demands.

Another database used in this study was provided by the **Edmund Mach Foundation (FEM)**, containing a set of highly accurate geolocated presence points (precision < 1 m) collected between 2007 and 2021. This dataset was used to supplement the Forest Unit data for seven minor species with fewer than 1000 points in the UFor (*Betula pendula* Roth, *Prunus avium* (L.) L., *Acer pseudoplatanus* L., *Fraxinus excelsior* L., *Populus tremula* L., *Sorbus aucuparia* L., *Tilia cordata* Mill.), which were selected, with several others, also due to their suitability for reforestation, as specified by the DGP No. 1343 of July 22, 2022 (Table 2.1).

iNaturalist (iNat) database: iNaturalist is an online citizen science platform that collects observations of living species from around the world. Its data are widely used in

scientific research, including ENM studies (deboas, 2024), with more than 6,100 publications to date referencing this database (GBIF, 2025). The presence points for the seven minor species were downloaded using the R package rinat. The retrieved data, which included species names and observation coordinates, were clipped to the boundaries of the provincial territory, checked for taxonomic errors and duplicate records, and then saved in CSV format. These records were also used to supplement those derived from the Forest Unit dataset, which provides limited coverage for minor species.

Table 2.1 Number of original presence points for each dataset (Edmund Mach Foundation, FEM; iNaturalist, iNat; and Forest Units, UFor), as well as the final number of points used after thinning for species with more than 6,000 points. The parameters *Thin_distance* and *Chunk_size* were adjusted during the thinning process using the R package GeoThinner in order to obtain a thinned dataset ranging between 4,200 and 5,800 points. In **bold** the species authorized for the reforestation by the DGP No. 1343 of July 22, 2022.

Species	Presence dataset			Number of points used (post-thinning)	Thin_distance (km)	Chunk_size
	FEM	iNat	UFor			
<i>Picea abies</i> (L.) H.Karst.			225,830	5,832	15	20,000
<i>Larix decidua</i> Mill.			142,551	5,068	18	20,000
<i>Fagus sylvatica</i> L.			115,699	4,536	15	18,000
<i>Ostrya carpinifolia</i> Scop.			75,105	4,531	11	12,000
<i>Fraxinus ornus</i> L.			70,510	4,536	2	10,000
<i>Abies alba</i> Mill.			63,067	4,526	2	10,000
<i>Pinus sylvestris</i> L.			55,564	4,450	7	9,000
<i>Quercus pubescens</i> Willd.			44,610	4,523	7	6,000
<i>Aria edulis</i> (Willd.) M.Roem.			27,488	4,531	5	4,000
<i>Pinus cembra</i> L.			19,953	4,494	4	3,000
<i>Pinus mugo</i> Turra			16,745	4,466	4	2,500
<i>Alnus alnobetula</i> (Ehrh.) K.Koch			14,755	4,814	4	2,000
<i>Pinus nigra</i> J.F.Arnold			10,209	4,206	4	1,500
<i>Castanea sativa</i> Mill			4,095	4,095		
<i>Quercus petraea</i> (Matt.) Liebl.			3,402	3,402		
<i>Quercus ilex</i> L.			1,488	1,488		
<i>Betula pendula</i> Roth	711	63	281	1,055		
<i>Prunus avium</i> (L.) L.	311	42	275	628		
<i>Acer pseudoplatanus</i> L.	454	131	206	791		
<i>Fraxinus excelsior</i> L.	494	51	175	720		
<i>Populus tremula</i> L.	686	45	158	889		
<i>Sorbus aucuparia</i> L.	367	157	149	673		
<i>Tilia cordata</i> Mill.	175	33	58	266		

For each of the seven less-represented species, the three presence datasets were aggregated and initially organized by species. The CSV files were then standardized to retain only the columns containing the scientific species name and the X and Y coordinates of the presence points.

2.3.2 Climatic Variables

This study utilised climatic data from the European CLimate Index ProjectionS (ECLIPS) dataset (Chakraborty, Dobor, et al., 2021), specifically from its high-resolution ECLIPS 2.0 version. This dataset includes spatially downscaled climate projections derived from the EURO-CORDEX ensemble, providing raster maps at a resolution of 30 arc-seconds (approximately 1×1 km), distributed in GeoTIFF format.

From the 42 available climatic indices in ECLIPS 2.0, 11 variables were selected for analysis, based on their ecological relevance in modelling forest species distributions. The selected indices are detailed in Table 2.2, which includes their acronyms, units of measurement, and calculation methods. These variables capture key climatic dimensions such as temperature, precipitation, seasonality, and moisture availability.

Table 2.2. Selected Climatic Indices for the Ecological niche modelling. The table shows the eleven climatic indices utilized as predictive variables for modelling both current and future forest species distributions. For each index, its unit of measurement and the methodology for its calculation are provided. Source: Chakraborty, Dobor, et al. (2021, supplementary material), modified.

Acronym	Variable name	Unit	Calculation
MWMT	Mean warmest month temperature	°C	$MWMT = (T_{mon.mean})$
MCMT	Mean coldest month temperature	°C	$MCMT = (T_{mon.mean})$
TD	Continentality	°C	$MWMT - MCMT$
AHM	Annual heat: moisture index	°C/mm	$AHM = \frac{MAT + 10}{MAP/1000}$
SHM	Summer heat: moisture index	°C/mm	$SHM = \frac{MWMT}{MPS/1000}$
DDbelow0	Degree-days below 0°C	°C	$DDbelow0 = \sum_{day} \{T, T < 0^{\circ}C \ 0^{\circ}C, T > 0^{\circ}C \}$
DDabove18	Degree-days above 18°C	°C	$DDabove18 = \sum_{day} \{T-18^{\circ}C, T > 18^{\circ}C \ 0^{\circ}C, T < 18^{\circ}C \}$
NFFD	Number of frost-free days	-	$NFFD = \sum_{day} \{1, T_{min} > 0^{\circ}C \ 0, T_{min} < 0^{\circ}C \}$
EMT	Extreme minimum temperature	°C	
MAP	Annual total precipitation	mm	Summary of daily precipitation over a year
Tmax_an	Annual mean of maximum temperature	°C	Average of daily maximum temperature over a year

Climatic data were extracted for the baseline period 1991–2010 – referred throughout the work as *present* or *current* climate – as well as for three future time periods: 2041–2060, 2061–2080, and 2081–2100.

Future climate projections were obtained under two **Representative Concentration Pathways (RCPs)**: RCP4.5 and RCP8.5, which represent alternative greenhouse gas concentration trajectories developed by the Intergovernmental Panel on Climate Change (IPCC) in its Fifth Assessment Report (AR5) (IPCC, 2014). The nomenclature of these pathways is directly linked to their projected **radiative forcing**, defined as the change in the net energy balance of the Earth-atmosphere system caused by an external factor, expressed in Watts per square meter (W/m²) (IPCC, 2014). Specifically, a positive radiative forcing indicates that more energy, primarily from solar radiation, is being absorbed by the Earth system than is being radiated back to space, leading to a warming effect (Gregor, 2025).

Under this framework:

- RCP4.5 assumes a moderate emissions and mitigations scenario, stabilising the radiative forcing at 4.5 W/m² by 2100;
- RCP8.5 represents a high-emission scenario with no mitigation (business-as-usual), resulting in a radiative forcing of 8.5 W/m² by the end of the century.

Each scenario is associated with projected increases in global mean surface temperature, as summarised in Table 2.3 and illustrated in Figure 2.2. These projections provide a basis for evaluating potential impacts on forest ecosystems under different emission pathways.

Table 2.3. Projected Global Mean Surface Temperature Increases Relative to 1986–2005 Baseline. The table illustrates the anticipated warming trends under various Representative Concentration Pathways (RCPs: RCP2.6, RCP4.5, RCP6.0, and RCP8.5) for two distinct future periods: 2046–2065 and 2081–2100. The 'Likely range' quantifies the uncertainty as the 5th to 95th percentile interval derived from climate model simulations.

Source: IPCC (2014), modified.

	2046–2065		2081–2100	
Scenario	Mean (°C)	Likely range (°C)	Mean (°C)	Likely range (°C)
RCP2.6	1.0	0.4 - 1.6	1.0	0.3 - 1.7
RCP4.5	1.4	0.9 - 2.0	1.8	1.1 - 2.6
RCP6.0	1.3	0.8 - 1.8	2.2	1.4 - 3.1
RCP8.5	2.0	1.4 - 2.6	3.7	2.6 - 4.8

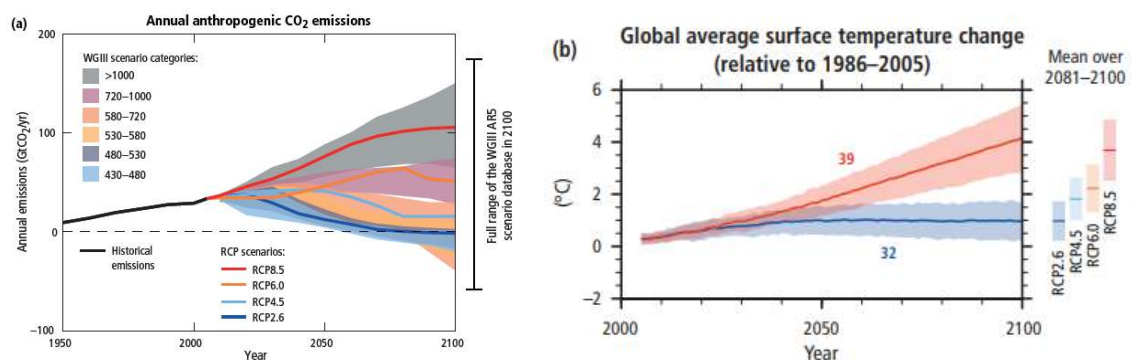


Figure 2.2. Annual anthropogenic CO₂ emissions and global average surface temperature change under IPCC RCP scenarios, compared with historical data. Panel (a) shows historical and projected CO₂ emissions. Panel (b) shows projected temperature changes (2081-2100) relative to 1986-2005 for RCP scenarios. Shaded areas: likely range.
Source: IPCC (2014).

To account for uncertainties in climate modelling, projections for each RCP and time period were derived from five Regional Climate Models (RCMs), whose specifications are listed in Table 2.4, along with their corresponding driving Global Climate Models (GCMs). For each combination of RCP and time period, the relevant raster maps from the five RCMs were averaged – using the raster package in R – to produce a consensus climate projection.

Table 2.4. Regional Climate Models (RCMs) and their driving Global Climate Models (GCMs) employed in the study. These models contributed to the averaged climate rasters utilized for modelling current and future species distributions.

Source: Chakraborty, Dobor, et al. (2021), modified.

Institute	RCM	Driving GCM
Climate Limited-Area Modelling Community (CLM-Community)	CLMcom-CLM4-8-17	CNRM-CERFACS-CNRM-CM5
Climate Limited-Area Modelling Community (CLM-Community)	CLMcom-CLM4-8-17	MPI-M-MPI-ESM-LR
Danish Meteorological Institute (DMI)	DMI-HIRHAM5	ICHEC-EC-EARTH
Royal Netherlands Meteorological Institute (KNMI)	KNMI-RACMO22E	MOHC-HadGEM2-ES
Helmholtz-Zentrum Geesthacht, Climate Service Center, Max Planck Institute for Meteorology (MPI-CSC)	MPI-CSC-REMO2009	MPI-M-MPI-ESM-LR

All raster layers were subsequently resampled to a spatial resolution of 50 m using the nearest neighbor algorithm via the R package terra. The coordinate reference system was also standardised by converting the spatial reference from EPSG:22232 to EPSG:25832, ensuring consistency with other geospatial datasets used in the study.

2.3.3 Topographic Variables

Topographic factors, alongside climatic variables, play a crucial role in determining plant-species distributions. All indices were derived from a 10 m Digital Terrain Model (DTM) obtained via the WebGIS portal of the Autonomous Province of Trento (PAT, 2025b) and resampled to 50 m resolution using the nearest neighbor algorithm in QGIS. The selected variables are:

- **Slope:** calculated in QGIS (degrees), it indicates terrain steepness and its influence on soil drainage and erosion.
- **Terrain Ruggedness Index (TRI):** computed using QGIS, it quantifies the elevation difference between adjacent cells.
- **Heatload Index (HLI):** obtained using slope, aspect and latitude, it quantifies the potential thermal energy received at a site in a year (Zelený & Lin, 2021). This index substitutes raw aspect, – which presents critical issues, for example, 1° and 360°, although numerically opposite, both correspond to north-facing – by providing a continuous, ecologically meaningful measure of thermal exposure.
- **Topographic Wetness Index (TWI):** it estimates soil-moisture accumulation based on the topography.

The last two variables were extracted using the R package *spatialEco* (Evans & Murphy, 2023).

Elevation was excluded as it does not directly drive species' occurrences but is rather correlated with other variables, such as mean annual temperature. While future projection models might partially base habitat suitability on elevation, it is crucial to consider that past climatic conditions associated with a specific altitude may no longer persist, potentially introducing bias and undermining the model's predictive accuracy.

2.3.4 Soil Variables

Soil-related features, important for understanding plant distribution, were derived from the provincial Geological Map (PAT, 2024). Specifically, soil pH was categorized into three binary raster layers. In these layers, a value of 1 signifies the presence of a specific soil property, while a value of 0 indicates its absence:

- **Acidic Soil:** areas with predominant acidic soil conditions.
- **Basic Soil:** areas with predominant basic soil conditions.

- **Mixed Soil:** areas where both acidic and basic soil types are present, or where conditions are neutral ($\text{pH} \approx 7$).

These raster layers were resampled to a 50 m resolution to align with other environmental predictors in the study.

2.3.5 Disturbance Variables

Disturbance variables were incorporated to account for geomorphological processes that could influence the species distributions. Two specific disturbance types were included as raster layers, sourced from the WebGIS portal (PAT, 2025c):

- **Rockfall:** A layer indicating areas prone to rockfall events;
- **Landslides:** A layer indicating areas affected by landslide phenomena.

These layers were initially rasterized and then binarized to represent hazard levels. A value of 0 was assigned to areas classified as "no hazards," "negligible," and "low" hazard, while a value of 1 corresponded to areas with "medium" and "high" hazard levels.

2.4 Model Framework

The modelling framework adopted in this study relies on the integration of single-species distribution models (ESDMs) into community-level predictions using the R package SSDM. The process includes the preparation of environmental predictors and species occurrence data (Section 2.3), the construction of ensemble models for each species, and the aggregation of these into stacked models to generate spatial predictions of species richness. A schematic overview of the entire workflow is presented in Figure 2.3. The diagram outlines key phases including data preparation, modelling, spatial outputs, and the elaboration of case-study examples.

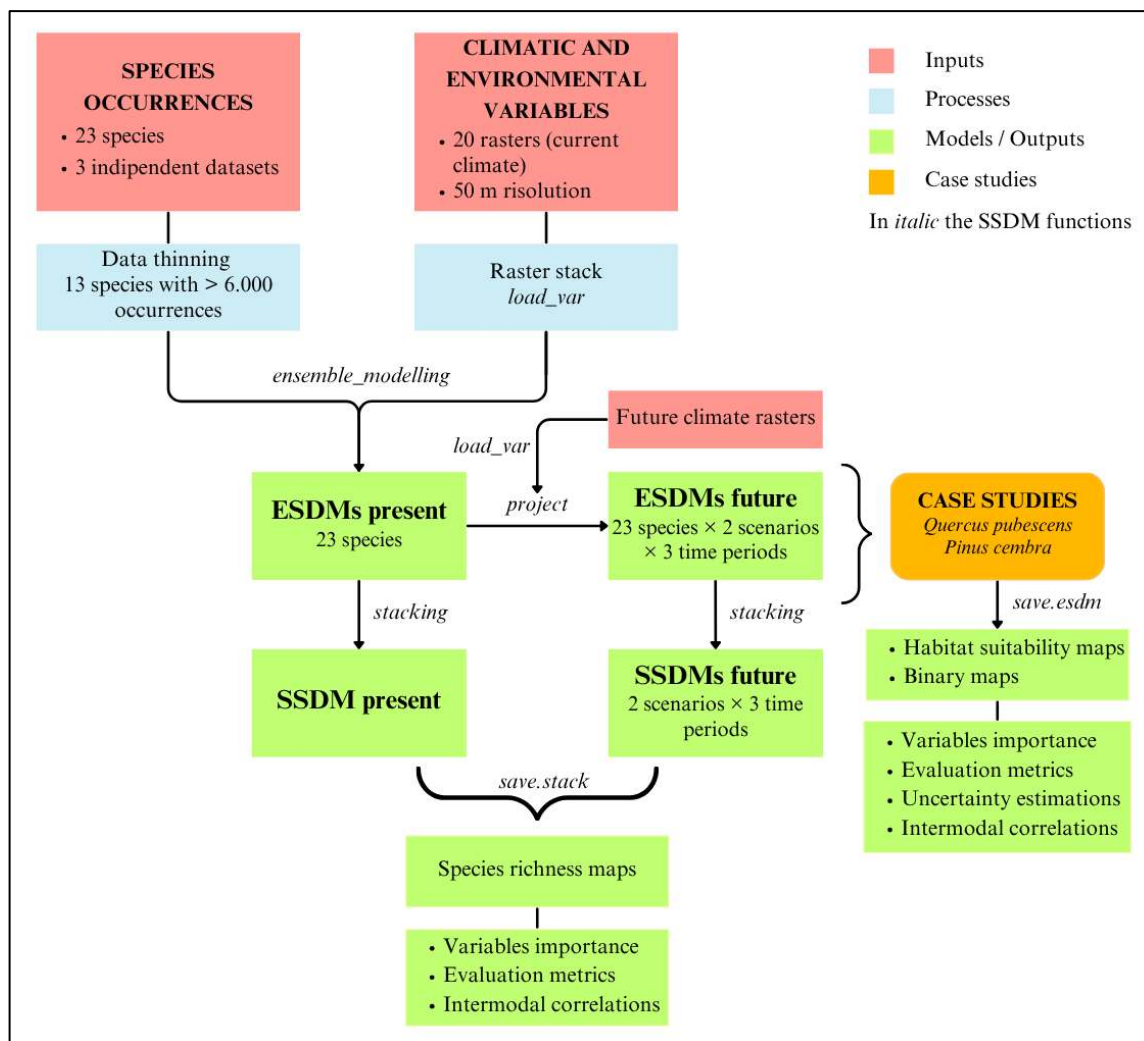


Figure 2.3. Workflow diagram of the ecological niche modelling process followed in the present work. The flowchart illustrates the main parts of the work's process, starting from the occurrence and environmental data, to the final outputs. In italic are written the main functions from the R package SSDM that were used to build the models. The 23 species are illustrated in Table 2.1. The 2 future scenarios are: intermediate (RCP4.5) and business-as-usual (RCP8.5). The time periods are: 2041-2060, 2061-2080, and 2081-2100.

The initial phase of the workflow consisted of two main steps. First, all raster layers of environmental and climatic variables – named according to their acronyms (see Section 2.3.3 and Table 2.2) – were stacked using the *load_var* function from the R package SSDM. In ecological niche modelling studies, it is crucial that all raster files share the same coordinate reference system, spatial extent and resolution (Guisan & Thuiller, 2005; Guisan & Zimmermann, 2000; Hijmans & Elith, 2025). The SSDM package automatically manages discrepancies in spatial extent and resolution between input layers, ensuring compatibility across all variables (Schmitt et al., 2017).

The second step of this phase involved a thinning process applied to species occurrence data, primarily to reduce computational effort. This step is described in detail in Section 2.3.1.

2.4.1 Ensemble Species Distribution Models

Ensemble Species Distribution Modelling (ESDM) combines multiple statistical algorithms, both machine learning and regression-based, to generate robust predictions of species distributions. By integrating outputs from different modelling approaches, ESDMs mitigate algorithm-specific biases and enhance ecological reliability (Araújo & New, 2007; Benito et al., 2013). In this study current habitat suitability of the 23 target forest species was modelled using the *ensemble_modelling* function from the package SSDM. This function requires two primary inputs: (i) a raster stack of environmental predictors and (ii) a CSV file containing the X and Y coordinates of species presence points (Table 2.1). Absence data were not required, as the model function automatically generates pseudo-absences beyond the known presence locations (Schmitt et al., 2017).

Eight algorithms were selected for ensemble modelling:

- Random Forest (RF): A machine-learning method that constructs numerous decision trees and outputs the mode of predictions. It captures complex, nonlinear interactions, handles large datasets, and is robust to overfitting and noisy data (Friedman, 2001; Hastie et al., 2009);
- Generalized Linear Model (GLM): Extends linear regression by allowing non-normal error distributions. In ENM, it models species presence-absence relationships and provides interpretable coefficients for predictor influence (Elith & Leathwick, 2009; Friedman, 2001; Guisan & Zimmermann, 2000);
- Generalized Additive Model (GAM): Enhances GLMs by incorporating smooth, non-parametric functions to capture nonlinear species-environment relationships, improving flexibility in ecological modelling (Hastie et al., 2009);
- Classification Tree Analysis (CTA): A decision-tree algorithm that forecasts presence or absence using environmental thresholds, offering transparent rules for interpreting species responses (De'Ath & Fabricius, 2000; Hastie et al., 2009);

- Generalized Boosted Regression Model (GBM): Combines multiple weak learners to minimize prediction error, effectively capturing complex nonlinear interactions and ranking variable contributions (Friedman, 2001; Hastie et al., 2009);
- Multivariate Adaptive Regression Splines (MARS): Constructs piecewise linear regressions, adapting to species occurrence data and variable structures, and effectively modelling shifting environmental responses (De'Ath & Fabricius, 2000; Friedman, 2001);
- Artificial Neural Network (ANN): Uses layered, interconnected nodes to process inputs through weighted pathways, capturing complex, nonlinear species-environment relationships (Hastie et al., 2009);
- Support Vector Machine (SVM): Finds the optimal boundary (hyperplane) that separates classes in multidimensional space, proving effective in distinguishing data even when relationships are non-linear (Hastie et al., 2009).

These algorithms represent a range of modelling strategies, each with specific strengths in handling non-linearity, variable interactions, and complex species-environment data structures (De'Ath & Fabricius, 2000; Hastie et al., 2009).

Other key parameters within the *ensemble_modelling* function were set as follows: presence coordinate columns were assigned to the Xcol and Ycol arguments; the number of repetitions per algorithm ("rep") was set to 5; and the cross-validation method ("cv") was configured as "holdout", with 75% of the data used for training and 25% for testing, with 5 repetitions to reduce the influence of random splits. Cross-validation plays a crucial role in evaluating model generalizability, as it provides an estimate of predictive accuracy on unseen data and helps identify potential overfitting by testing model performance on independent subsets. The SSDM package provides other two methods to split the initial dataset into training and evaluation sets.

Different core counts were tested (up to 120), in order to optimize the computational time and efficiently handle the parallelization process. The SSDM package offers two parallelization mode within the "parmode" parameter: "algorithms" and "replicates". Both were tested in order to find the most efficient one. Under the given conditions, the "replicates" option was the most suitable and the less time-consuming one. Adding more cores than the number of replicates (5 in this case), did not remarkably reduce the computation time. An important aspect of these computations is the requirement of high

amount of temporary memory (RAM), in the order tens to hundreds of Gigabytes, in the case of projecting the SSDM into the future. In this case, a High Performance Computing (HPC) environment is necessary.

To convert the continuous habitat suitability maps into binary presence/absence outputs, a threshold was calculated using the **sensitivity-specificity equality (SES)**. This metric, which is the default setting in the *ensemble_modelling* function (Schmitt et al., 2017), minimises the difference between the sensitivity and the specificity (Liu et al., 2005). Consequently, the threshold is unique for each model, ensuring an optimal, species-specific calibration between predicted presence and absence. While the SES is the default, the function offers the flexibility to choose alternative thresholding methodologies, providing a versatile tool for species distribution modelling.

All other parameters were kept at their default values as specified by Schmitt et al. (2017).

An automated loop was implemented in R to iterate the modelling process across all the 23 species. For each species, the analysis produced three main outputs in GeoTIFF format: a habitat suitability map, a binary presence/absence map, and an uncertainty estimation map showing the between-algorithm variance. In addition, a *rda* (R Data format) file was generated to store all relevant model outputs, facilitating organized access and further analysis of the species/scenario within the R environment. The present-day ESDMs also yielded fundamental outputs essential for assessing model reliability: evaluation metrics (Section 2.4.3), variable importance scores, and algorithm correlation matrices. These metrics provide insights into model performance, the relative contribution of predictor variables, and the degree of agreement between algorithms.

Future projections were generated using the *project* function, which recalculates the current ESDMs under updated climatic conditions corresponding to two RCP scenarios and three temporal horizons (Section 2.3.2). The resulting outputs include projected habitat suitability maps, binary presence/absence maps, and updated algorithm correlation matrices. It is important to note that only the algorithm correlation values are recalculated in future projections, as they depend on model consensus under new climatic conditions; all other metrics – evaluation scores, variable importance values, and thresholding parameters – remain consistent with those from the present-day models. A total of 138 future ESDMs (23 species $\times$ 2 scenarios $\times$ 3 time periods) were produced, in addition to the 23 present ESDMs, resulting in a complete set of 161 models. All model outputs and associated data are fully accessible in the Zenodo repository (link provided in

Supplementary Material). Two representative species were selected for detailed discussion in the Case Studies sections (2.4.4 and 3.3), serving as examples for how the modelling results can be analysed and applied.

Two faceted plots were generated with the ggplot2 package to illustrate the ecological implications of predictions for all 23 species in the two scenarios for the three time horizons:

- Suitability Change by Class

A stacked histogram, faceted by species, illustrating the changes in surface area across three suitability classes: 0.41–0.60 (low), 0.61–0.80 (medium), and 0.81–1.0 (high). Surface areas below 0.40 were considered non-suitable and subsequently excluded from further analysis. As no standardized threshold values are established in the literature for defining suitability classes, these categories were defined arbitrarily and considered appropriate for capturing meaningful variation relevant to this study.

- Elevation Distribution of Suitable Areas

A violin plot, faceted by species, illustrating changes in elevation for pixels with medium and high suitability.

Additionally, two Figures representing the absolute and relative gains and losses in suitable surface area of the future scenarios compared to the present one were created (Figure 3.2 and Figure 3.3).

All distribution maps were first masked using **CORINE Land Cover** data (raster format from Copernicus Land Monitoring Service, 2025), which were resampled from 100 m to 50 m resolution using the terra package with the default nearest neighbor algorithm, to match the prediction map resolution. The mask excluded land-cover classes unlikely to be colonized by vegetation by the end of the century, specifically:

- Class 1: Artificial surfaces;
- Class 3.3: Open spaces with little or no vegetation (excluding subclass 3.3.3, sparsely vegetated areas);
- Class 5: Water bodies.

The raster file was binarized, with the “1” values being the “non masked” land cover classes. The total masked surface accounts for 724 km², corresponding to 11.7% of the provincial area. Masking in this way ensures that subsequent area and elevation computations focused only on potentially colonizable areas.

2.4.2 Stacked Species Distribution Models

The integration of individual ESDMs into a single community-level model was performed using the *stacking* function from the SSDM package. This process enables the simultaneous analysis of all 23 species, allowing the creation of community-level indicators such as the species richness.

Species richness maps were computed by summing the binary presence/absence maps of the 23 species produced through thresholding (bSSDM method), as proposed by D'Amen et al. (2015). In this approach, richness is estimated by counting how many species are predicted as present in each cell, providing an intuitive and easily interpretable output. In addition to this method, the SSDM package offers five alternative approaches for estimating species richness, here presented for future further improvements:

- Bernoulli resampling: richness is estimated by summing multiple binary maps generated through repeated draws from a Bernoulli distribution based on each species' predicted occurrence probability;
- Probabilistic stacking (pSSDM): richness is calculated by summing raw habitat suitability values (i.e., probabilities) across all species, avoiding thresholding but potentially smoothing richness gradients;
- PRR.pSSDM: the SESAM framework's Probability Ranking Rule is applied, selecting species in decreasing order of predicted probability until reaching the richness estimated via pSSDM;
- PRR.MEM: a constrained stacking approach similar to PRR.pSSDM, but using richness predictions derived from a macroecological model (MEM) as the limiting value;
- Maximum-likelihood adjustment: a statistical correction that adjusts species-level probabilities to match site-level richness, reducing biases caused by thresholding and model assumptions.

Projections of species richness under the two climate scenarios in three time periods were produced also by stacking the relative 23 future ENMs for each scenario and time period.

For the stacks, no uncertainty maps were produced since there were some issues with the temporary files saved by the previous *project* function.

All results were saved using the *save.stack* function. In addition to the spatial outputs, stacked-level evaluation metrics were computed, aggregating those from the individual

ESDMs and providing additional insights into the reliability of community-level predictions.

Two primary visualizations were generated from the species richness maps, previously masked with the selected CORINE Land Cover classes (Section 2.4.1), using the ggplot2 package:

1. **Mean Species Richness change over time:** To show the overall change in species richness, the mean value of all non-masked pixels was calculated for each raster using the terra package. The results were plotted as a line graph illustrating the trend of mean species richness over the different time periods and climate scenarios.
2. **Surface Area Distribution:** To analyse how the landscape composition changes, a frequency analysis was performed on each masked raster using the terra package. This analysis counted the number of pixels corresponding to each specific richness value. These pixel counts were then converted into surface area (km²), quantifying how the total area for each richness level changes across the different time periods and climate scenarios.

2.4.3 Evaluation Metrics and Uncertainty Estimations

The SSDM package provides a comprehensive suite of metrics to evaluate the performance and reliability of species distribution models at both the individual and community levels.

Metrics applied to both ESDMs and SSDMs:

- **Variable importance:** this metrics allows to have and insight of which predictors have more influence on the distribution of the single species (in the case of the ESDMs) as well as over all the 23 species (after the SSDM). Higher is the percentage, higher is the influence that the variable has on the prediction of the species spatial distribution. The metric is based on the performance drop when each variable is omitted in turn from the full model with the complete pool of variables;
- **Algorithm correlation matrix:** it tests the agreement between pairs of statistical methods, giving the Pearson's coefficient (Schmitt et al., 2017);
- **AUC (Area Under the receiver operating characteristic Curve):** Threshold-independent measure of model discrimination capacity, based on true positive and

true negative range (Liu et al., 2009). It ranges from 0 to 1. Values approaching to 1 indicate the model has excellent discriminatory capacity, conversely, values near 0.5 suggest that the model's predictions perform no better than a random classification (Thakur et al., 2022);

- **Sensitivity** (true positive rate) and **Specificity** (true negative rate): Indicate the proportion of actual presences and absences correctly predicted (Liu et al., 2009);
- **Proportion of Correct Predictions**: The mean between the sensitivity and specificity. It ranges from 0 to 1, with higher values indicating better model performance, with fewer false negatives and false positives;
- **Omission Rate**: Proportion of true presence points incorrectly predicted as absent. Equivalent to 1 minus the proportion of correct predictions;
- **Cohen's Kappa**: Measures agreement between predicted and observed data beyond chance (Guisan & Zimmermann, 2000). It ranges from -1 to 1. A value of -1 means the model performs worse than random guessing, 0 means the model is no better than random chance, and 1 means the model has a strong agreement with the observed data;
- **Calibration or overall accuracy**: Reflects the correspondence between predicted probabilities and observed frequencies of presence/absence. Values near to 1 indicates great calibration (Liu et al., 2009; Raveendra et al., 2024).

For the SSDMs, an additional community-level metric were computed:

- **Mean Species Richness Error**: Difference between predicted and observed species richness (Schmitt et al., 2017). Observed richness was computed as the count of unique species per 50-m cell from the cross-validation method (75/25 hold-out, 5 replicates); predicted richness is the sum of species presences in the binary stack (bSSDM).

2.4.4 Case studies

To illustrate the outputs and capabilities of the modelling framework without redundantly presenting results for all 23 species, two representative species were selected as case studies: *Pinus cembra* (Swiss stone pine) and *Quercus pubescens* (downy oak). These two species were chosen for their contrasting responses to climate change – *Pinus cembra* being projected to decline dramatically under future climate scenarios, and

Quercus pubescens expected to show an expansion under moderate conditions (Section 3.3). This targeted approach provides a clear and concise example of the typical outputs generated by the SSDM package, including continuous habitat suitability maps, binary presence–absence projections, uncertainty estimates, variable importance plots, and algorithm performance metrics (e.g., AUC, Kappa).

Their selection serves as a representative illustration of the broader ensemble modelling process. All the results, included the other species, are available in the Zenodo digital repository (link in Supplementary Material).

3 RESULTS

3.1 Projected Ecological Niches of 23 Forest Tree Species in Trentino

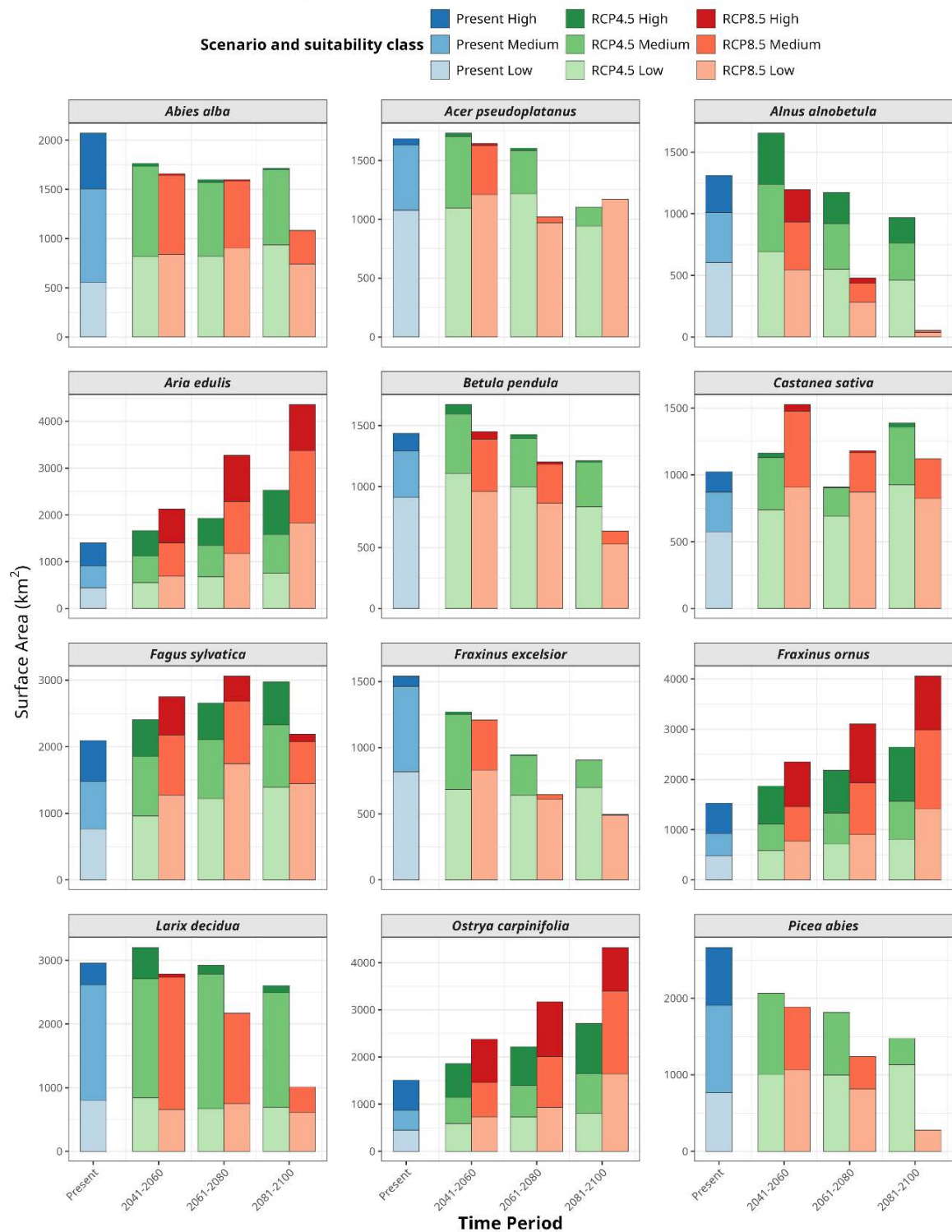
This section presents the primary findings from the ecological niche modelling of 23 forest tree species within the province of Trento. The analysis is structured into three main sections. First, it examines the projected changes in suitable habitat area and altitudinal shifts for each species, comparing the current scenario with future projections under two Representative Concentration Pathways (RCP 4.5 and RCP 8.5) across three distinct time periods (2041–2060, 2061–2080, and 2081–2100). Second, the section analyses species richness at the community level as an aggregate indicator of forest biodiversity, evaluating its evolution in response to climate change. Finally, two detailed case studies are presented for downy oak (*Quercus pubescens*) and Swiss stone pine (*Pinus cembra*), selected for their contrasting projected responses to future climatic conditions. All the results are uploaded in Zenodo platform (link in Supplementary Material).

The projected impacts of climate change on the suitable habitat area for the 23 studied forest tree species are presented in Figure 3.1. The responses vary significantly among species, allowing for their classification into three categories based on their projected trends:

- "Gainers": This group includes predominantly thermophilous species that are expected to expand their suitable habitat. Species such as common whitebeam (*Aria edulis*), manna ash (*Fraxinus ornus*), European hop-hornbeam (*Ostrya carpinifolia*), black pine (*Pinus nigra*), holm oak (*Quercus ilex*), and downy oak (*Quercus pubescens*) show a consistent positive trend across future scenarios and time periods. Notably, the Mediterranean species holm oak is projected to increase in habitat suitability by an order of magnitude. The mountain pine (*Pinus mugo*) and the European beech (*Fagus sylvatica*) will also have a positive trend throughout the decades. The sweet chestnut (*Castanea sativa*), the wild cherry (*Prunus avium*), the sessile oak (*Quercus petraea*) and the small-leaved lime (*Tilia cordata*) can also fit into this category, despite their high suitability areas are expected to decline.

- "Losers": This category comprises species facing a stable reduction in suitable habitat area. The decline is especially dramatic for the two high-altitude, cold-adapted species Norway spruce (*Picea abies*) and Swiss stone pine (*Pinus cembra*). For this last species in particular the projections indicate a near-total disappearance of its habitat under almost all future scenarios, highlighting its extreme vulnerability. A strong decline is expected also for the common ash (*Fraxinus excelsior*), while silver fir (*Abies alba*) and Scots pine (*Pinus sylvestris*) will face a prevalent reduction of their high suitable areas.
- "Different behaviours": A third group of species, including sycamore maple (*Acer pseudoplatanus*), green alder (*Alnus alnobetula*), Silver birch (*Betula pendula*), European larch (*Larix decidua*), European aspen (*Populus tremula*), and rowan (*Sorbus aucuparia*) exhibits non-linear temporal trend, with initial gain offset by consequent losses, especially in the business-as-usual scenario RCP8.5. The gains in higher elevations are compensated by the losses at lower elevations.

Changes in suitable surface area (Page 1 of 2)



Changes in suitable surface area (Page 2 of 2)

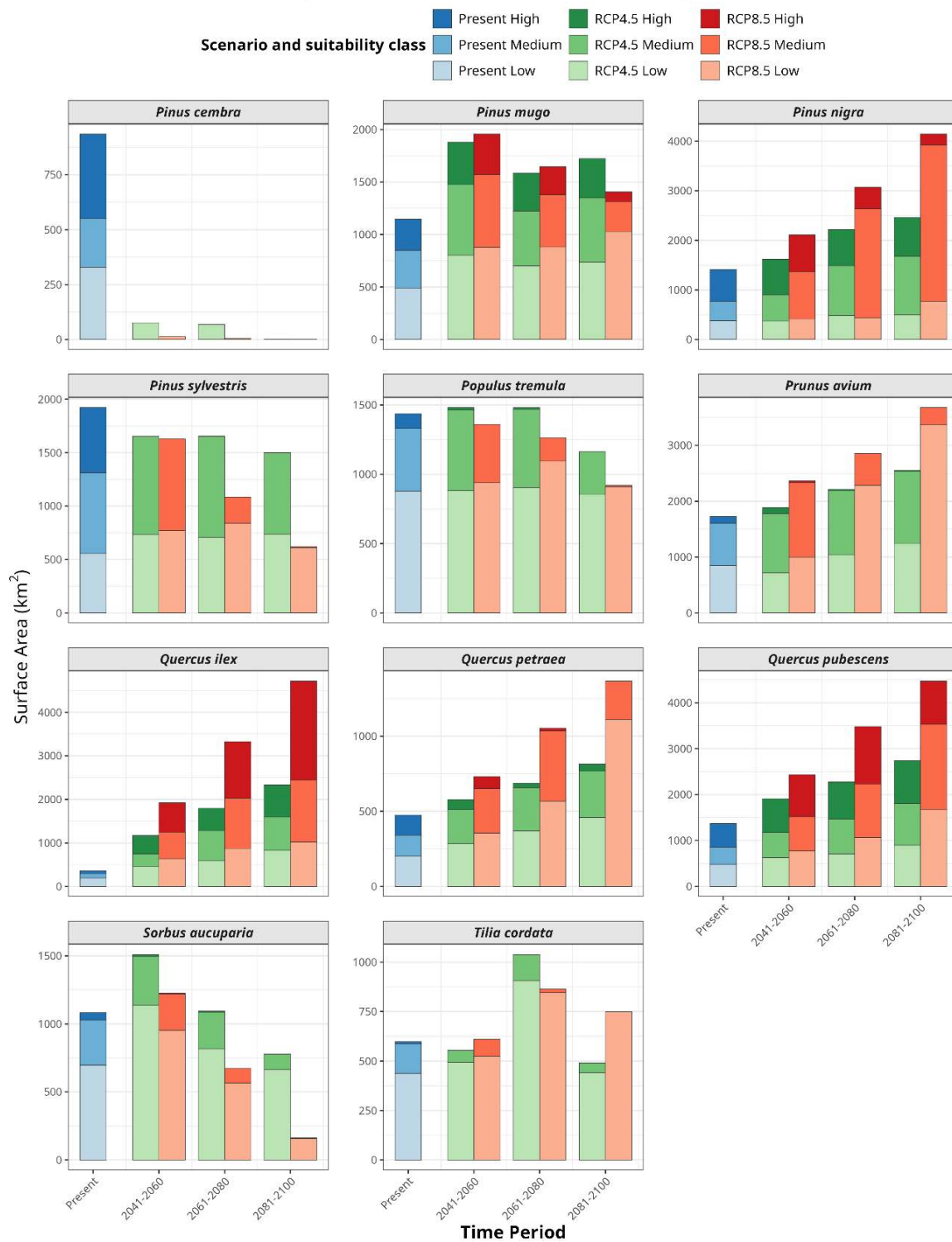


Figure 3.1. Changes in suitable surface area (in km²) for the 23 studied species, across the two RCP climate scenarios (4.5 and 8.5) in the three future time periods (2041-2060, 2061-2080 and 2081-2100), compared with the present scenario. Responses to climate change are very diversified, with the extremes being the *Pinus cembra* that is projected to almost disappear in all the scenarios, and *Quercus ilex* that is projected to increase its potential habitat suitability by one order of magnitude.

The absolute differences in the suitable surface area of the future scenarios and time periods, compared with the present climate, are illustrated in Figure 3.2. The holm oak (*Quercus ilex*) is the species with the most important increase in potential suitable area, for all scenarios and timeframes, gaining, in the intermediate-emission scenario RCP4.5, about 2000 km² by the end of the century. In absolute terms the major suitable area loss will be experienced by the Norway spruce (*Picea abies*) in all scenarios and time periods (-1500 km² by the end of the century in the RCP4.5).



Figure 3.2. Absolute difference in suitable surface area in km² compared with the present climate.

In relative terms, for the holm oak the gain in relative potential suitable area is evident in all scenarios (Figure 3.3). By the end of the century for this species the potential suitable area, considering the medium-emission scenario, could increase by 20 times. The major loss will be experimented by the Swiss stone pine, that will lose 100% of its area in all the suitability classes by the end of the century (Section 3.3.1).

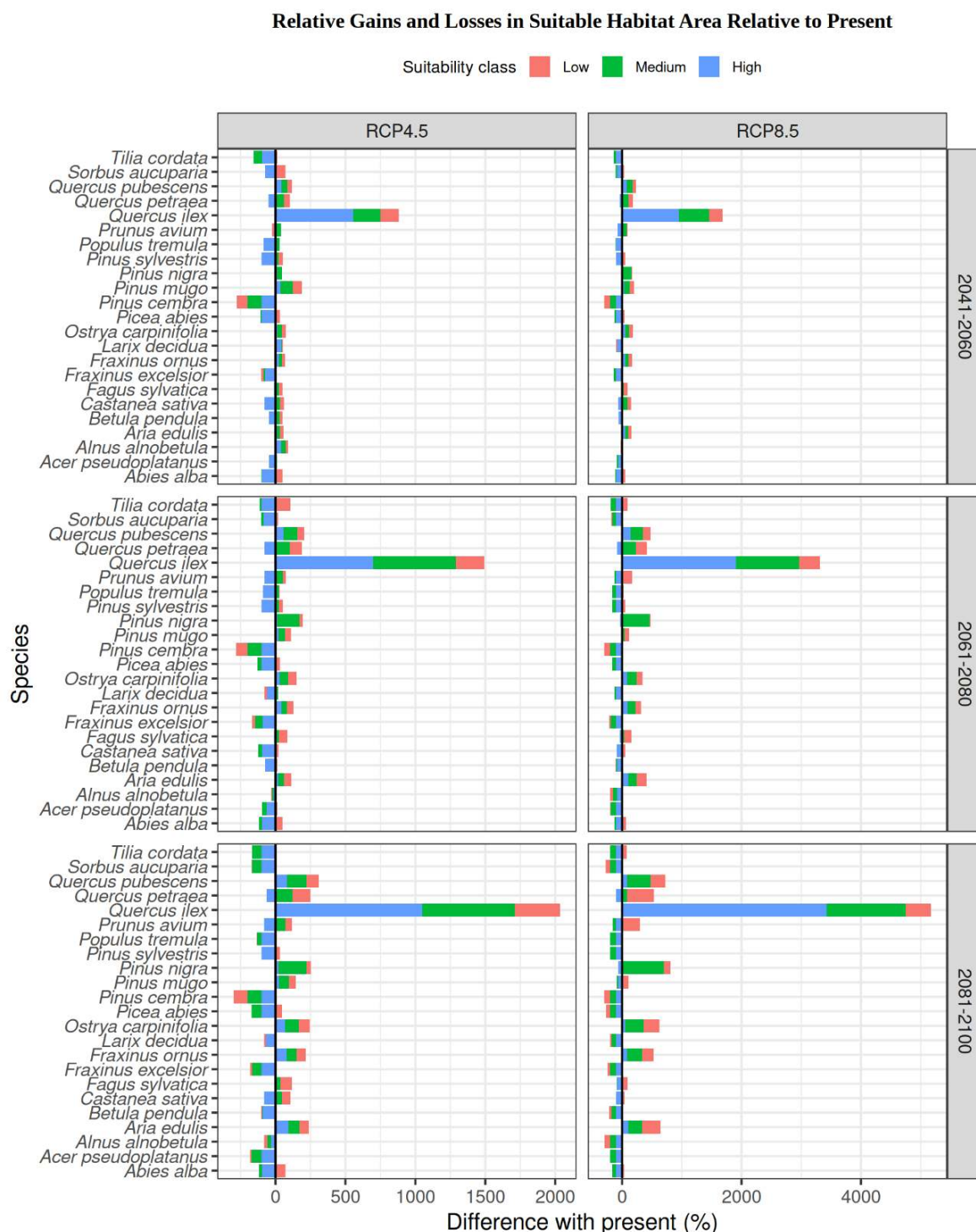
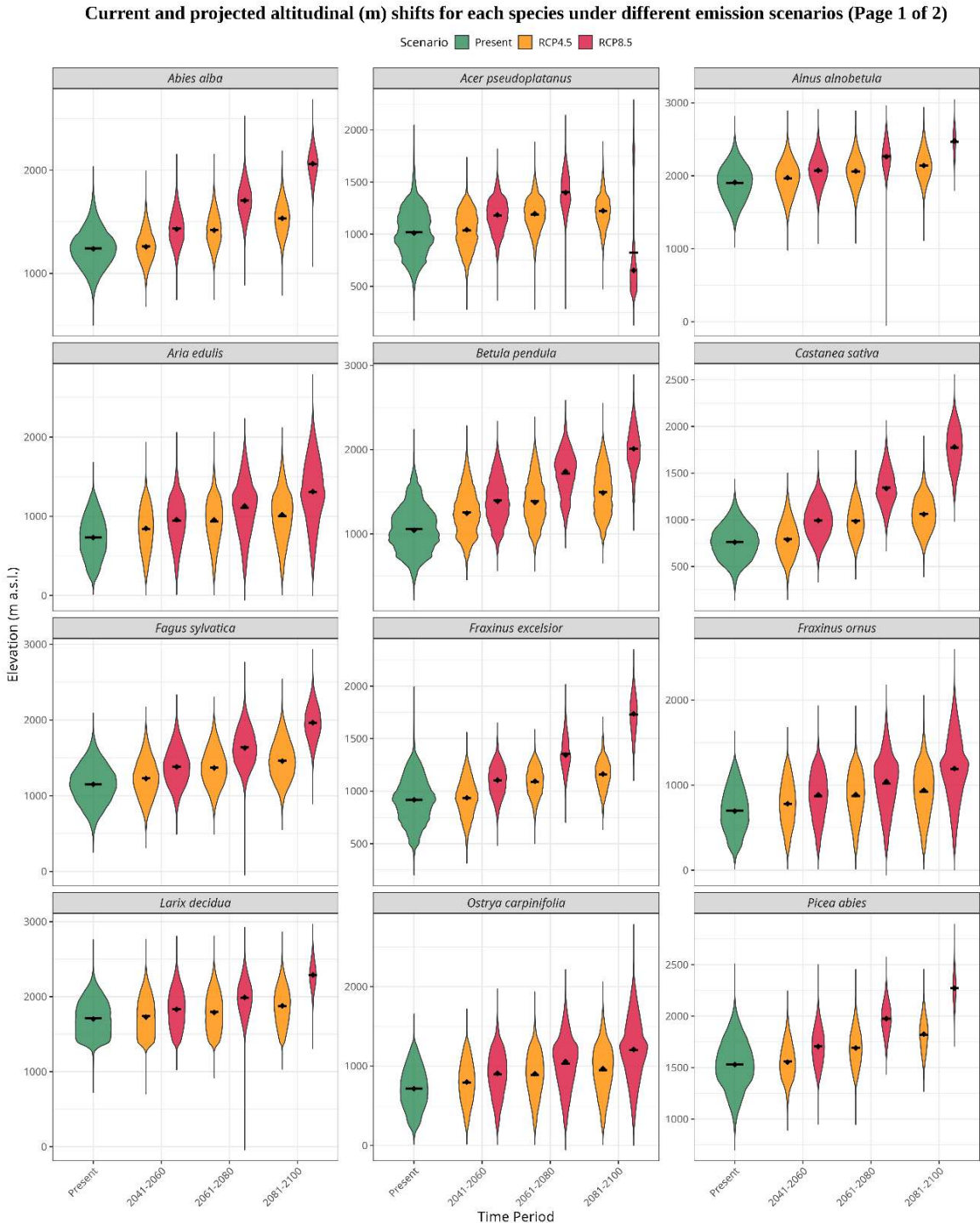


Figure 3.3. Relative difference in suitable surface area compared with the present climate.

The analysis of altitudinal shifts – for the medium and high suitability areas – revealed a general upward migration trend for all the 23 species (Figure 3.4). For instance, the Norway spruce, currently abundant at 1200 - 1800 m a.s.l., is projected to shift its optimal suitability to 1600 - 2100 m a.s.l. under RCP4.5 by the end of the century while the holm oak, now with the optimum at 250 – 750 m a.s.l. will expand its suitable habitat beyond 1000 m a.s.l.



Current and projected altitudinal (m) shifts for each species under different emission scenarios (Page 2 of 2)

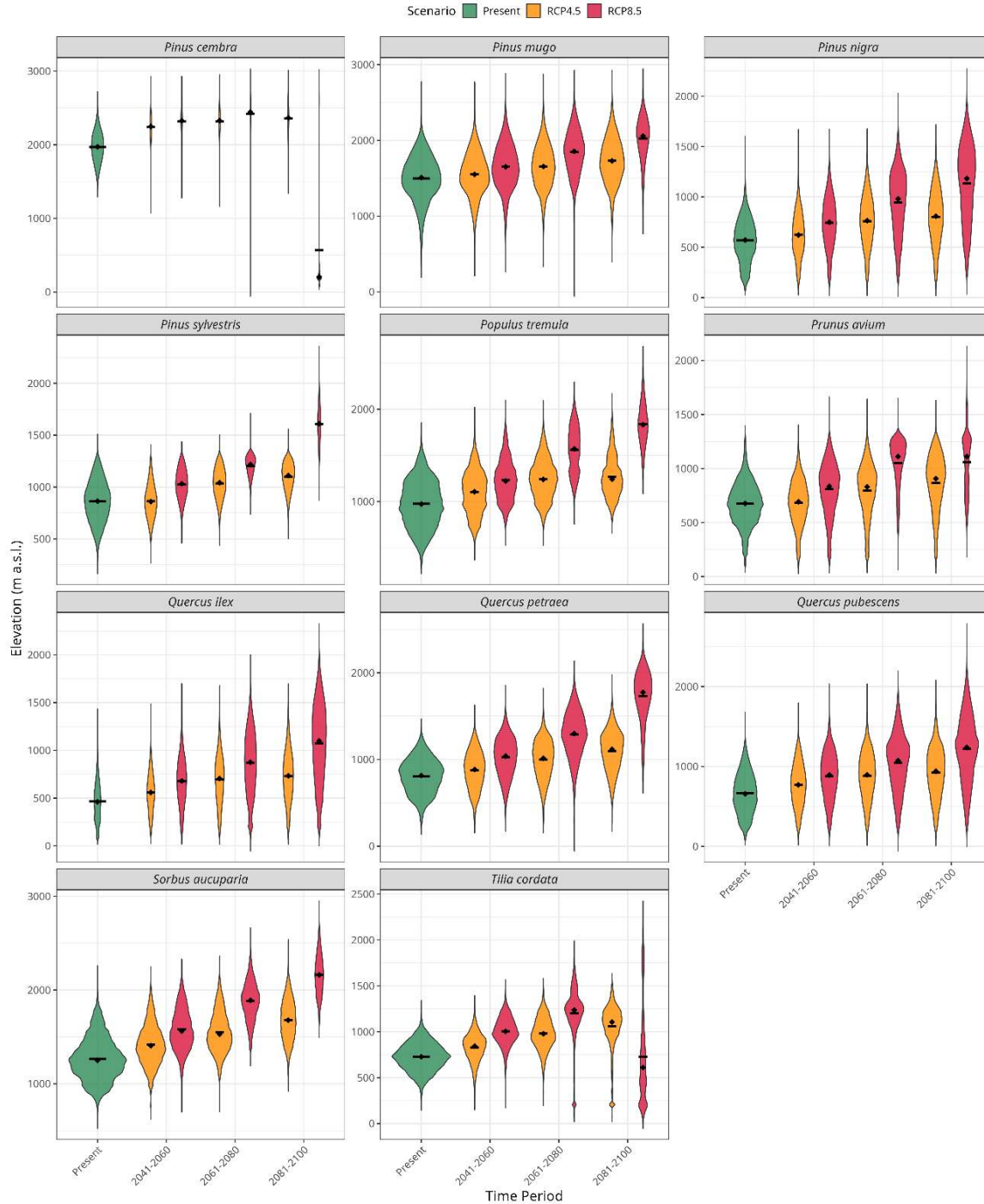


Figure 3.4. Variation in the altitudinal range of 23 tree species across four temporal periods (Present, 2021-2040, 2041-2060, 2081-2100) and two emission scenarios (RCP4.5 and RCP8.5). Only medium and high suitability classes are included in the plot. Altitudinal distributions are presented using violin plots, which indicate the probability density for each species, scenario, and period. The mean is represented by the line, the median by the dot.

The average elevation shift for the medium and high suitable areas for all the 23 species is 83 m by the mid-century and 265 m by the end of the century, considering the RCP4.5 scenario (Table 3.1). High variance across the species is registered (the standard deviation

is 83 and 75 m respectively). Under the RCP8.5 scenario, altitude shifts are anticipated to double, comparing of those projected under the intermediate scenario.

Table 3.1. Mean elevation gain (in m a.s.l.) for the two emission scenarios in the three time-periods referred to the present scenario. The overall mean indicate elevation shift across all the 23 species.

Species	Present	RCP4.5			RCP8.5		
		2041-2060	2061-2080	2081-2100	2041-2060	2061-2080	2081-2100
<i>Abies alba</i>	1247	18	180	284	189	456	809
<i>Acer pseudoplatanus</i>	1018	16	171	201	159	369	521
<i>Alnus alnobetula</i>	1898	56	154	232	162	367	667
<i>Aria edulis</i>	750	97	181	248	189	358	543
<i>Betula pendula</i>	1062	200	334	434	338	656	989
<i>Castanea sativa</i>	762	36	225	305	238	582	1011
<i>Fagus sylvatica</i>	1143	85	220	309	233	480	804
<i>Fraxinus excelsior</i>	917	14	173	237	184	369	651
<i>Fraxinus ornus</i>	725	62	140	195	142	289	467
<i>Larix decidua</i>	1708	29	82	151	112	263	556
<i>Ostrya carpinifolia</i>	733	66	145	208	154	290	473
<i>Picea abies</i>	1529	41	170	291	183	445	-
<i>Pinus cembra</i>	1968	414	459	-	-	-	-
<i>Pinus mugo</i>	1489	58	160	233	155	342	509
<i>Pinus nigra</i>	592	50	168	210	155	338	520
<i>Pinus sylvestris</i>	857	9	177	237	168	348	625
<i>Populus tremula</i>	969	125	267	299	259	605	839
<i>Prunus avium</i>	681	-4	93	165	111	340	379
<i>Quercus ilex</i>	464	101	232	271	223	411	603
<i>Quercus petraea</i>	807	66	190	291	216	474	920
<i>Quercus pubescens</i>	689	89	185	226	185	350	520
<i>Sorbus aucuparia</i>	1272	150	278	387	306	587	880
<i>Tilia cordata</i>	720	126	281	418	296	516	
Mean (m a.s.l.)	1043	83	203	265	198	420	664
Standard deviation	423	88	81	75	60	112	190

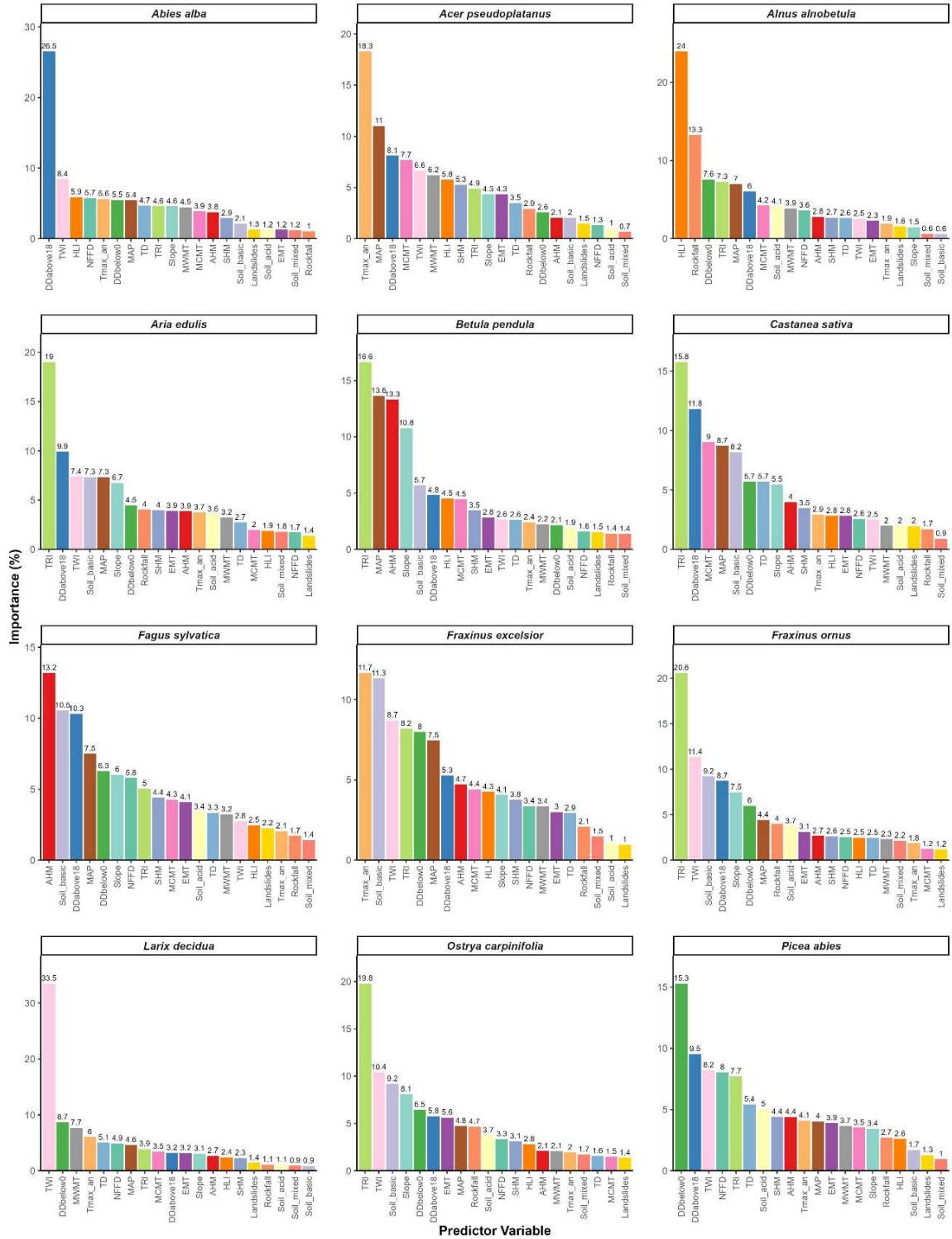
The relative importance of predictor variables differs notably among the analysed species (Figure 3.5). Climatic and topographic variables generally show the highest contributions. For some species, topographic variables were found to be the most important. The most prominent example is the Topographic Ruggedness Index (TRI), which is the most influential variable for six species (*Aria edulis*, *Betula pendula*, *Castanea sativa*, *Fraxinus ornus*, *Ostrya carpinifolia*, and *Quercus petraea*), with an importance constantly over 15%. The heatload index is the most important factor for *Alnus alnobetula*,

accounting for 24.0%, while the Topographic Wetness index proved to be the best predictor for *Larix decidua* (33.5%) and *Prunus avium* (15%).

Climatic factors are predominant for other species. The Mean Annual Precipitation (MAP) is the most influential predictor for *Populus tremula* (18%) and *Quercus ilex* (25.3%) and among the firsts for nine other species. The Degree-Days Above 18°C influences more the distribution for *Abies alba* (26.5%) and *Pinus nigra* (16.8%). Notably, for *Fagus sylvatica*, the models predicted the Annual Heat-Moisture Index (AHM) as the most important predictor variable (13.2%).

Conversely, some variables consistently demonstrated low importance across nearly all species models. Soil characteristics, including Soil_acid and Soil_mixed, and disturbance factors like Landslides, generally contributed less than 3% to the predictive power of the models. Exceptions are the Soil_basic, important predictor for *Pinus mugo* (14.4%) *Quercus pubescens* (14.5%), *Fraxinus excelsior* (11.3%), and *Fagus sylvatica* (10.5%), and the Rockfall, second most important factor for *Pinus mugo* (13.5%) and *Alnus alnobetula* (13.3%).

Variable importance by species (Page 1 of 2)



Variable importance by species (Page 2 of 2)

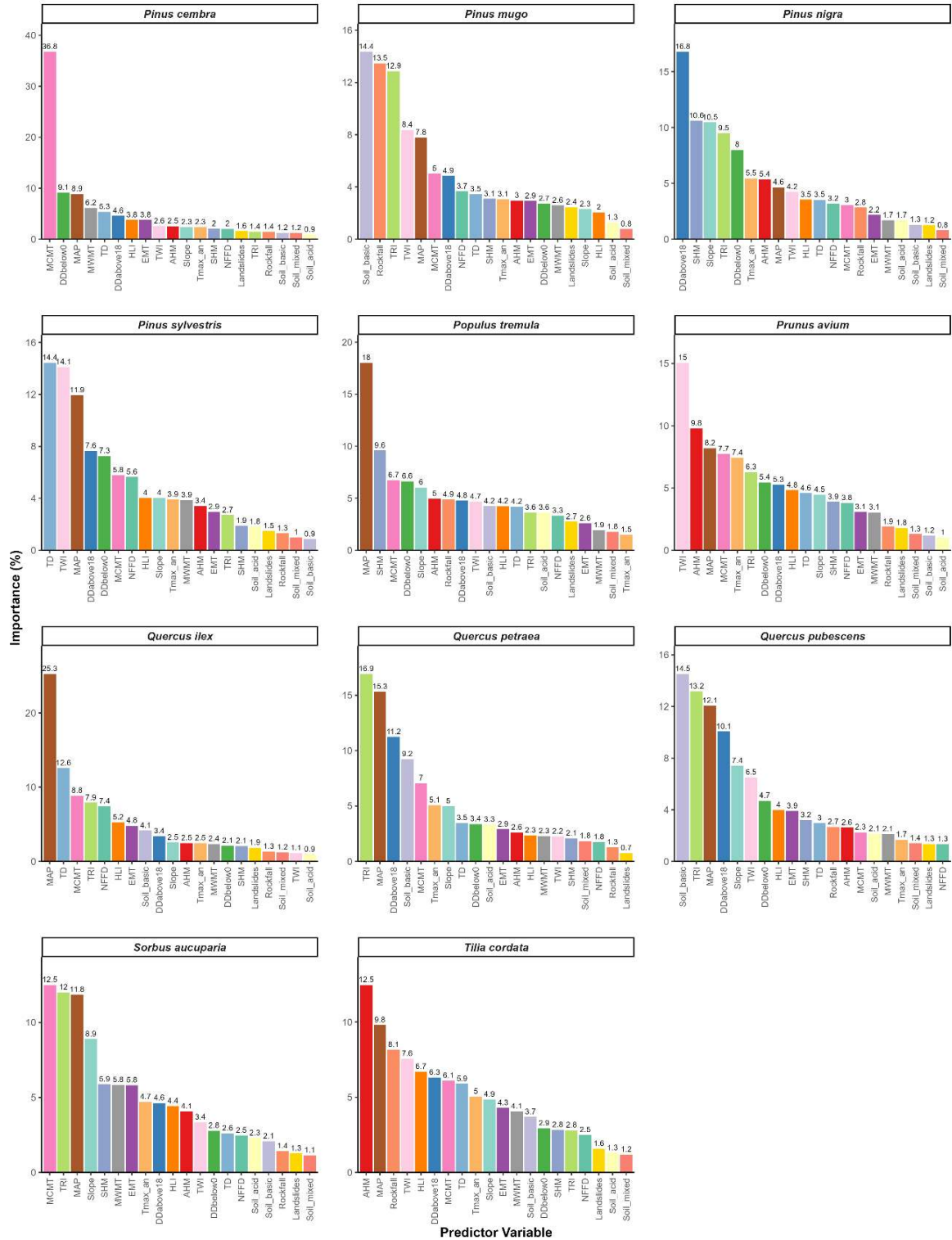


Figure 3.5. Variable importance in predicting the distribution for the 23 studied species. For each species, the bars indicate the percentage contribution of each predictor to the final distribution model.

The analysis of mean variable importance across all 23 species revealed that the most influential predictors are the Topographic Ruggedness Index (TRI), Mean Annual Precipitation (MAP), and Degree-Days above 18°C (DDabove18). As shown in Figure 3.6, each of these variables accounts for more than 8% of the total importance. Conversely, the least influential predictors were Soil_acid, Landslides, and Soil_mixed, with each contributing less than 2.5%.

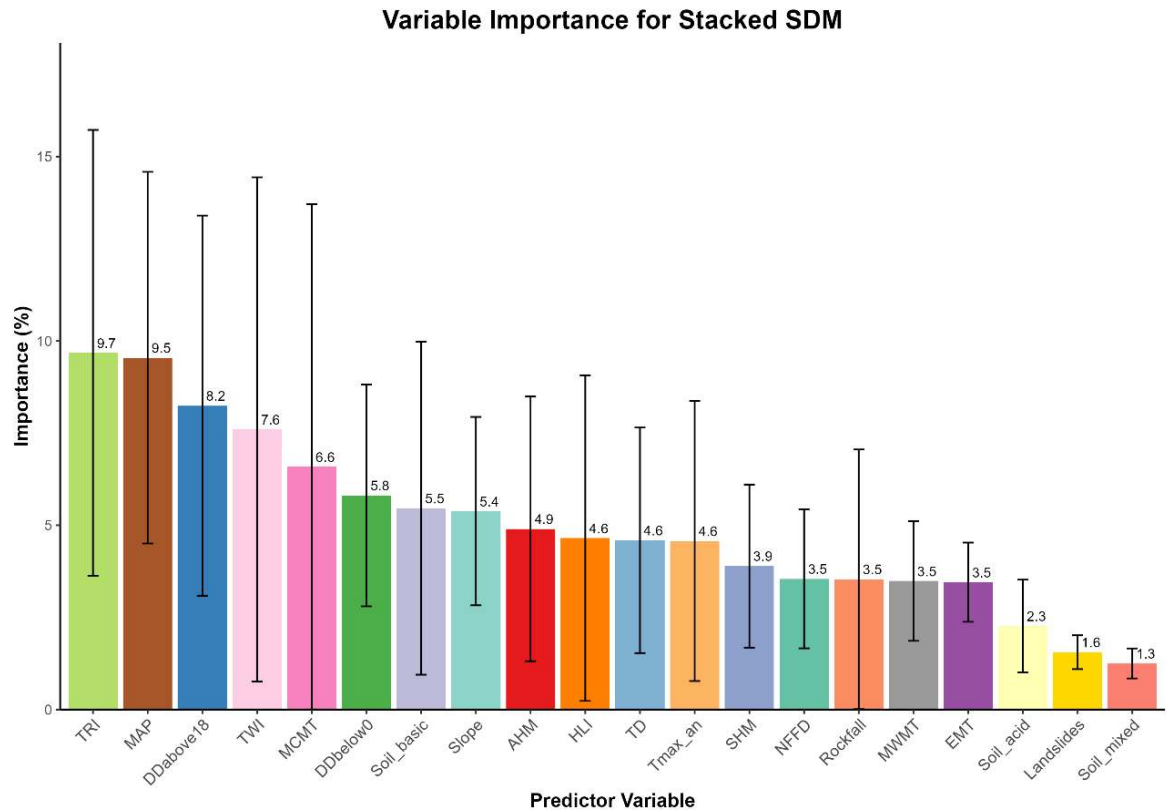


Figure 3.6. Ranked importance of predictor variables for the Stacked Species Distribution Model (SSDM). The bars represent the mean importance of each variable, expressed as a percentage, calculated across all model runs. Error bars represent the standard deviation across the 23 species.

3.1.1 Evaluation metrics

The predictive performance of the modelling framework was assessed at both the algorithm and individual species levels.

An evaluation of the eight different algorithms across the 23 species revealed that Random Forest (RF) was the most accurate individual model (AUC = 0.96, Kappa = 0.80, overall accuracy or proportion of correct predictions = 0.90), while Artificial Neural network (ANN) exhibited the weaker performance (AUC = 0.83, Kappa = 0.60, overall accuracy = 0.80) (Table 3.2). Notably, while GBM showed high discrimination (AUC = 0.09), it suffered from extremely poor calibration (-0.30), rendering its probability

outputs unreliable. The final stacked model demonstrated strong overall predictive performance across the 23 tree species, achieving a mean AUC of 0.90 ± 0.04 and a mean Kappa of 0.66 ± 0.12 .

Table 3.2. Performance evaluation of the eight individual algorithms used in the ensemble species distribution models. All metrics, including the Area Under the Curve (AUC) and Cohen's Kappa, are averaged across the 23 modelled tree species (individual ESDMs). The final rows show the mean performance ('Assemblage mean') and standard deviation across the suite of algorithms and it corresponds to the overall performance of the stacked species distribution model.

Algorithm evaluation	Threshold	AUC	Omission rate	Sensitivity	Specificity	Prop. correct	Cohen's Kappa	Calibr.
ANN	0.64	0.83	0.20	0.87	0.72	0.80	0.59	0.88
CTA	0.66	0.88	0.16	0.86	0.83	0.84	0.68	0.89
GAM	0.72	0.93	0.13	0.87	0.87	0.87	0.66	0.79
GBM	0.48	0.90	0.18	0.83	0.82	0.83	0.65	-0.30
GLM	0.71	0.90	0.17	0.83	0.83	0.83	0.57	0.78
MARS	0.73	0.92	0.14	0.86	0.86	0.86	0.64	0.81
RF	0.60	0.96	0.10	0.90	0.90	0.90	0.80	0.87
SVM	0.73	0.92	0.14	0.86	0.86	0.86	0.72	0.75
Assemblage Mean	0.66	0.90	0.15	0.86	0.84	0.85	0.66	0.68
Std Dev	0.08	0.04	0.03	0.02	0.05	0.03	0.07	0.40

Despite the strong average performance, model accuracy varied significantly among species (Table 3.3). Predictions were highly accurate for species with well-defined niches, such as *Quercus ilex* (Kappa = 0.92) and *Quercus petraea* (Kappa = 0.86). In contrast, the model was less successful for other species, notably *Larix decidua* (Kappa = 0.42), *Picea abies* (Kappa = 0.47) and *Fagus sylvatica* (Kappa = 0.55).

This species-specific evaluation is crucial for understanding the model's reliability across different ecological profiles and for identifying which species' distributions were modelled most accurately. This variability highlights that while the stacked model is robust overall, its reliability is species-dependent, likely reflecting differences in ecological specialization and data quality.

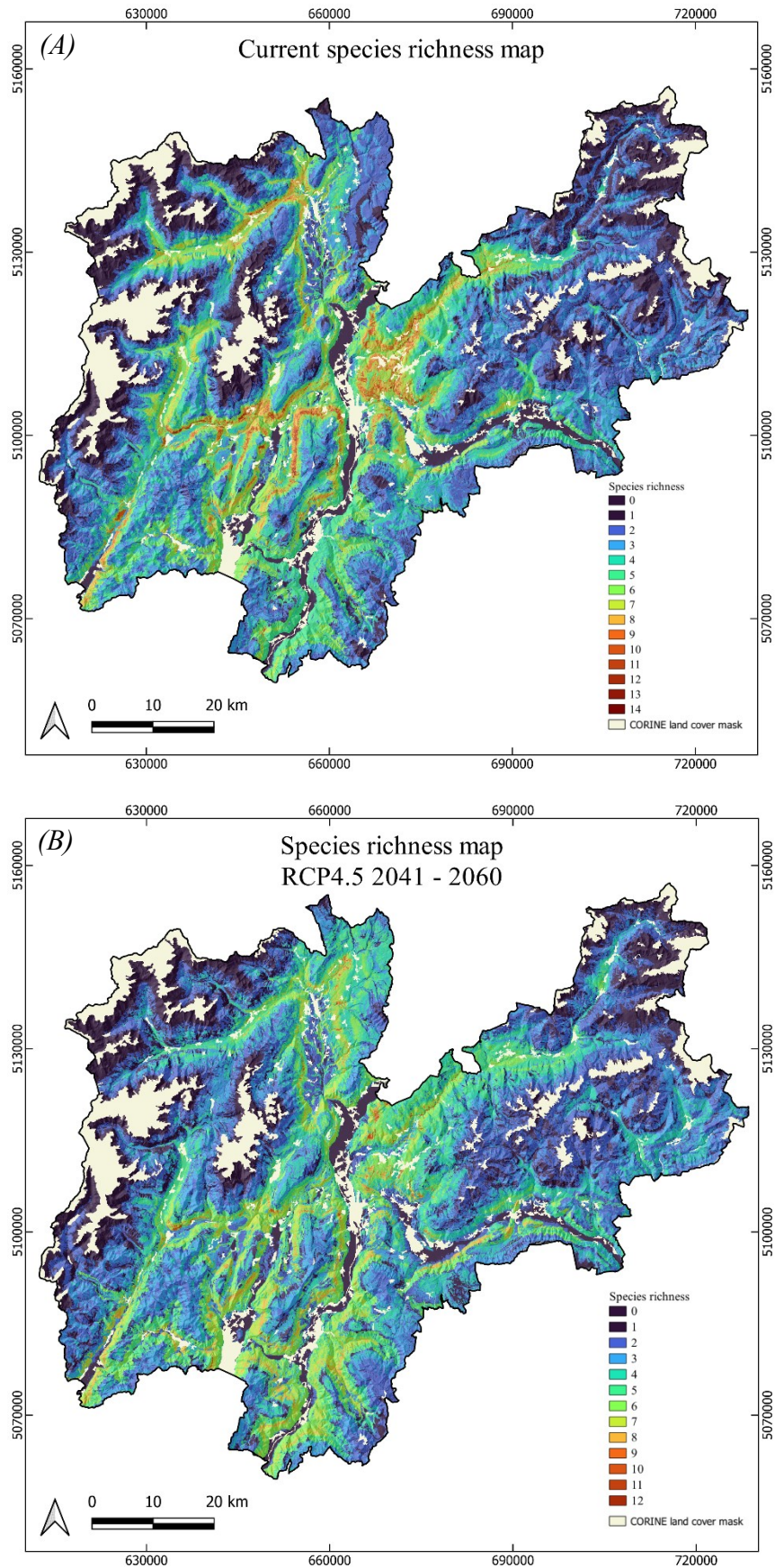
Table 3.3. Species-specific performance evaluation of the final ensemble model. Metrics are reported for each of the 23 modelled tree species individually. The final rows summarize the mean performance ('Assemblage mean') and standard deviation of the final model across all species, indicating its overall accuracy and consistency.

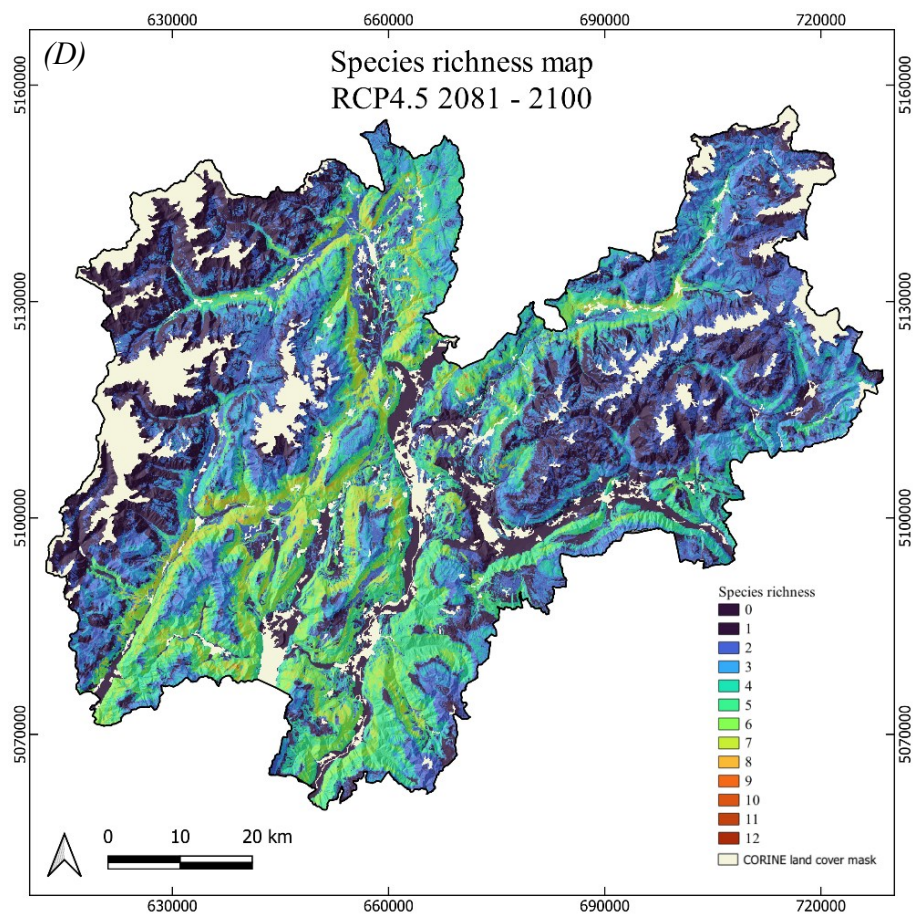
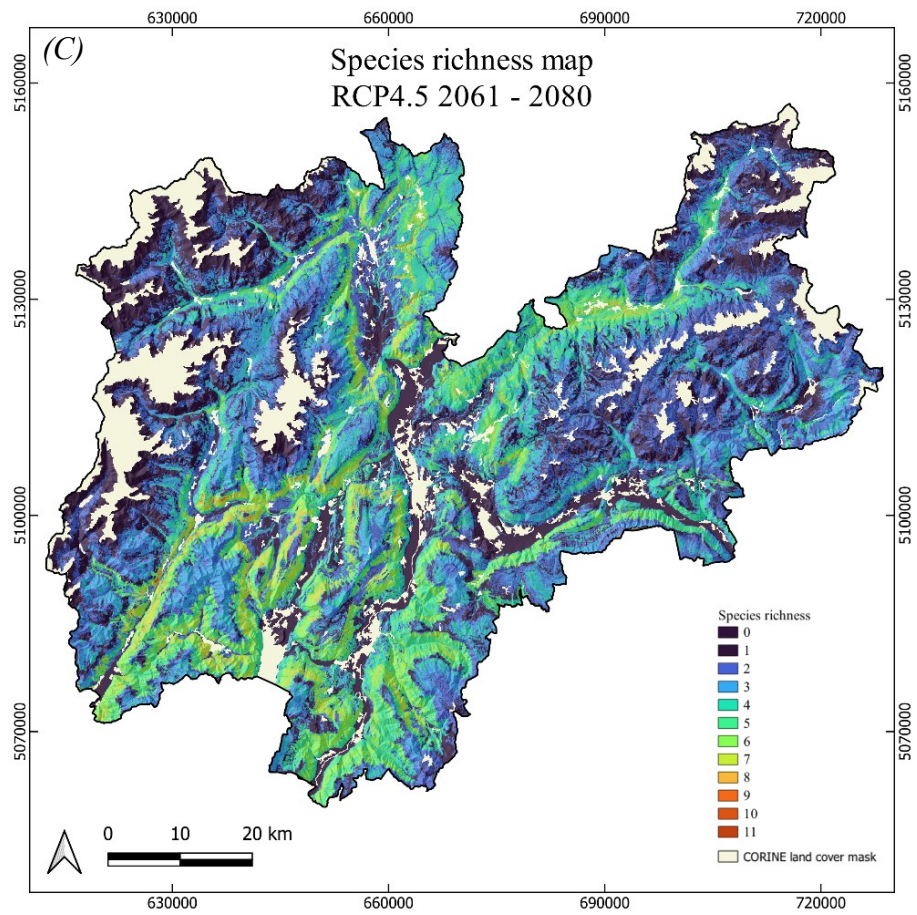
Species	Thresh.	AUC	Omission rate	Sens.	Spec.	Prop. correct	Cohen's Kappa	Calibr.
<i>Abies alba</i>	0.71	0.89	0.18	0.84	0.80	0.82	0.59	0.72
<i>Acer pseudoplatanus</i>	0.54	0.87	0.20	0.80	0.80	0.80	0.59	0.63
<i>Alnus alnobetula</i>	0.65	0.92	0.14	0.89	0.84	0.86	0.68	0.72
<i>Aria edulis</i>	0.71	0.93	0.12	0.88	0.87	0.88	0.72	0.69
<i>Betula pendula</i>	0.52	0.87	0.20	0.81	0.80	0.80	0.61	0.67
<i>Castanea sativa</i>	0.66	0.95	0.09	0.92	0.90	0.91	0.80	0.68
<i>Fagus sylvatica</i>	0.66	0.87	0.20	0.81	0.79	0.80	0.55	0.73
<i>Fraxinus excelsior</i>	0.57	0.88	0.20	0.79	0.81	0.80	0.60	0.63
<i>Fraxinus ornus</i>	0.71	0.92	0.14	0.87	0.84	0.86	0.67	0.70
<i>Larix decidua</i>	0.69	0.80	0.26	0.76	0.71	0.74	0.42	0.66
<i>Ostrya carpinifolia</i>	0.73	0.92	0.14	0.87	0.85	0.86	0.68	0.70
<i>Picea abies</i>	0.72	0.84	0.23	0.79	0.75	0.77	0.47	0.71
<i>Pinus cembra</i>	0.79	0.95	0.09	0.91	0.90	0.91	0.78	0.72
<i>Pinus mugo</i>	0.61	0.94	0.11	0.88	0.89	0.89	0.73	0.71
<i>Pinus nigra</i>	0.74	0.92	0.13	0.89	0.85	0.87	0.70	0.67
<i>Pinus sylvestris</i>	0.75	0.89	0.17	0.84	0.82	0.83	0.62	0.71
<i>Populus tremula</i>	0.57	0.88	0.18	0.84	0.80	0.82	0.64	0.66
<i>Prunus avium</i>	0.62	0.87	0.20	0.82	0.78	0.80	0.60	0.62
<i>Quercus ilex</i>	0.82	0.98	0.04	0.97	0.96	0.96	0.92	0.67
<i>Quercus petraea</i>	0.68	0.96	0.06	0.95	0.92	0.94	0.86	0.71
<i>Quercus pubescens</i>	0.70	0.93	0.13	0.88	0.86	0.87	0.71	0.71
<i>Sorbus aucuparia</i>	0.46	0.88	0.19	0.81	0.80	0.81	0.61	0.64
<i>Tilia cordata</i>	0.51	0.93	0.12	0.89	0.87	0.88	0.72	0.61
Assemblage mean	0.66	0.90	0.15	0.86	0.84	0.85	0.66	0.68
Standard deviation	0.09	0.04	0.06	0.06	0.06	0.06	0.12	0.03

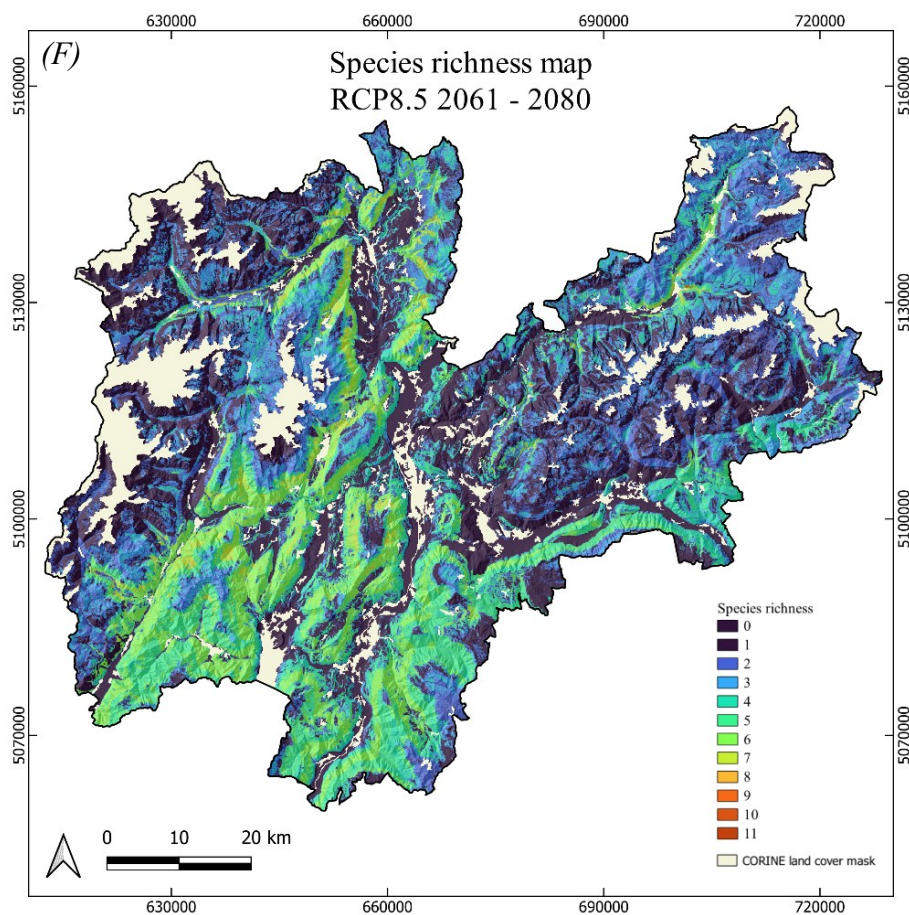
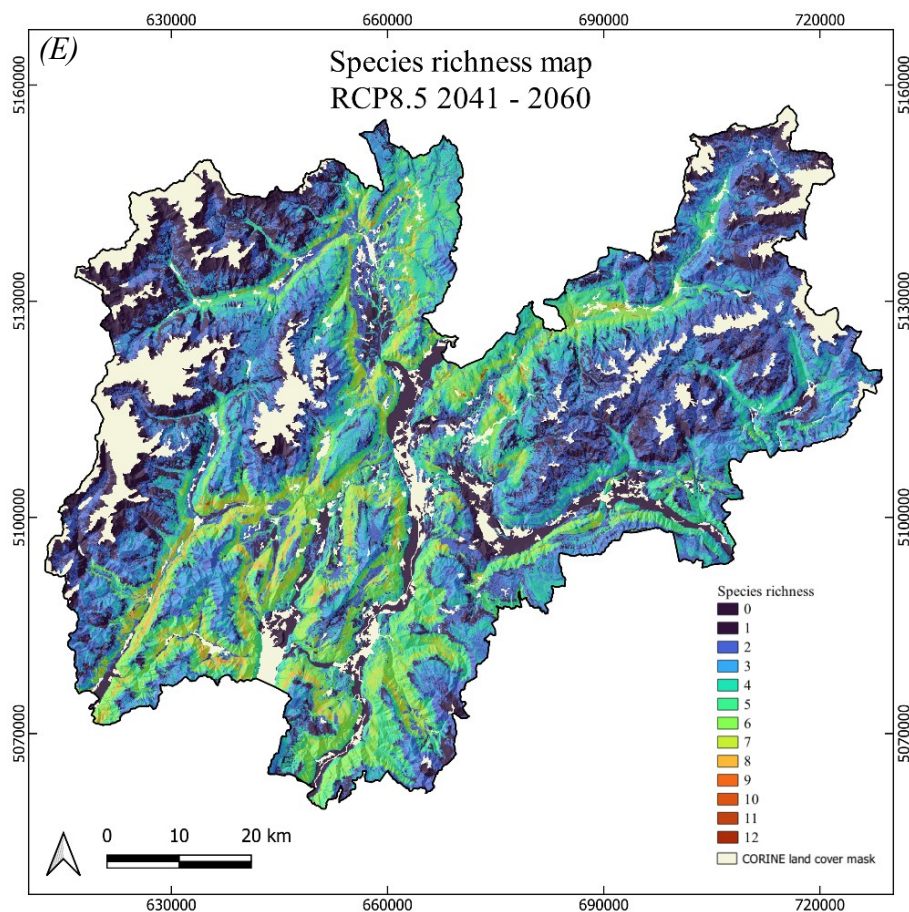
3.2 Species Richness

Species richness is an important community-level metric that offers an aggregate indication of habitat suitability across all species within the studied territory. The species richness maps under both current and projected future climatic scenarios show a moderate general decline across all time periods of the RCP4.5 scenario (Figure 3.7, A – G). Under current conditions (Figure 3.7, A), areas of high species richness (dark red) are prevalent in the side slopes of the main valleys (e.g. Valle dei Laghi, Adige, Cembra, Non and

Valsugana Valley). Notably, the model predicted a strong reduction in species richness for area with predominant acid soil (e.g. Lagorai mountain chain area, east of the study area).







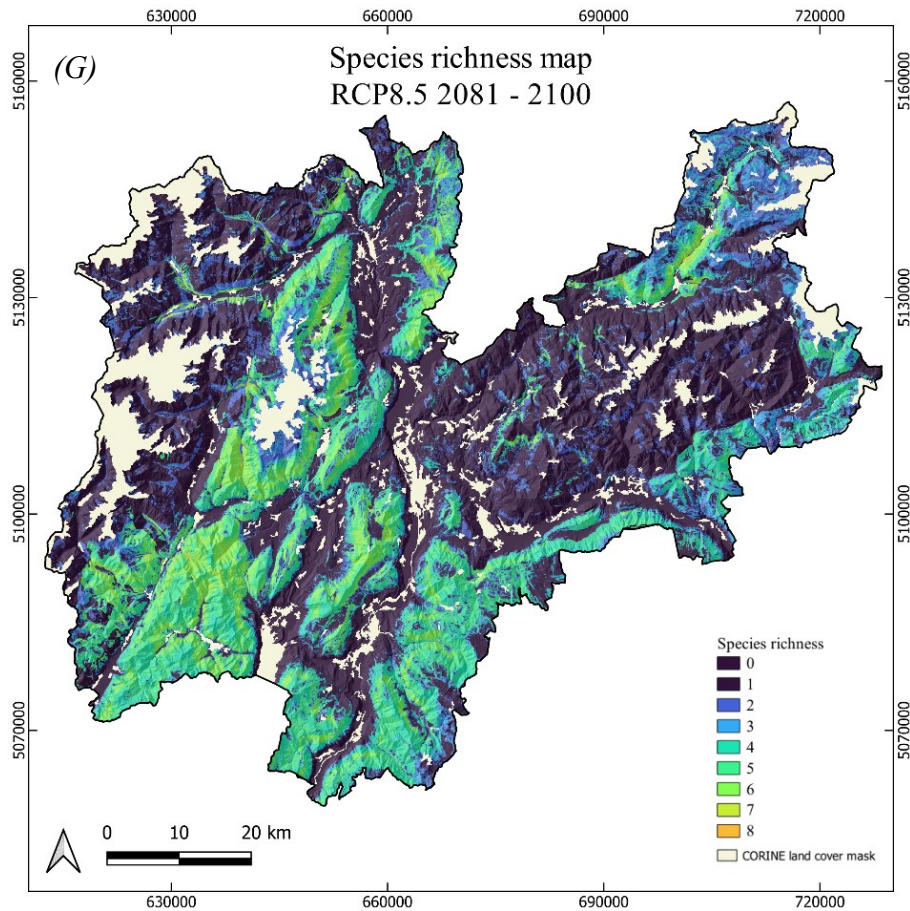


Figure 3.7. Future species richness map under present (A) and two future climate scenarios in three time periods: RCP4.5 for 2041–2060 (B), 2061–2080 (C), and 2081–2100 (D); and RCP8.5 for 2041–2060 (E), 2061–2080 (F), and 2081–2100 (G).

The projected impact of climate change on the spatial distribution of species richness varies significantly depending on the climate scenario considered (Figure 3.8). Under the intermediate scenario, RCP4.5, the distribution of species richness is projected to remain relatively stable throughout the 21st century. The overall shape of the curve, which peaks with a richness of two species occupying approximately 1,400 km², shows minimal deviation across the future time periods compared to the present-day baseline. This pattern suggests a certain resilience of the species assemblage to the climatic changes expected under this scenario. In stark contrast, the business-as-usual RCP8.5 scenario is projected to cause severe alterations to the species richness landscape. A clear trend of biodiversity decline is evident, characterized by two primary phenomena. Firstly, a progressive loss of areas with high species richness is projected; for instance, areas supporting six or more species are expected to shrink substantially and nearly vanish by the 2061–2080 period. Secondly, and most dramatically, a shift towards landscapes dominated by low species richness is predicted. This is highlighted by the sharp increase in the area suitable for only

a single species, which is projected to grow from approximately 900 km² in the present day to over 1,500 km² by the 2081-2100 period (Figure 3.9). Such a trend indicates a future of increasing biotic homogenization under a high-emissions trajectory.

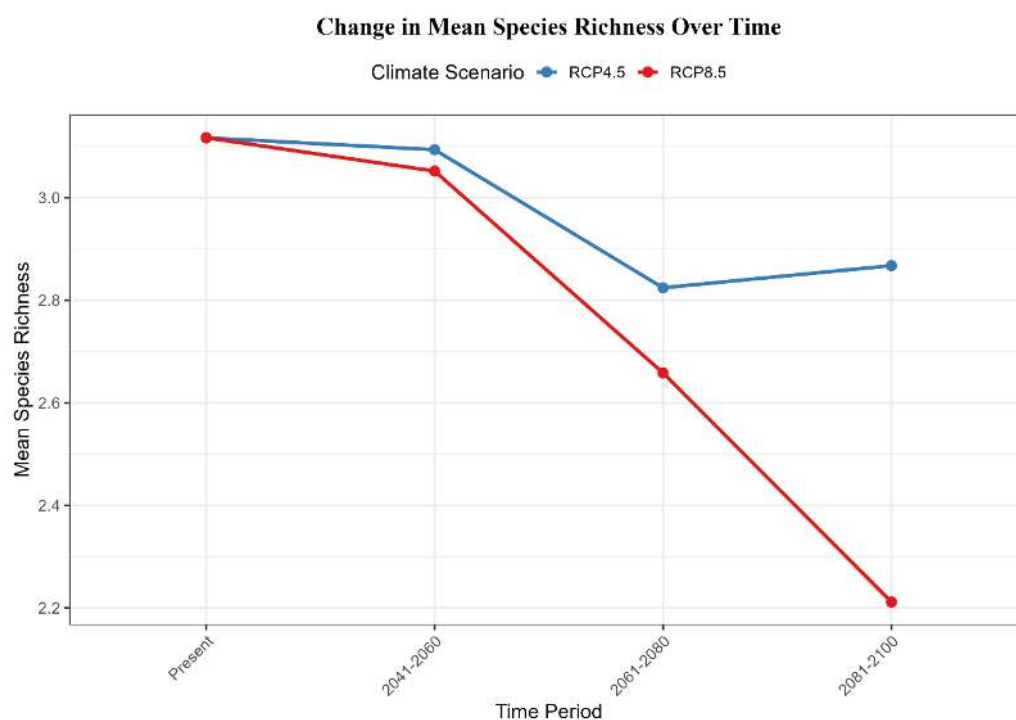


Figure 3.8. Changes in mean species richness in the entire study area: confront between the RCP4.5 and RCP8.5 scenarios.

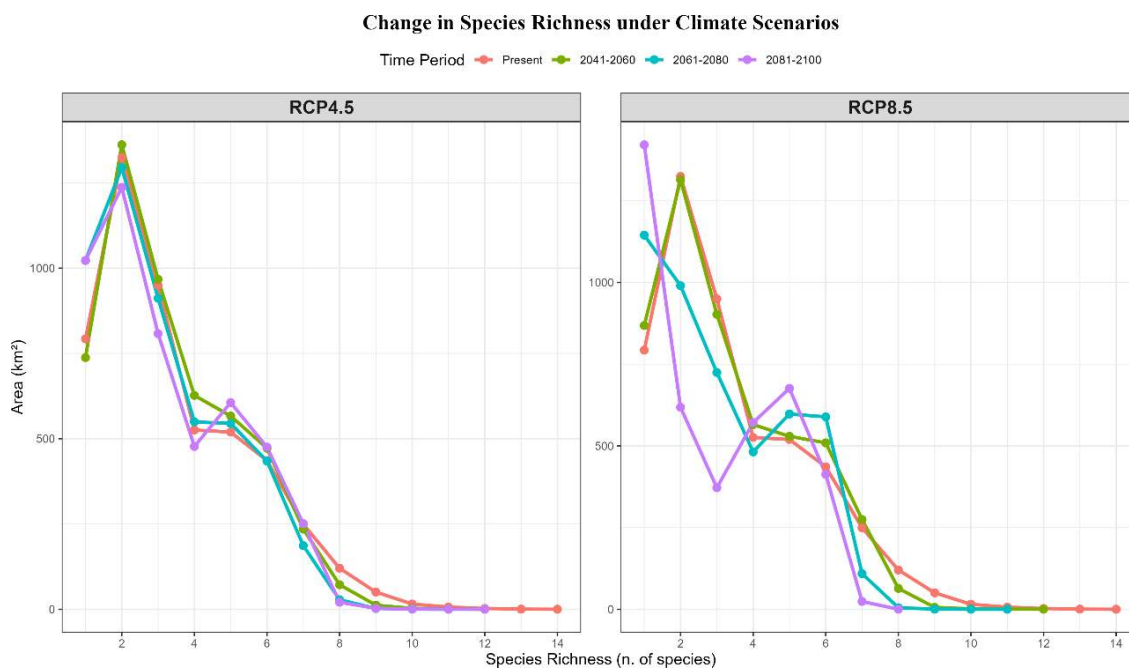


Figure 3.9. Distribution of species richness under two climate change scenarios. The plots show the total surface area (km²) occupied by a given number of species (species richness). The analysis is presented for the two RCP scenarios (4.5 and 8.5) across four time periods: Present, 2041-2060, 2061-2080, and 2081-2100.

The mean species richness error (mean absolute error per cell) is 3.14 species for the present (Std Dev = 2.19) and decreases under future scenarios – reaching 1.39 for RCP8.5 (2081–2100) – with intermediate values for the other time frames (Table 3.4). These values represent the average absolute difference between predicted and observed species richness per raster cell, computed from the retained occurrence data in the holdout cross-validation (75/25 split, 5 replicates); full details are reported in Section 2.4.

Table 3.4. Mean species richness error of the stacked SDMs across two scenarios and four time periods.

	Mean species richness error	Std Dev
Present	3.14	2.19
RCP4.5 2041-2060	3.00	2.07
RCP4.5 2061-2080	2.55	1.93
RCP4.5 2081-2100	2.62	2.07
RCP8.5 2041-2060	2.84	2.04
RCP8.5 2061-2080	2.21	2.13
RCP8.5 2081-2100	1.39	2.04

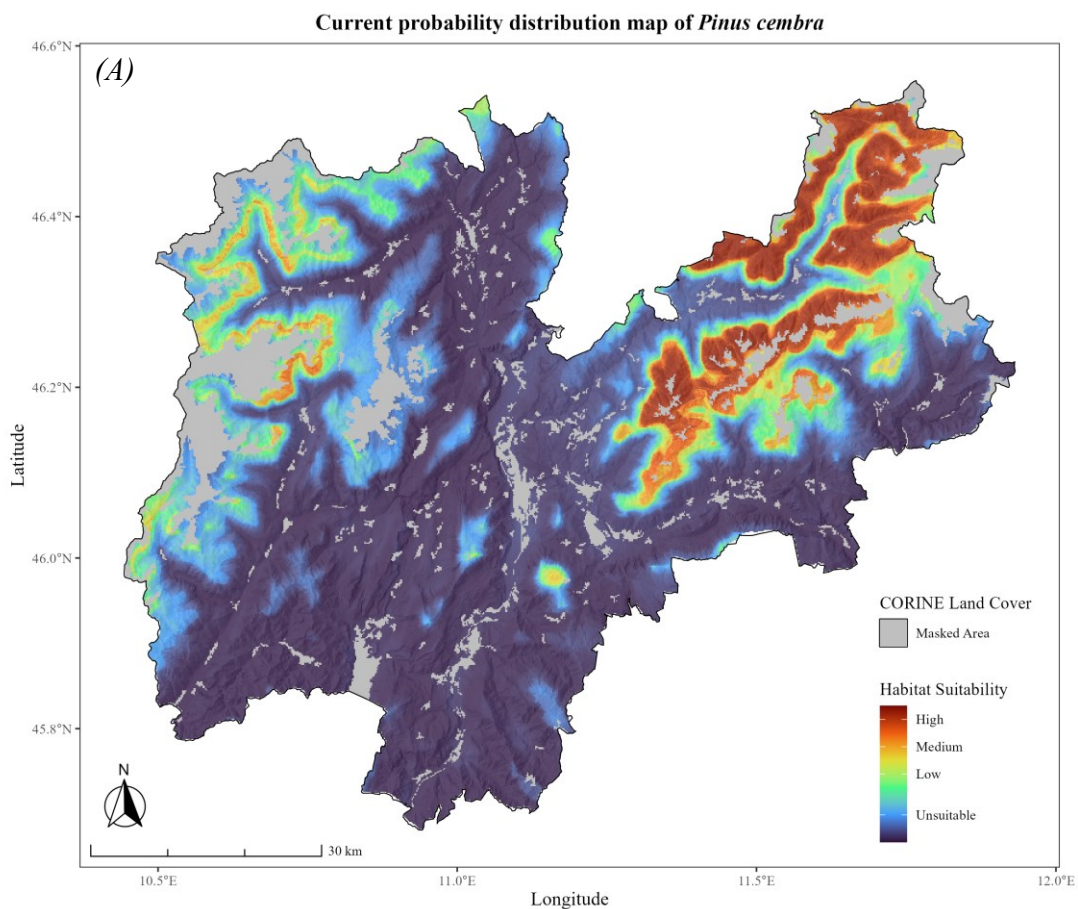
3.3 Case Studies

Among the 23 species modelled, *Pinus cembra* (Swiss stone pine) and *Quercus pubescens* (downy oak) were selected as representative examples to illustrate the outputs and interpretative potential of the ESDMs. These species were chosen due to their ecological relevance and contrasting projected trends under future climate conditions in the Province of Trento: The Swiss stone pine is expected to experience a severe reduction in suitable habitat, while the downy oak is projected to benefit from future climatic shifts.

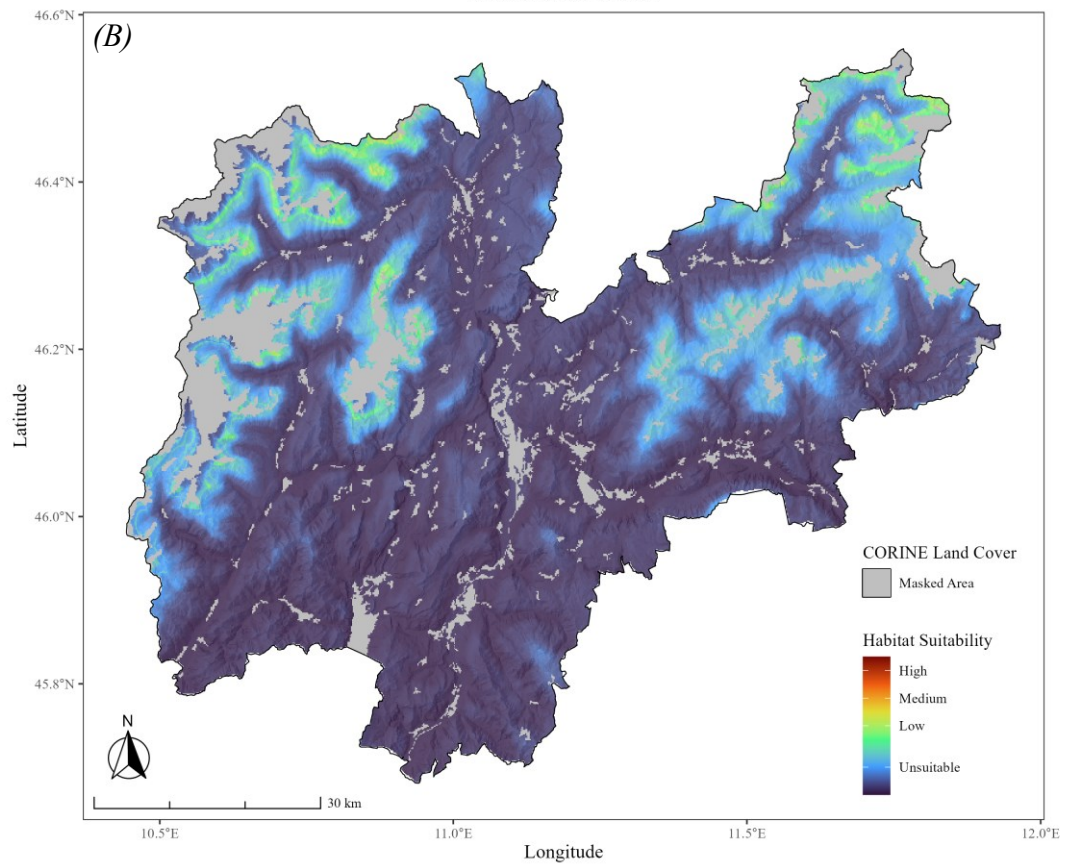
This section serves as a practical demonstration of how model outputs – developed in the Section 2.4.1 – can be analysed and interpreted for ecological and conservation purposes. Results from the ESDM comprise: habitat suitability maps, binary presence/absence maps, algorithm correlation heatmaps, and uncertainty estimations. The graphs showing the suitable area changes, the elevation shifts and the variable importance ranking were presented in Section 3.1.

3.3.1 *Pinus cembra*

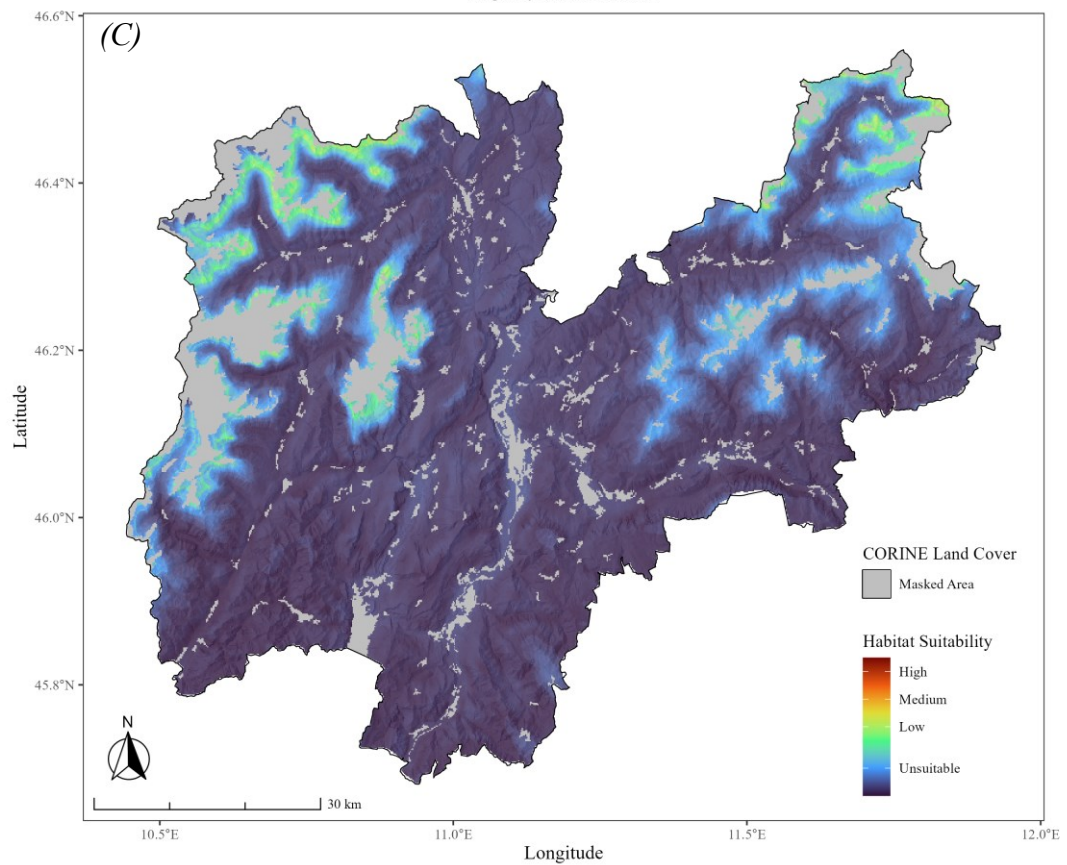
The habitat suitability maps for the Swiss stone pine project a severe and rapid spatial contraction of its climatic niche under all future scenarios (Figure 3.10, A – G). The current distribution shows extensive areas of optimal (dark red; 385 km²) and medium (orange/yellow; 221 km²) suitability at the highest elevations of the study area, as well as other 329 km² of low-suitability areas (green). This trend of decline begins in the near-term and becomes progressively more pronounced over time. Even under the intermediate RCP4.5 scenario, optimal and medium-suitability habitats almost completely disappear by mid-century (-99.9%), replaced by fragmented patches of low suitability (reduced by 76.8% by the decades 2041 – 2060). The reduction is greatly accelerated and more profound under the business-as-usual scenario, leaving only small low-suitability areas (- 96% in 2041 – 2060). In these scenarios, the study area becomes entirely unsuitable for the species by the end of the century, indicating a high risk of regional extinction for Swiss stone pine due to climate change.



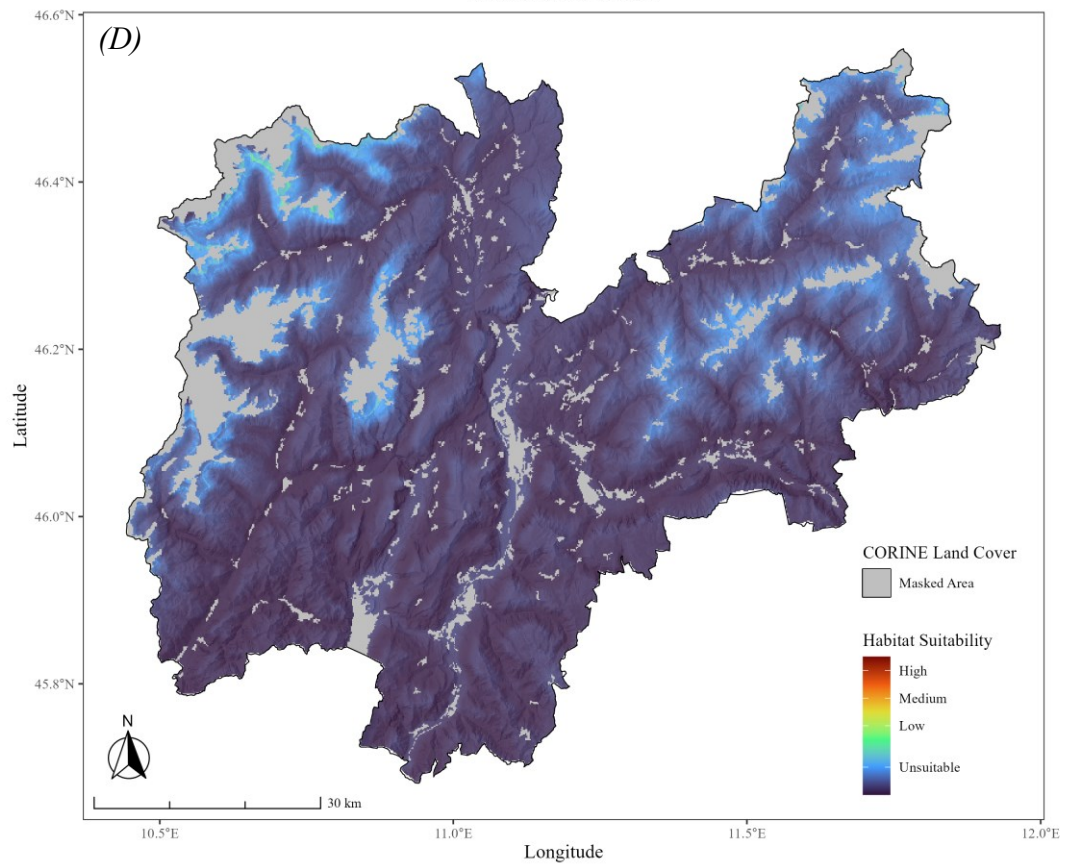
Future probability distribution map of *Pinus cembra*
RCP4.5 2041 - 2060



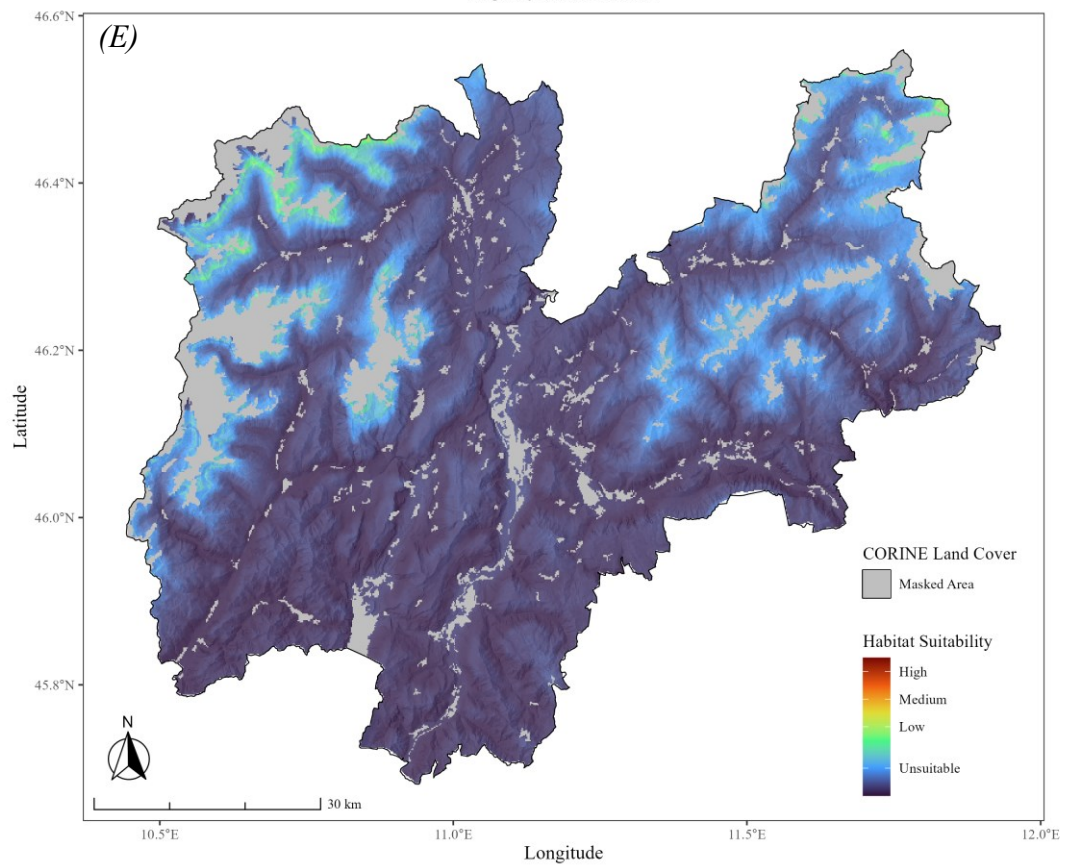
Future probability distribution map of *Pinus cembra*
RCP4.5 2061 - 2080



**Future probability distribution map of *Pinus cembra*
RCP4.5 2081 - 2100**



**Future probability distribution map of *Pinus cembra*
RCP8.5 2041 - 2060**



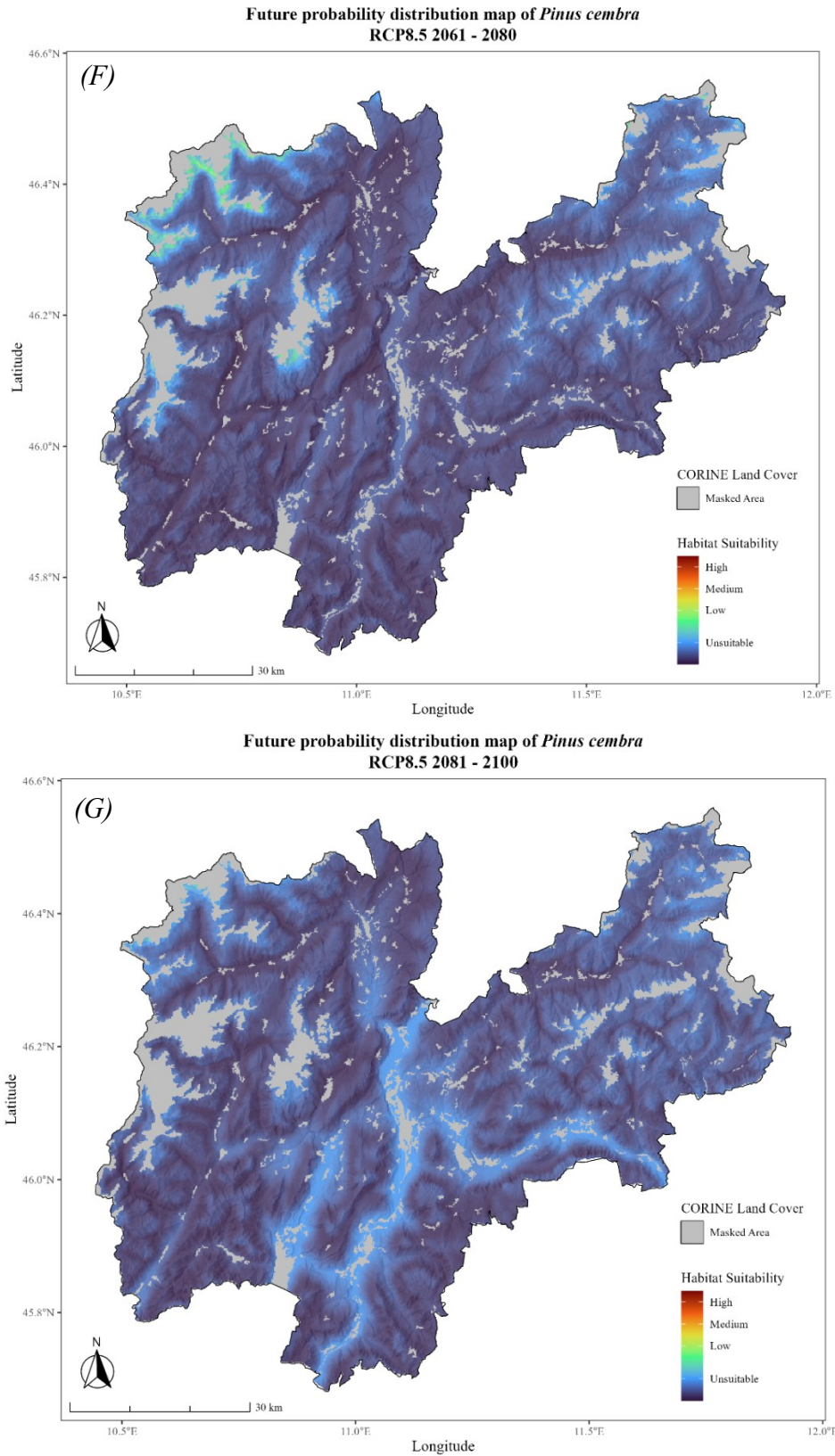
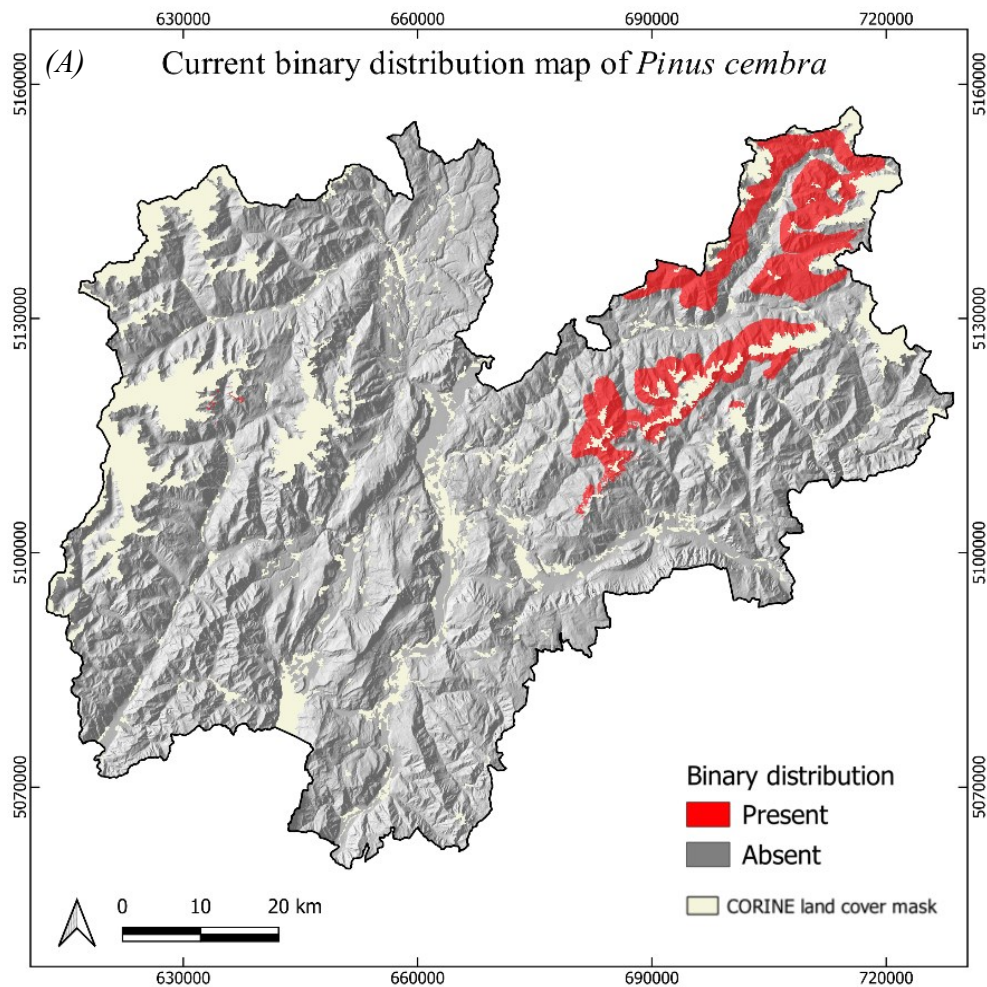


Figure 3.10. Habitat suitability maps of *Pinus cembra* under present (A) and future (B–G) climatic scenarios. Suitability is represented as a continuous gradient from unsuitable (dark blue) to optimal (dark red). A CORINE land cover mask has been applied to exclude areas unlikely to be colonized. Future projections are shown for two emission scenarios across three time periods: RCP 4.5 for 2041–2060 (B), 2061–2080 (C), and 2081–2100 (D); and RCP 8.5 for 2041–2060 (E), 2061–2080 (F), and 2081–2100 (G).

Elevation shift of the medium and high suitable areas is extremely high and rapid (+414 m by the mid-century; Table 3.1).

Complementing the habitat suitability maps, the binary maps illustrate the simple presence/absence probability for the species (Figure 3.11), with the threshold calculated using the Sensitivity Specificity Equality (SES; Section 2.4.1) and resulted in a value of 0.79 (Table 3.5). Red areas denote predicted presence, while grey areas indicate absence, with the underlying Digital Terrain Model (DTM) providing topographic context.

A complete disappearance is expected under the business-as-usual RCP8.5 scenario. This evident decline is partially explained by the particularly high threshold that the program identifies for the species.



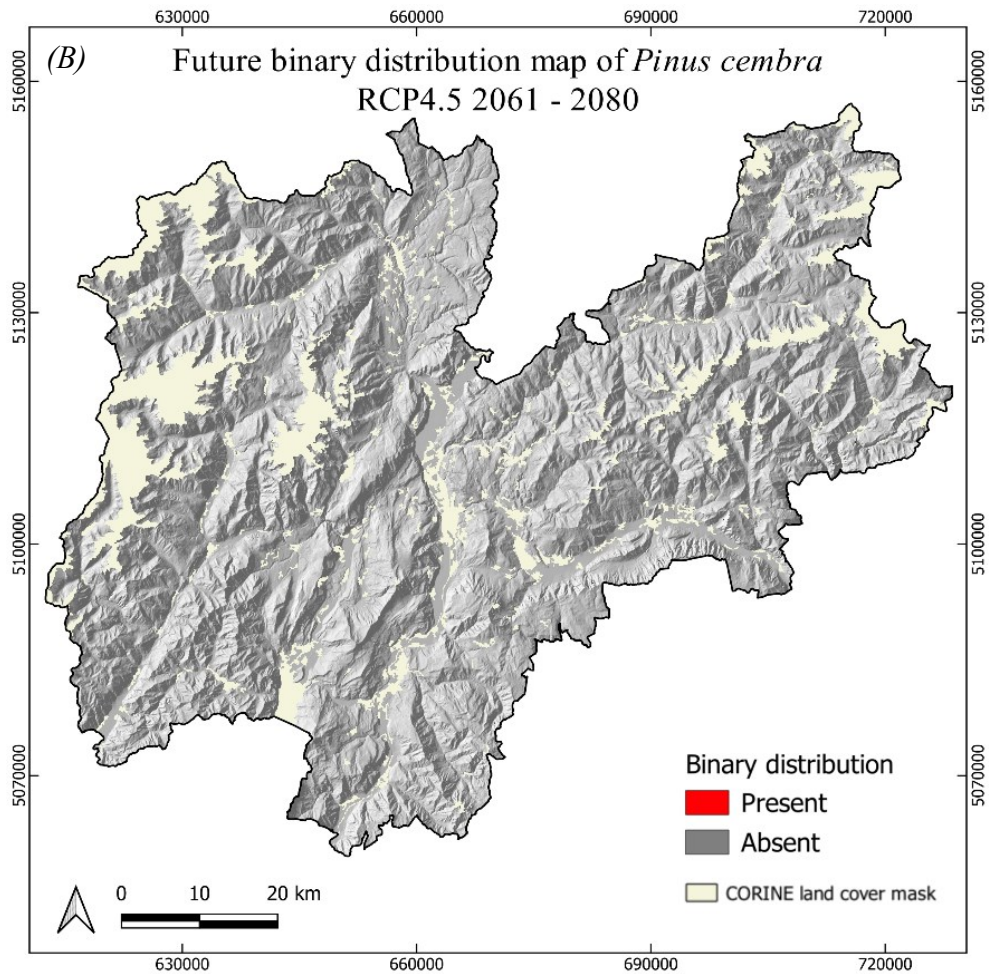


Figure 3.11. Binary distribution maps of *Pinus cembra* under present (A) and one future (B) climatic scenarios. Red areas indicate predicted presence, while grey areas represent absence and simultaneously display the underlying Digital Terrain Model (DTM) to provide topographic context. With this high threshold (0.79) the *Pinus cembra* is projected to disappear by the decades 2061 – 2080.

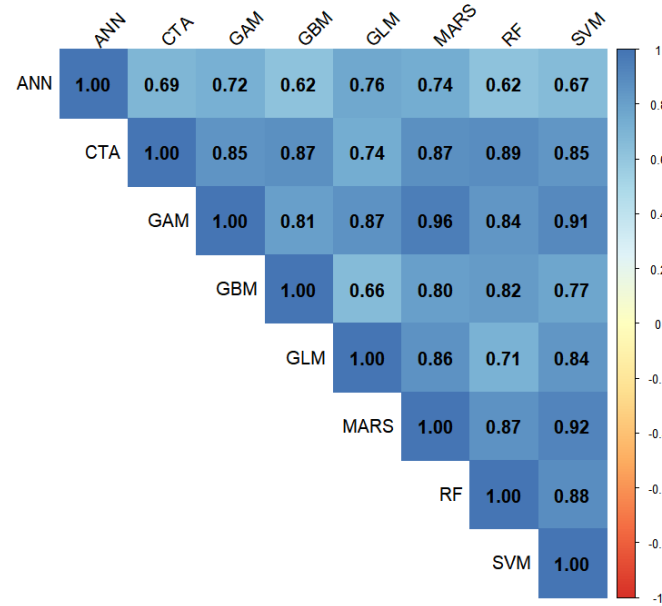
The individual algorithms contributing to the *Pinus cembra* ensemble model demonstrated a robust and reliable performance. An analysis of the evaluation metrics reveals excellent discriminative ability across the suite of models, with a mean AUC of 0.95, a mean Cohen's Kappa of 0.78, a proportion of correct predictions of 0.91 and a calibration of 0.72 (Table 3.5). Random Forest (RF) consistently emerged as the top-performing algorithm, achieving the highest scores for both AUC (0.98) and Kappa (0.89). A more varied result was observed in model calibration. Although most algorithms were well-calibrated, the Generalized Boosted Regression Model (GBM) returned a severe negative calibration score of -0.33. This indicates that while GBM has strong discriminative power (AUC = 0.94), its probability outputs are systematically distorted.

Table 3.5. Performance evaluation of the eight individual algorithms comprising the ensemble model for *Pinus cembra*. The table displays key metrics including the Area Under the Curve (AUC), omission rate, sensitivity, specificity, Cohen's Kappa, and a calibration index. All algorithms were successfully run and retained for the final ensemble (Kept model: 5/5 repetitions).

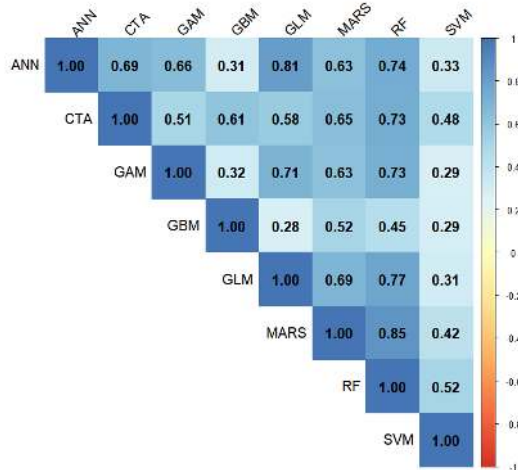
Algorithm evaluation	Threshold	AUC	Omission rate	Sensitivity	Specificity	Prop correct	Cohen's Kappa	Calibr.	Kept model
RF	0.69	0.98	0.06	0.94	0.94	0.94	0.89	0.91	5
GLM	0.81	0.95	0.10	0.90	0.90	0.90	0.70	0.79	5
ANN	0.75	0.89	0.13	0.93	0.81	0.87	0.74	0.92	5
GAM	0.85	0.95	0.09	0.91	0.91	0.91	0.73	0.84	5
MARS	0.88	0.95	0.09	0.91	0.91	0.91	0.73	0.84	5
SVM	0.78	0.96	0.07	0.93	0.93	0.93	0.85	0.81	5
CTA	0.79	0.94	0.10	0.90	0.90	0.90	0.80	0.95	5
GBM	0.77	0.94	0.11	0.89	0.89	0.89	0.78	-0.33	5
Mean	0.79	0.95	0.09	0.91	0.90	0.91	0.78	0.72	-
Std Dev	0.06	0.03	0.02	0.02	0.04	0.02	0.07	0.43	-

The correlation between the spatial predictions of the eight Species Distribution Model (SDM) algorithms was analysed for the present day and for six future scenarios (Figure 3.12, A – G). Under present-day conditions, the algorithms show a high degree of agreement. Most pairwise correlations are strong and positive, with many exceeding 0.80. For example, the correlation between GAM and MARS is 0.96, and between MARS and SVM is 0.92. This agreement decreases progressively in future projections. The decline is more pronounced for scenarios further in the future and is most severe under the high-emissions RCP8.5 scenario. For instance, the correlation between GAM and GBM drops from 0.81 in the present-day model to -0.12 by 2081-2100 under RCP4.5, and to -0.18 in the same period under RCP8.5. By the end of the century under RCP8.5, many algorithm pairs show weak or even negative correlations.

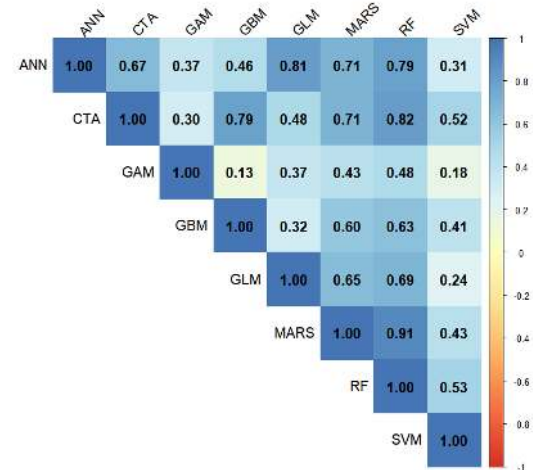
(A) Correlation Matrix of SDM Algorithms for *Pinus cembra* present



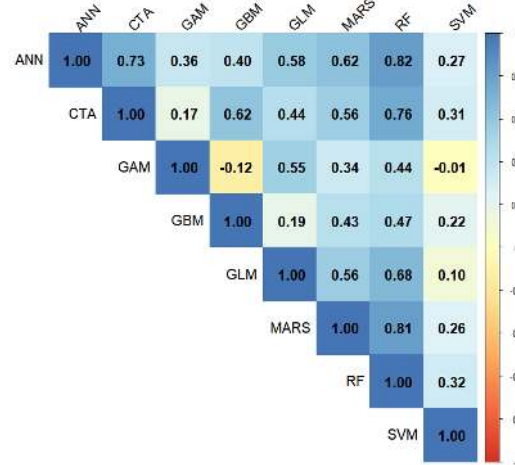
(B) *Pinus cembra* RCP4.5 2041 - 2060



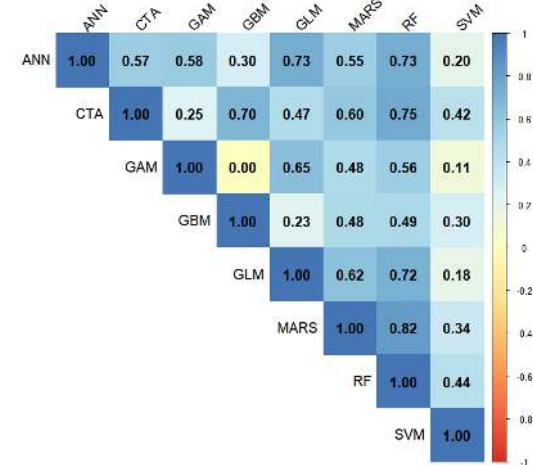
(C) *Pinus cembra* RCP4.5 2061 - 2080



(D) *Pinus cembra* RCP4.5 2081 - 2100



(E) *Pinus cembra* RCP8.5 2041 - 2060



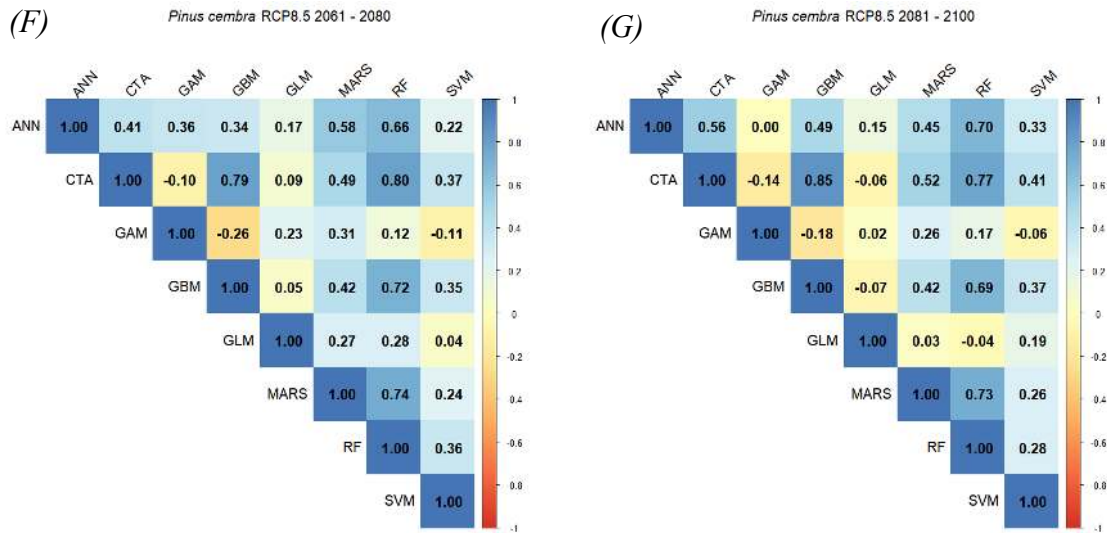


Figure 3.12. Pairwise correlation matrix of present predictions from the eight individual algorithms used in the ensemble model for *Pinus cembra*. The values represent the Pearson correlation coefficient between the continuous habitat suitability predictions of each algorithm pair. The colour scale indicates the strength of the correlation, with dark blue representing high positive correlation (strong agreement) and red representing high negative correlation (strong disagreement).

To assess the robustness of the ensemble predictions generated by the SSDM package, uncertainty maps were created for each scenario, illustrating the between-methods variance for the current and future distribution of *Pinus cembra* (Figure 3.17).

For the current distribution, model agreement is highest (low uncertainty) in core habitats and clearly unsuitable low-elevation areas. The greatest disagreement among algorithms is found at the transitional margins of the species' range, with a maximum variance value of 0.176. When projecting into the future (RCP4.5, 2061–2080), the pattern of uncertainty shifts. The maximum level of disagreement between models is notably lower, with the peak variance decreasing to 0.098. This reduction suggests that as climatic conditions become increasingly unfavourable, a stronger consensus emerges among the algorithms in predicting widespread habitat unsuitability. While the peak disagreement is lower, the spatial extent of moderate uncertainty becomes concentrated in the few remaining high-elevation zones where models diverge on the precise location of potential future refugia.

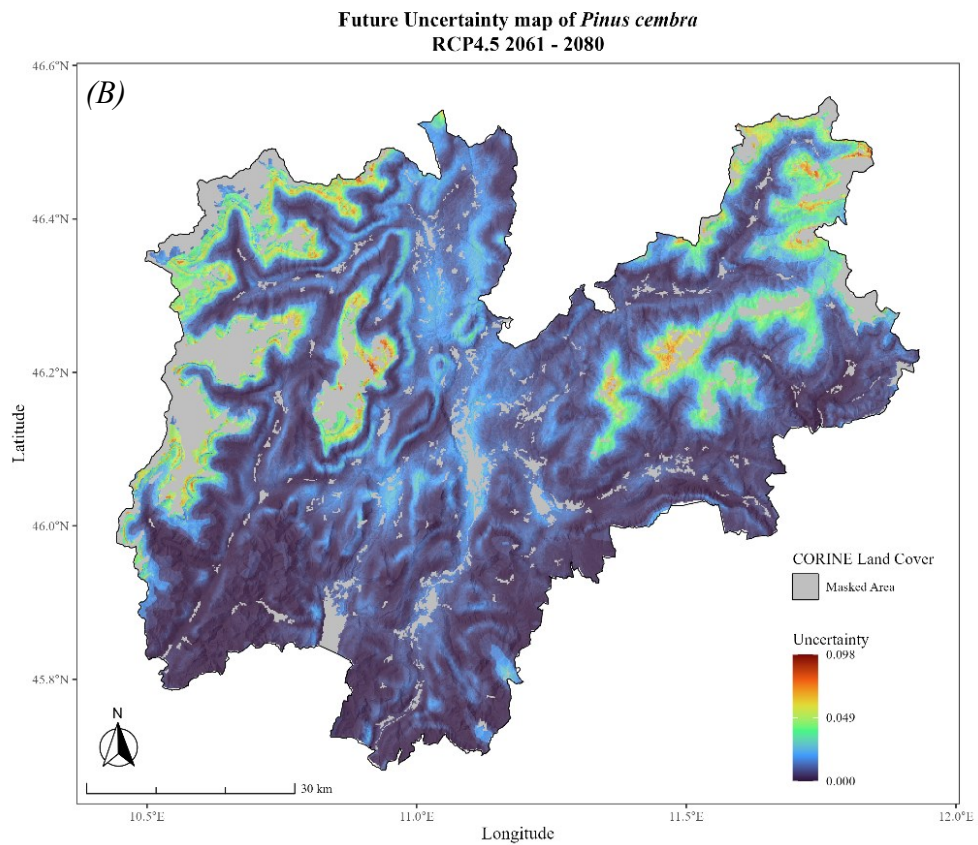
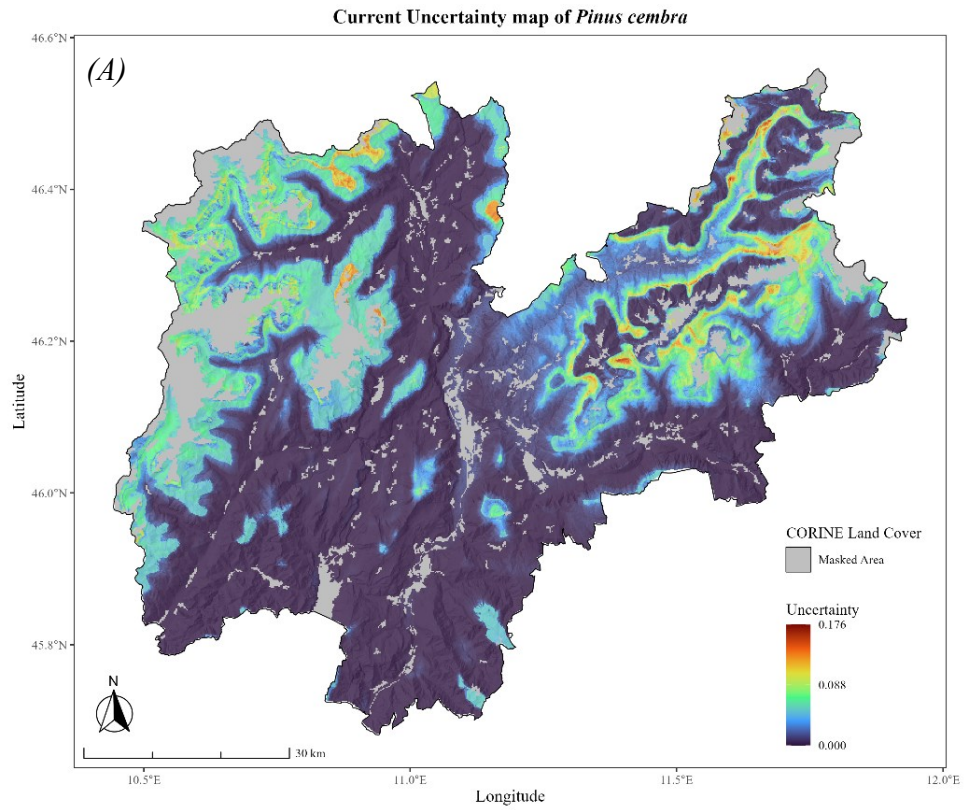
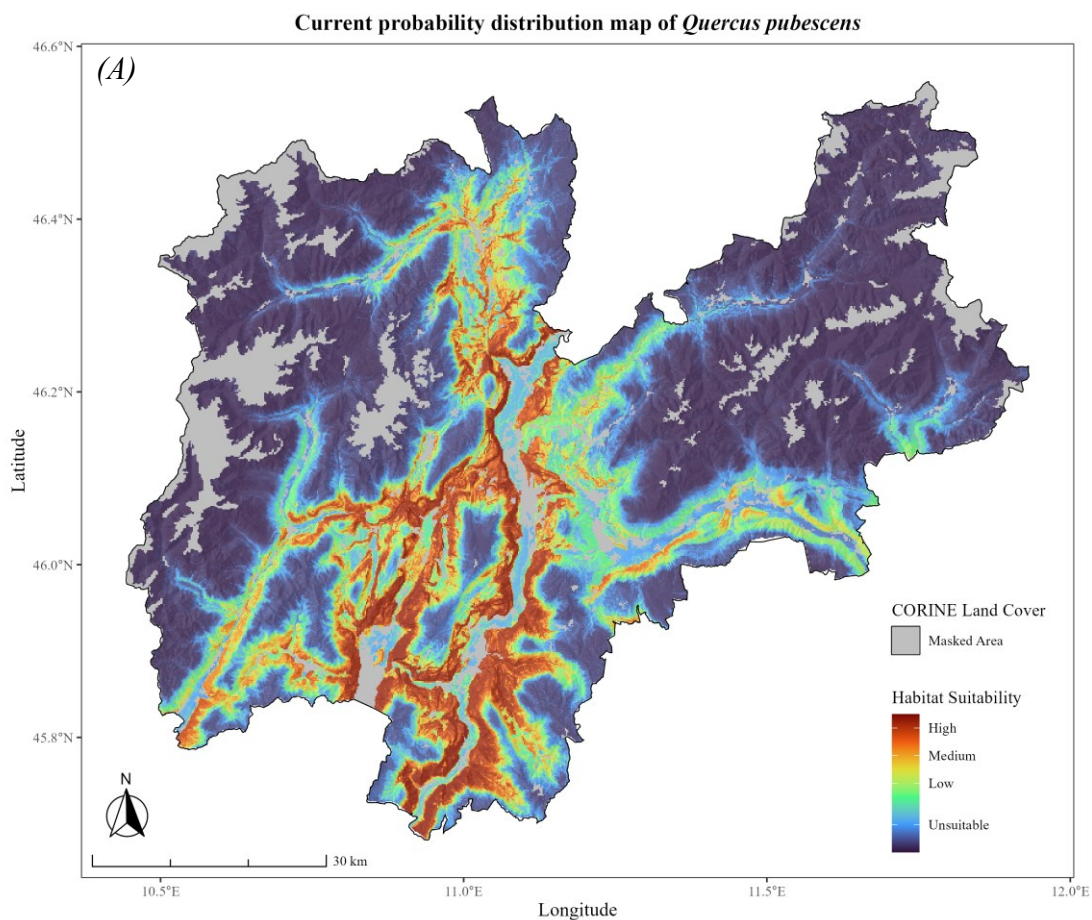


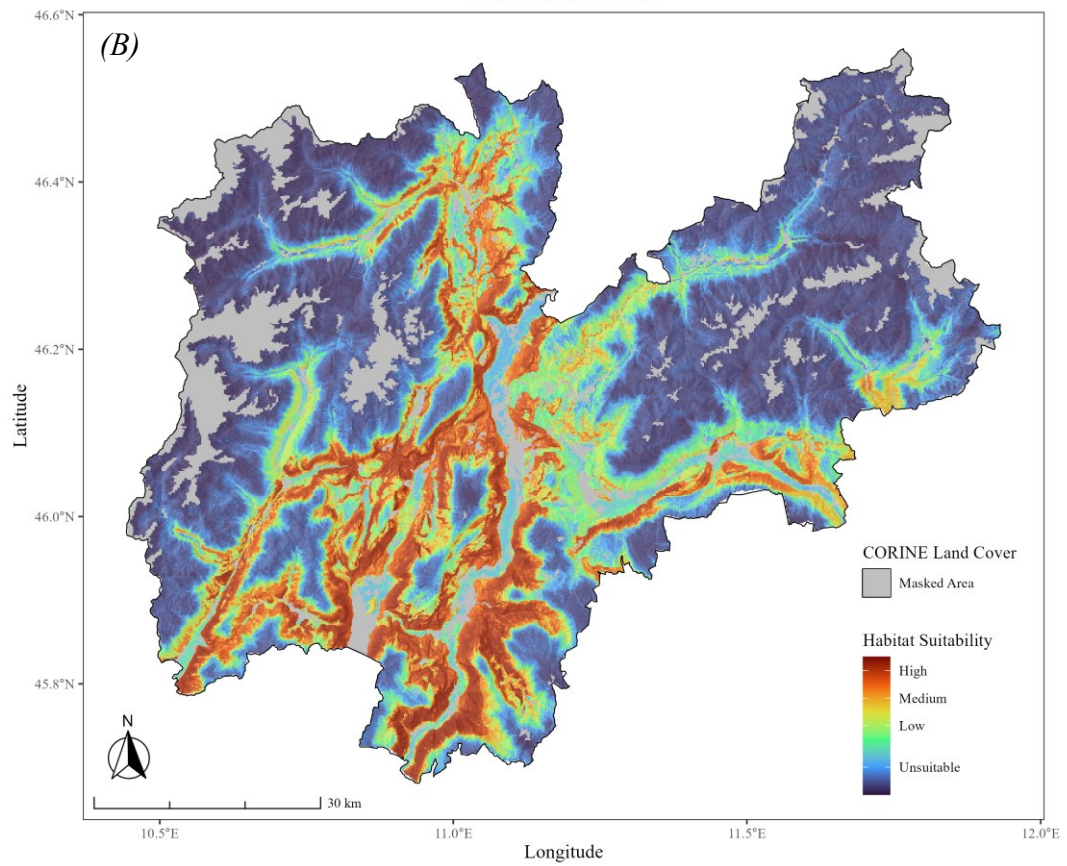
Figure 3.13. Uncertainty of the Ensemble Species Distribution Model for *Pinus cembra*. The maps illustrate the between-algorithm variance for the present (A) and a future scenario (B; RCP4.5, 2061–2080). Warmer colours indicate higher disagreement among the models. The maximum observed variance is 0.176 in the present map and decreases to 0.098 in the future projection, reflecting a shift in model consensus as climatic conditions change.

3.3.2 *Quercus pubescens*

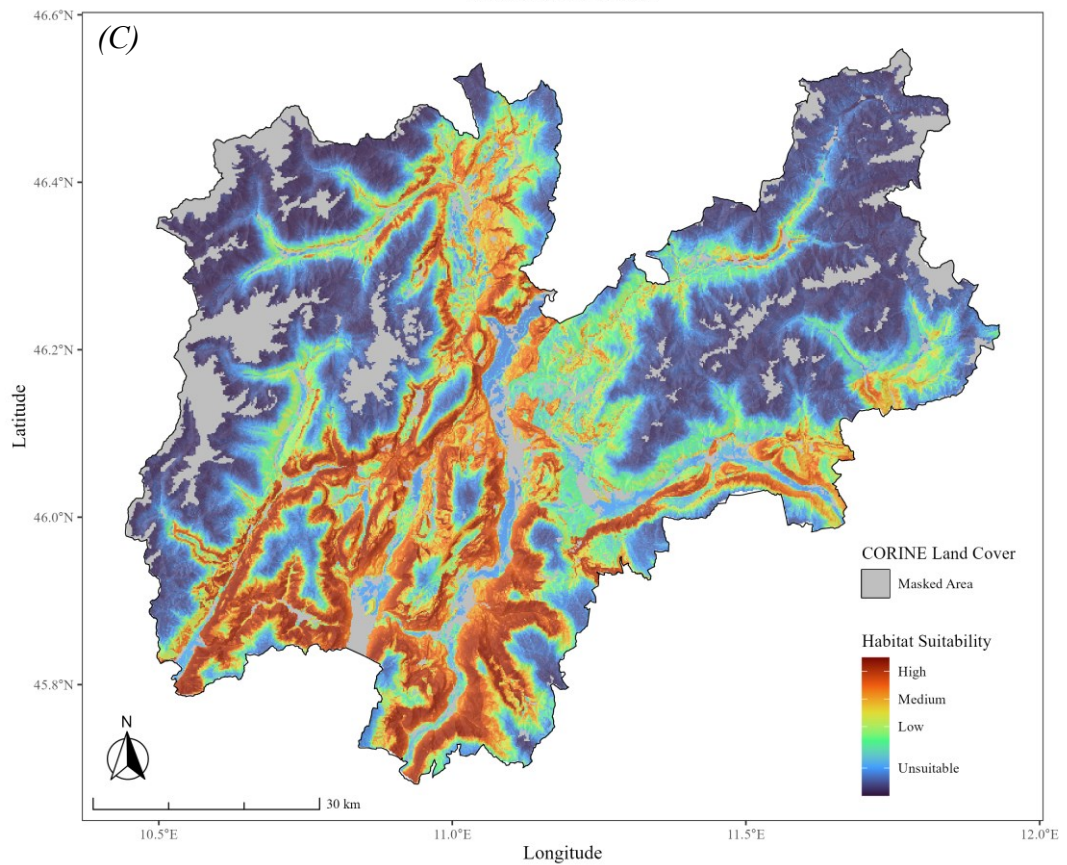
The habitat suitability maps for the downy oak indicate that this thermophilous species is projected to be a significant beneficiary of future climate change in the region. Currently, its optimal- and medium-suitability areas (514 and 379 km² respectively) are largely confined to the low-elevation valley floors (Figure 3.14, A). Under all future scenarios, a notable expansion of suitable habitat is projected (Figure 3.14, B – G). This change is characterized by a significant upward altitudinal shift, with high-suitability zones expanding from the valley floors to occupy the mid-elevation slopes that are currently sub-optimal or marginal. For RCP4.5 scenario in 2061 – 2080 is expected an increase of 57.8% for the high-suitability areas, +99.0% for medium-suitability areas and +48% for low-suitability areas. This trend of habitat expansion becomes progressively more pronounced over time and is substantially more rapid and extensive under the high-emission RCP8.5 pathway. By the end of the century for both emission scenarios, optimal conditions for downy oak are projected to dominate much of the region's valleys, included the Inner-alpine ones like Fiemme, Fassa and Sole valleys.



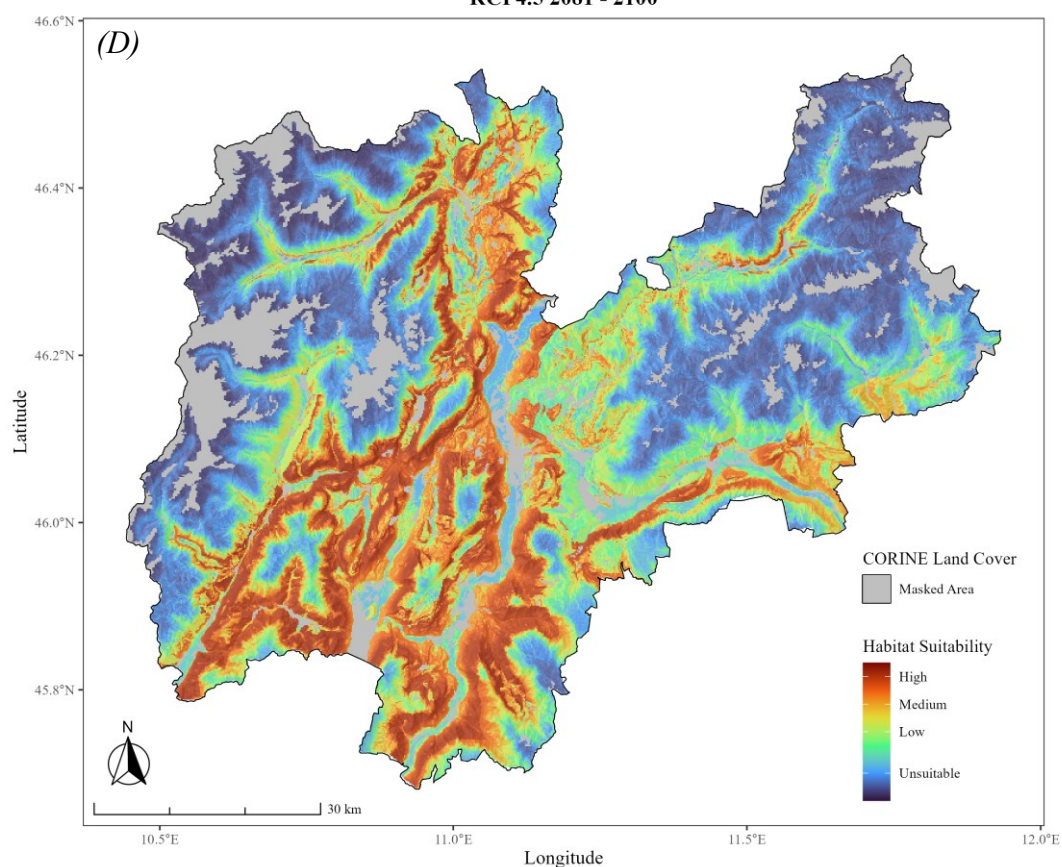
Future probability distribution map of *Quercus pubescens*
RCP4.5 2041 - 2060



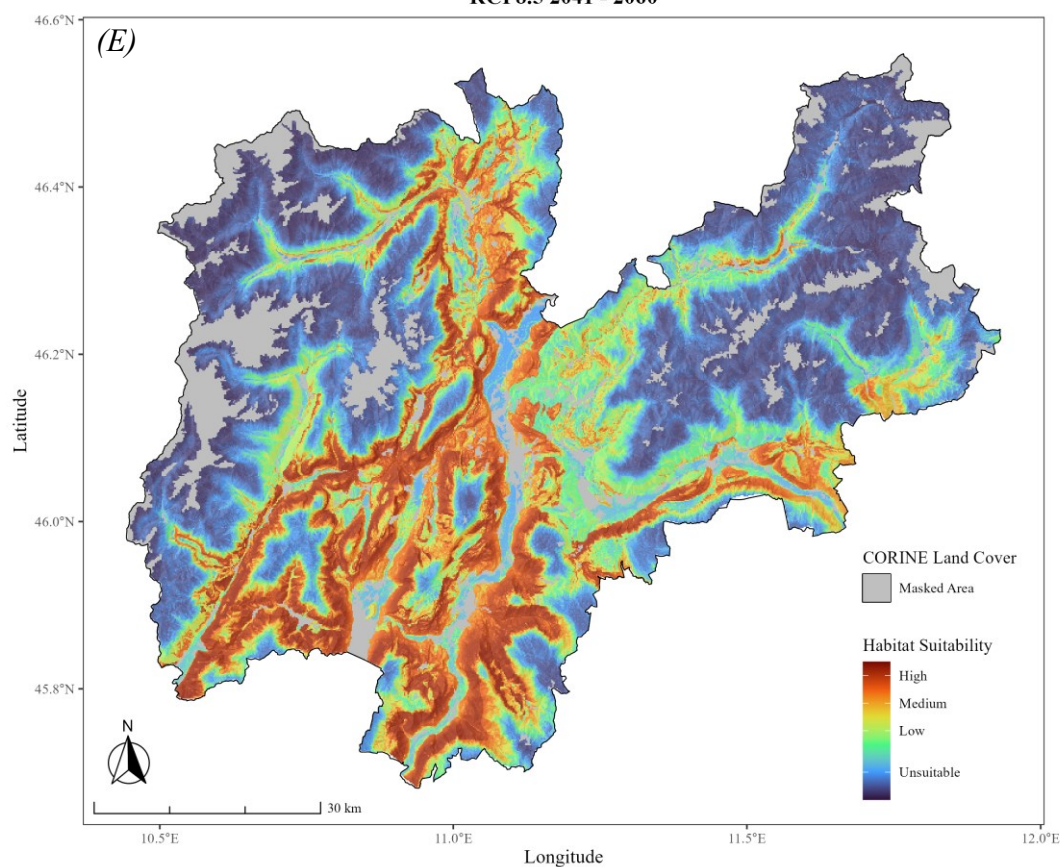
Future probability distribution map of *Quercus pubescens*
RCP4.5 2061 - 2080



Future probability distribution map of *Quercus pubescens*
RCP4.5 2081 - 2100



Future probability distribution map of *Quercus pubescens*
RCP8.5 2041 - 2060



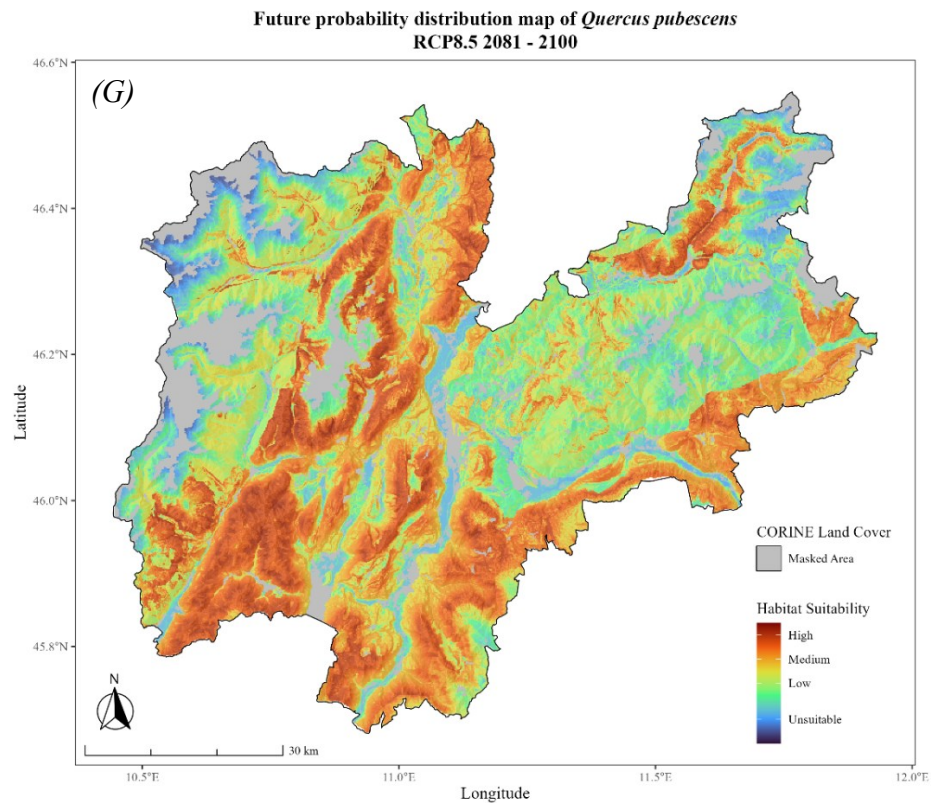
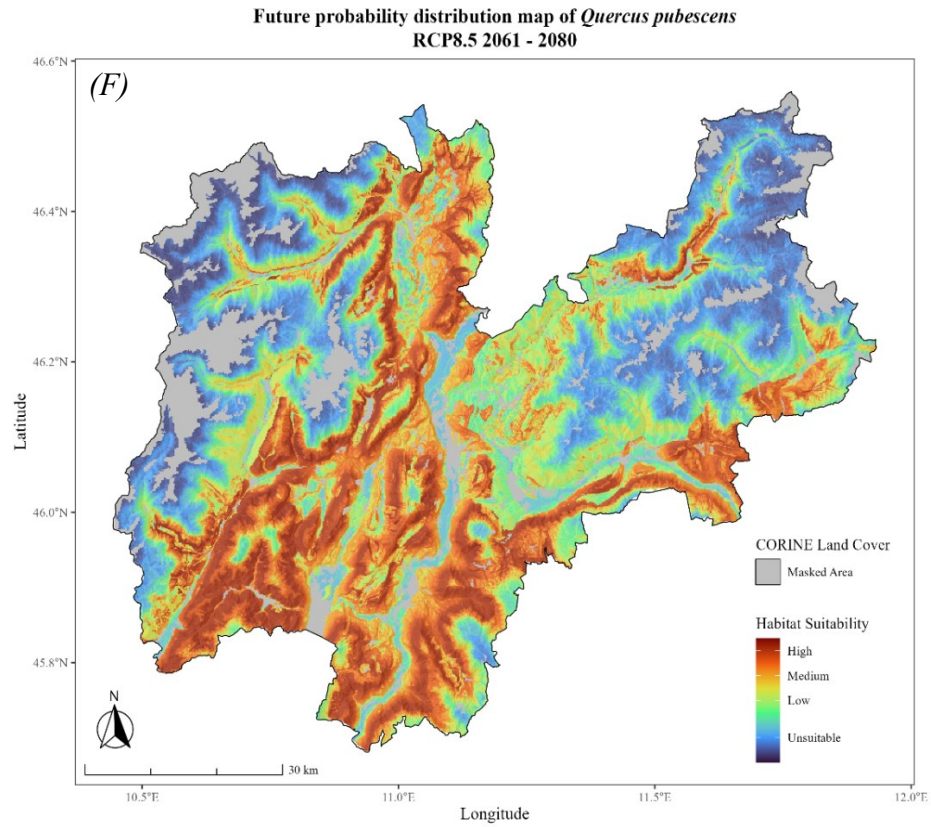
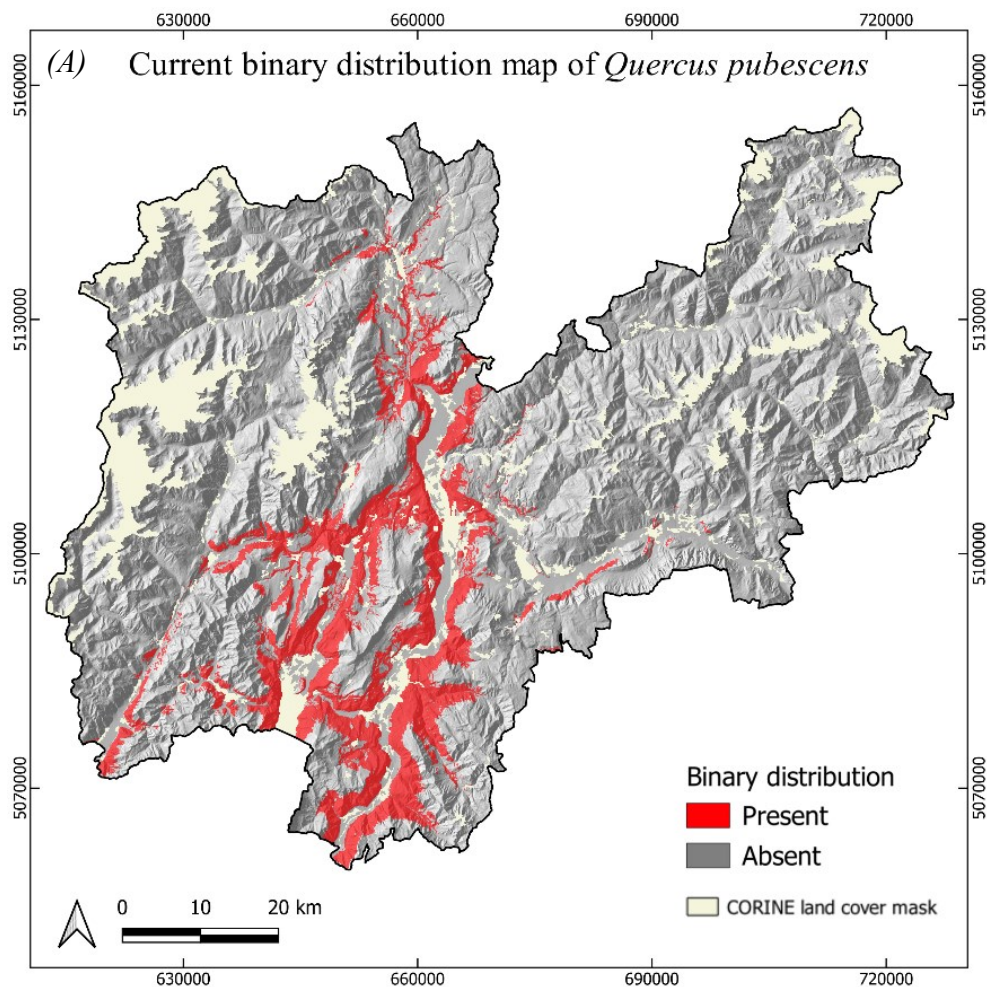


Figure 3.14 Habitat suitability maps of downy oak under present (A) and future (B–G) climatic scenarios. Suitability is represented as a continuous gradient from unsuitable (Unsuitable, dark blue) to optimal (dark red). A CORINE land cover mask is applied in order to exclude unlikely colonizable areas (see Section 2.4.1 for the classes). Future projections are shown for two emission scenarios across three time periods: RCP4.5 for 2041–2060 (B), 2061–2080 (C), and 2081–2100 (D); and RCP8.5 for 2041–2060 (E), 2061–2080 (F), and 2081–2100 (G).

Under the intermediate RCP4.5 scenario, the projected upward elevation shift for downy oak is +89 m by mid-century and +226 m by the end of the century (Table 3.1). These shifts are projected to be more than double under the business-as-usual RCP8.5 scenario, reaching +185 m and +520 m, respectively.

To translate the continuous habitat suitability projections into binary presence/absence maps, a threshold of 0.70, calculated using the SES method, was applied. The resulting map for the current period shows the predicted presence of the downy oak is largely confined to the low-elevation valley floors and sun-exposed lower slopes (Figure 3.15). The projection for the 2061–2080 period under the RCP4.5 scenario reveals a significant expansion of the species' potential range. This expansion is characterized by a distinct upward altitudinal shift, with the predicted presence extending further up the valley slopes and into adjacent areas that are currently classified as unsuitable. This result provides a clear spatial representation of the gains in suitable area for *Quercus pubescens*, reinforcing the finding that it is a likely beneficiary of future climatic warming in the region.



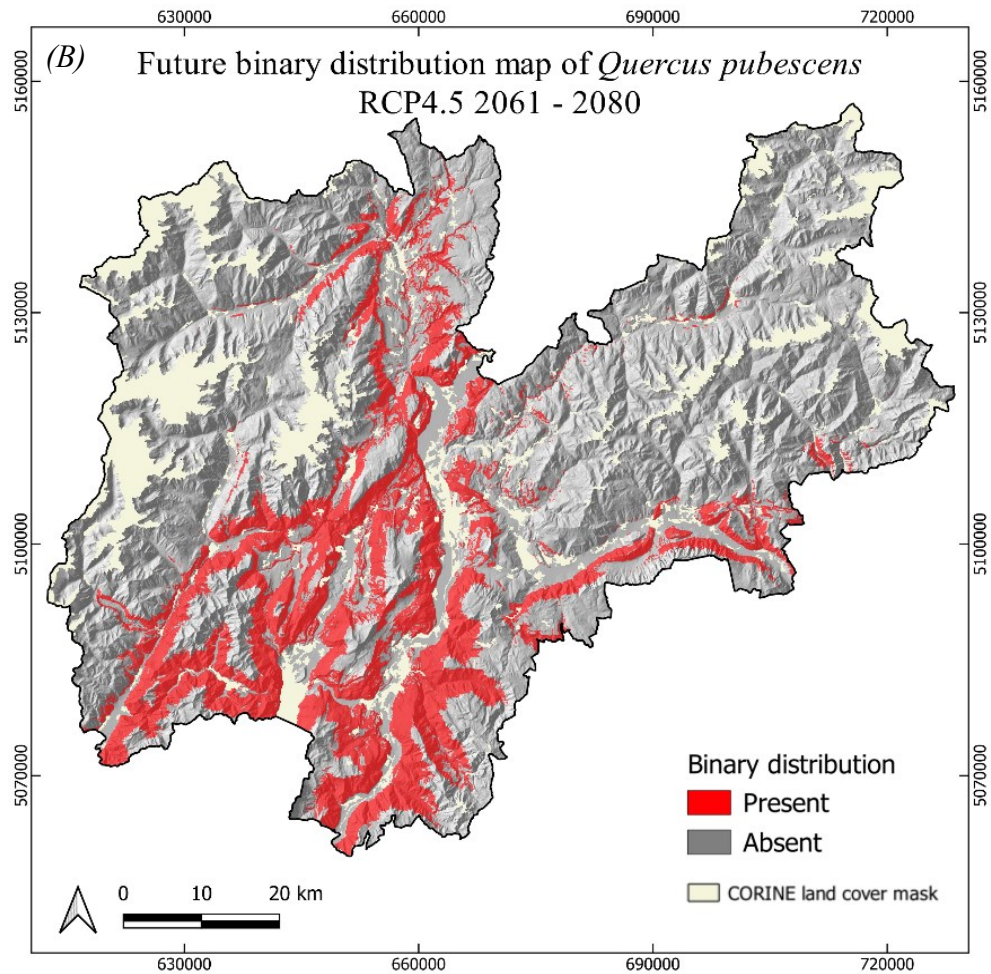


Figure 3.15. Binary distribution maps of *Quercus pubescens* under present (A) and future (B–G) climatic scenarios. Red areas indicate predicted presence, while grey areas represent absence and simultaneously display the underlying Digital Terrain Model (DTM) to provide topographic context. Future projections refer to two emission scenarios across three time periods: RCP 4.5 for 2041–2060 (B), 2061–2080 (C), and 2081–2100 (D); and RCP 8.5 for 2041–2060 (E), 2061–2080 (F), and 2081–2100 (G). Even with a relatively high threshold (0.70), *Quercus pubescens* is projected to increase their range by the year 2080.

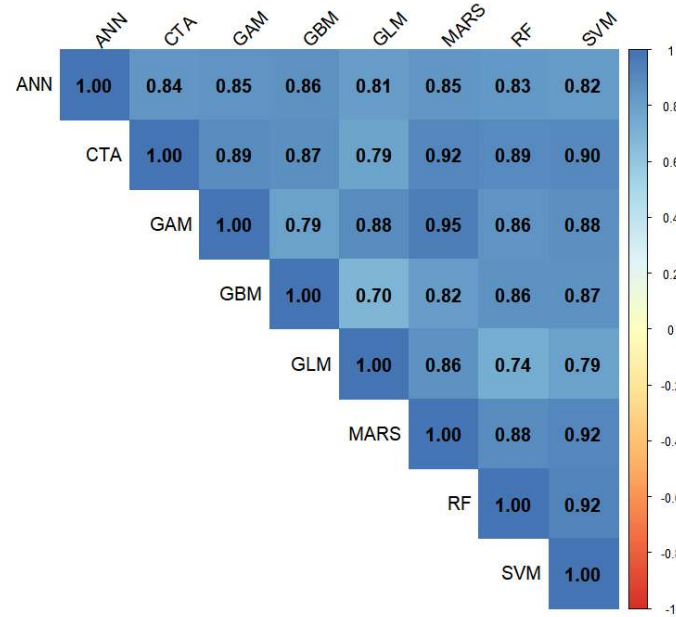
An evaluation of the individual algorithms reveals a high overall quality for the downy oak ensemble model (Table 3.6). The strength of the ensemble is supported by a mean AUC of 0.93 and a mean Cohen's Kappa of 0.71, indicating excellent discrimination and substantial agreement with observations, respectively (Table 3.6). The performance of the individual models varied. Random Forest (RF) stood out as the most consistently accurate algorithm for this species too, achieving the highest scores for both AUC (0.96) and Kappa (0.81), coupled with a strong calibration index of 0.90. In stark contrast, the Generalized Boosted Regression Model (GBM) presented a significant caveat. While its discriminative ability was high (AUC = 0.94), its severely negative calibration score (-0.29) renders its raw probability outputs untrustworthy.

Table 3.6. Performance evaluation of the eight individual algorithms comprising the ensemble model for *Quercus pubescens*. The table displays key metrics including the Area Under the Curve (AUC), omission rate, sensitivity, specificity, Cohen's Kappa, and a calibration index. All algorithms were successfully run and retained for the final ensemble (Kept model: 5/5 repetitions).

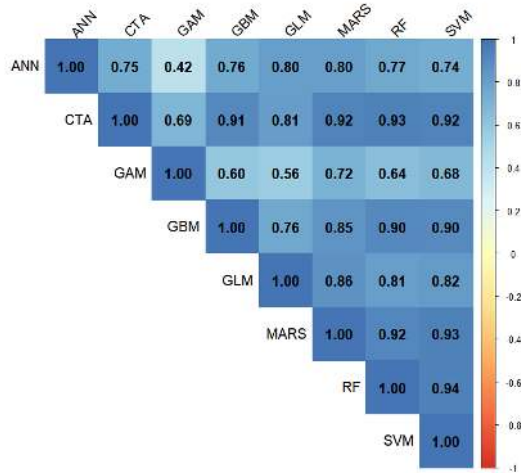
Algorithm evaluation	Threshold	AUC	Omission rate	Sensitivity	Specificity	Prop correct	Cohen's Kappa	Calibr.	Kept model
ANN	0.60	0.86	0.16	0.92	0.75	0.84	0.67	0.93	5
CTA	0.64	0.91	0.14	0.86	0.86	0.86	0.72	0.95	5
GAM	0.81	0.95	0.11	0.89	0.89	0.89	0.69	0.78	5
GBM	0.52	0.93	0.14	0.86	0.86	0.86	0.71	-0.29	5
GLM	0.80	0.93	0.13	0.87	0.87	0.87	0.63	0.79	5
MARS	0.85	0.94	0.12	0.88	0.88	0.88	0.64	0.81	5
RF	0.65	0.96	0.09	0.91	0.91	0.91	0.81	0.90	5
SVM	0.77	0.95	0.11	0.89	0.89	0.89	0.77	0.82	5
ESDM Mean	0.70	0.93	0.13	0.88	0.86	0.87	0.71	0.71	5
Std Dev	0.12	0.03	0.02	0.02	0.05	0.02	0.06	0.41	0

For *Quercus pubescens*, the predictions from all eight algorithms show very high positive correlation under present-day conditions, with most pairwise correlations exceeding 0.85 (e.g., GAM and MARS at 0.95; Figure 3.16). In future projections, a decline in overall agreement is observed, again being most pronounced in the late-century RCP8.5 scenario. However, a key pattern for this species is that the decrease in concordance is disproportionately driven by the GAM. While most other algorithms remain highly correlated with each other, their agreement with GAM diminishes significantly. This is best illustrated in the RCP8.5 2081-2100 scenario: the correlation between many model pairs like CTA and GBM remains extremely high at 0.90. In stark contrast, the correlation between GAM and most other models collapses, becoming strongly negative in several cases (e.g., GAM vs. GLM at -0.34; GAM vs. CTA at -0.17).

(A) Correlation Matrix of SDM Algorithms for *Quercus pubescens* present



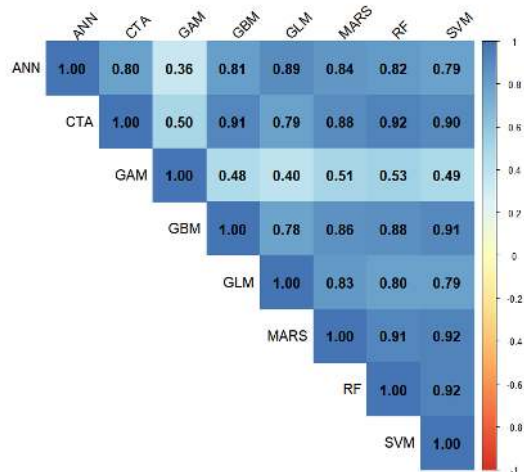
(B) *Quercus pubescens* RCP4.5 2041 - 2060



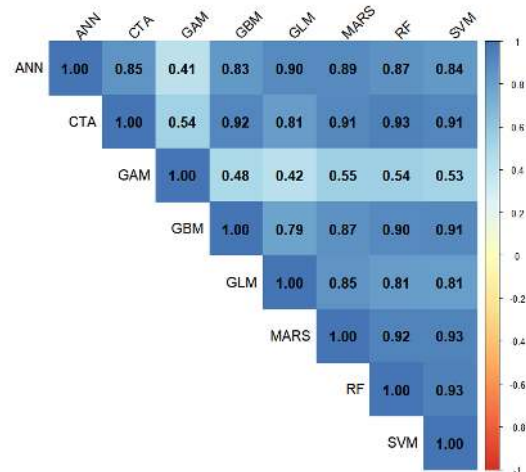
(C) *Quercus pubescens* RCP4.5 2061 - 2080



(D) *Quercus pubescens* RCP4.5 2081 - 2100



(E) *Quercus pubescens* RCP8.5 2041 - 2060



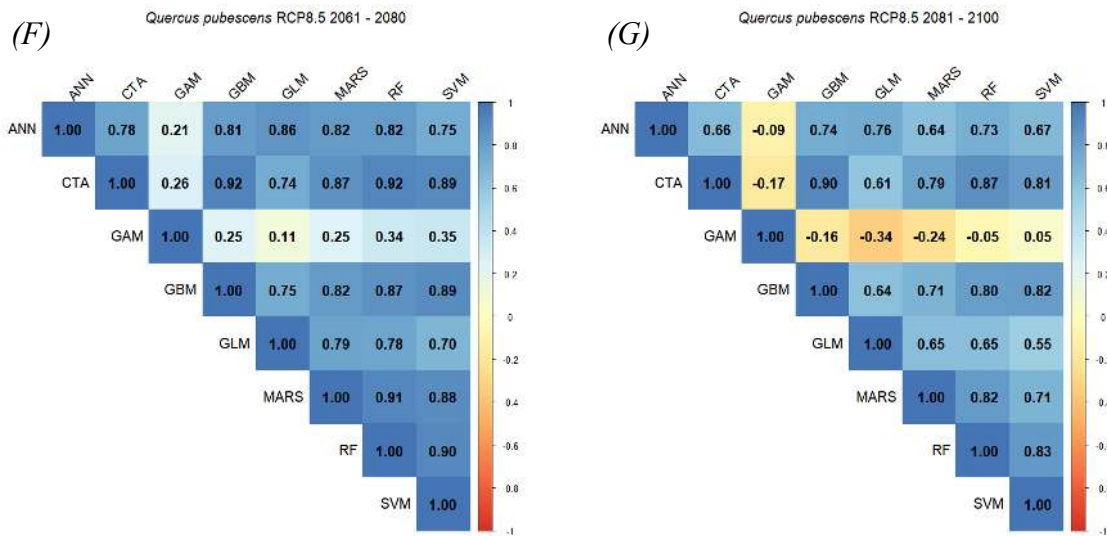


Figure 3.16. Pairwise correlation matrix of present predictions from the eight individual algorithms used in the ensemble model for *Quercus pubescens*. The values represent the Pearson correlation coefficient between the continuous habitat suitability predictions of each algorithm pair. The colour scale indicates the strength of the correlation, with dark blue representing high positive correlation (strong agreement) and red representing high negative correlation (strong disagreement).

The spatial distribution of model uncertainty for *Quercus pubescens* reveals a distinct altitudinal pattern (Figure 3.17, A – B). Under current conditions, areas of lowest uncertainty (i.e., highest model agreement) are found in the high-elevation alpine areas. Conversely, the greatest uncertainty is concentrated in the low-elevation floors of the main valleys and in clear bands at mid-elevations (Figure 3.17, A). These transitional zones, which represent the current lower and upper limits of the species' core habitat, show a maximum uncertainty value of 0.185. In the future projection for 2061–2080 (RCP4.5), this pattern shifts. The maximum uncertainty value across the landscape decreases slightly to 0.168 (Figure 3.17, B). Spatially, the high-uncertainty bands are no longer located at the same mid-elevations; instead, they have moved noticeably upwards in altitude.

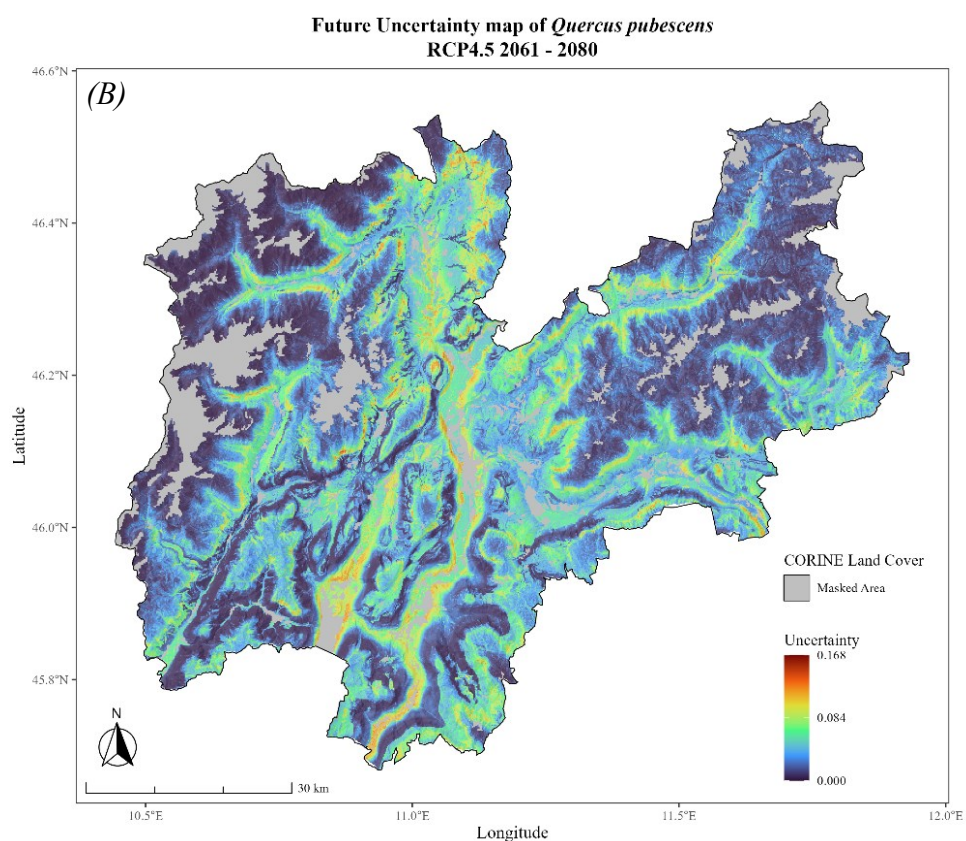
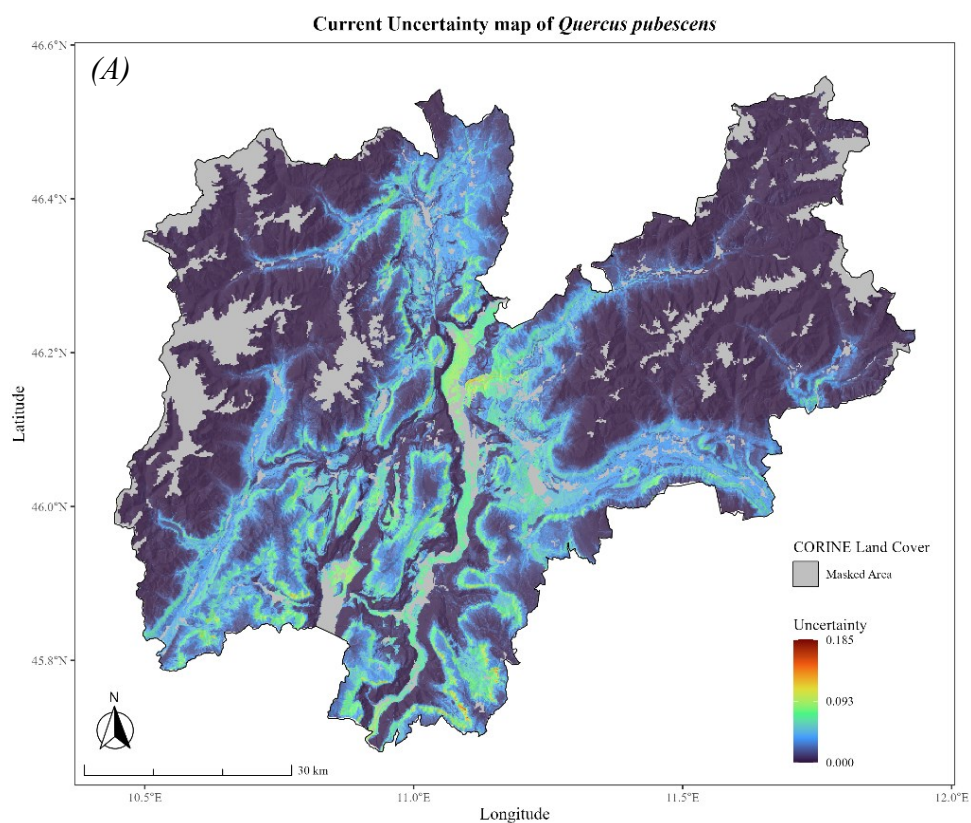


Figure 3.17 Uncertainty of the Ensemble Species Distribution Model for *Quercus pubescens*. The maps illustrate the between-algorithm variance for the present (A) and a future scenario (B; RCP4.5, 2061–2080). Warmer colours indicate higher disagreement among the models. The maximum observed variance is 0.185 in the present map and decreases to 0.168 in the future projection, reflecting a growing consensus on the suitability of mid-elevation habitats as the climate warms.

4 DISCUSSION

This study aimed to test and develop a methodology for generating high-resolution maps of current and future potential distributions of 23 dominant tree species in the Autonomous Province of Trento, producing species richness maps via Stacked Species Distribution Modelling (SSDM) and evaluating model performance and computational demands. This research paves the way for further improvements. In the following paragraphs, both ecological and methodological findings, as well as practical applications and limitations, will be discussed.

4.1 Interpretation of Distributional Changes

We found that changes in climatic conditions caused by greenhouse-gas emissions will substantially influence the distribution of the province's major forest tree species. Depending on the emission path taken, we could expect a limited impact (RCP4.5) or a substantial and strong one (RCP8.5). Mean upslope shift of medium-to-high suitability areas is 265 m (RCP4.5, 2081–2100), and ≈ 540 m under RCP8.5 scenario (Table 3.1). The rate of change in the RCP4.5 scenario – approximately 41 m per decade – may be slow enough for tree species to migrate and track their shifting climatic niche (Parolo & Rossi, 2008). In contrast, the rapid changes projected under the RCP8.5 scenario would likely outpace the adaptive capacity of these species, given the slow migration rates of tree species (Vacek et al., 2023).

The models predicted a decline in the ecological suitability in the lower altitudinal range of species, particularly for the two microthermal species *Picea abies* and *Pinus cembra*. The Swiss stone pine is in a “summit trap” scenario, with the velocity of climate change outpacing the species' ability to migrate upwards, and available high-elevation areas not likely colonizable because of the shallow soil (Figure 3.11). The species exhibits a particularly high value of upward shift (+414 m by mid-century; Table 3.1), which can be attributed to the severe reduction of suitable habitat at its lower margins (Figure 3.11; B – G). Other threatened species are *Abies alba*, *Fraxinus excelsior* and *Pinus sylvestris*, consistently with prediction at European scale did by Dyderski et al., 2025.

Conversely, thermophilous and generalist species such as *Quercus ilex*, *Quercus pubescens*, *Ostrya carpinifolia*, and *Fraxinus ornus* are projected to thrive. This trend is consistent with findings from another study (Noce et al., 2023). These species may colonize

mid- to high-elevations as climate warming progresses, although they are potentially constrained by soil, competition, topographic barriers, and dispersal limitation.

4.2 Species Richness Patterns and Community-Level Insights

The species richness analysis is based only on the 23 modelled forest tree species and therefore represents just a potential "tree-specific richness" rather than the total floristic diversity of the study area. While this metric does not account for other vegetation components, such as shrubs, herbaceous and allochthonous species, it can serve as an indicator of how the composition and co-occurrence of dominant forest species may shift under future climate scenarios. Moreover, it can help to identify high-richness areas and biodiversity hotspots that can be protected for conservation purposes.

At the community level, the SSDM projects a minor decline in mean tree species richness across the province for the intermediate scenario, but this trend is dramatically accelerated under the business-as-usual scenario. The mean species richness is projected to drop by the end of the century from 3.11 to 2.88 (intermediate scenario) and to 2.20 (high-emission scenario; Figure 3.9). This decline is not uniform and reflects a fundamental restructuring of forest communities. Spatially, the models predict a contraction of current high-richness zones at mid-elevations and a significant expansion of low-richness areas, particularly under the business-as-usual future scenario.

4.3 Environmental Variable Selection and Importance

The reliability and interpretability of the final model outcomes are critically dependent on the importance of the selected variables, encompassing climatic, topographic, and soil-related factors. Among these, the inclusion of elevation and aspect in forest tree species distribution modelling presented several key issues. Although elevation is sometimes used as a predictor variable in various Species distribution modelling studies (Hof et al., 2012), it is not a direct ecological driver of plant species distribution. Elevation functions primarily as a proxy for climatic conditions (especially temperature); thus, including elevation alongside direct temperature predictors risks redundancy and can constrain future projections if elevation is treated as static. Instead, temperature features are the main limiting factor that makes elevation an apparent indicator for tree distribution. If elevation is included as a static predictor based on present-day conditions, future projections become inadvertently limited by these current altitudinal predictions, despite the negligible direct

impact of elevation (within reasonable ranges) on tree distribution due to factors like gravity or air density. Therefore, since its inclusion can lead to misleading interpretations regarding potential future range shifts, it was ultimately excluded from the analysis.

Similarly, the aspect variable introduces a methodological challenge due to its circular nature. Since its 1-to-360-degree range means that extremes represent the same northern orientation, it can be misinterpreted by modelling algorithms. Therefore, this variable was substituted with the Heatload Index (HLI), a more robust predictor for species distribution that directly accounts for potential solar radiation and slope (Section 2.3.3).

This study did not assess the presence of potential collinearity (i.e. a reciprocal dependency) among predictor variables for instance by using tests such as the Kendall's rank correlation coefficient (Puth et al., 2015). Implementing a species-specific variable selection procedure could reduce the issue, but would undermine the standardisation of predictor sets across species, which is essential for aggregating individual models (i.e., stacking) and producing internally consistent species richness maps.

A crucial aspect of interpreting the results is understanding that a variable's high relative importance does not reveal the direction of the species' response. A predictor can be highly influential because a species is either positively associated with it (i.e., it prefers high values of that variable) or negatively associated with it (i.e., it avoids them). For instance, while topographic ruggedness is an important predictor for both manna ash (*Fraxinus ornus*) and sessile oak (*Quercus petraea*), the ecological relationship is opposite. The manna ash often colonizes steep, rocky, and topographically complex terrain, suggesting a positive correlation. In contrast, the sessile oak typically thrives on deeper, more stable soils found in less rugged landscapes, implying a negative correlation. Therefore, a comprehensive ecological interpretation that considers the species' known autecology is essential for correctly understanding its habitat requirements as predicted by the model.

The results highlight a clear hierarchy of factors controlling tree species distribution at a regional scale. Consistent with ecological niche theory, macroclimatic variables such as the Mean Annual Precipitation (MAP), the Degree-Days Above 18°C (DDabove18), and the lower temperature limits (Minimum Coldest Month Temperature, MCMT and Degree-Days Below 0°C, DDbelow0; Figure 3.5) act as a first-order filter, defining the climatically suitable envelope for most of the considered species. However, the study reveals the crucial role of topography as a second-order factor that shapes distribution at the local scale within this climatic envelope. The high importance of the Topographic Ruggedness Index (TRI)

and the Topographic Wetness Index (TWI; Figure 3.6) for many other species suggests that microclimate and substrate conditions, as modulated by terrain, are decisive for the species' actual presence. *Ostrya carpinifolia*, for instance, is known as a thermophilous pioneer species that thrives on steep, rocky, and well-drained slopes – conditions perfectly captured by a high TRI value.

A noteworthy finding is the low predictive importance attributed to soil characteristics and geomorphological disturbances like landslides. This does not necessarily imply that these factors are ecologically irrelevant. Additionally, the 50-m spatial resolution used in this study limits the detectability of fine-scale soil and geomorphological heterogeneity: many available soil and disturbance layers are produced at coarser resolutions and require downscaling, which can omit patches of different soil type and composition. It is more likely that at the regional scale of this study, broad climatic and topographic gradients are more significant determinants of species distribution, or that the categorical variables used are not capable of describing the geomorphological processes (including landslides, rockfall, and debris flows) which shape species distribution. For example, a categorical variable like “landslide presence/absence” fails to capture the frequency, intensity, and time from the last disturbance, all of which are critical for ecological succession. A pioneer species might colonize a recent landslide, but this nuanced relationship would not be captured by the model. Additionally, the layers used are often at a coarser resolution than the 50 m of this study – meaning that a downscaling process is necessary that inevitably reduce the data quality.

4.4 Performance and Uncertainty Assessment

Overall performances of the individual ESDMs are deemed good, considering the specific objectives of this study. The use of an ensemble of algorithms (both regression-based and machine learning) mitigates potential failures of any single model, resulting in acceptable mean values for AUC (0.90, Std Dev = 0.04), Cohen's Kappa (0.66, Std Dev = 0.12), proportion of correctly predicted pixels (0.85, Std Dev = 0.06), and Calibration (0.68, Std Dev = 0.03; Table 3.3). These values are in line with another study (Bedair et al., 2023).

Conversely, the specific SSDM metrics require further consideration as the performance in predicting the species composition was moderate. An average error of ~3 species per 50-m cell (Table 3.4) indicates limited accuracy of stacked predictions at the

regional scale and suggests caution when using these outputs for site-level decisions (Pottier et al., 2013). Nevertheless, the systematic decline of mean error across scenarios – particularly under RCP8.5, with a mean value of 1.39 and a Std Dev = 2.04 (Table 3.4) – does not imply improved composition forecasting, but reflects how predictions under all these scenarios diverge from current withheld observations and also reflects the overall species richness decline. Therefore, stacked outputs are most robust only for identifying broad spatial patterns (e.g., potential refugia or relative changes in richness) and should be supported by targeted monitoring and sensitivity analyses before operational use.

To identify the most efficient methodology for modelling 23 species under both current and future climatic conditions, various configurations of the R package SSDM were tested. The development of an organized and well-structured R script, capable of balancing computational effort with the desired scientific outcomes, proved fundamental for this study. The integration of high-resolution raster data, a substantial number of occurrence points across 23 species, and their projection across two climate scenarios in three time periods, collectively demanded a considerable amount of computational effort. Specifically, calibration and projection of the Ensemble Species Distribution Models (ESDMs) required over two weeks on both the Windows computer and the High-Performance Computing (HPC) machine, despite the latter's substantially greater CPU and memory capacity (Section 2.2) – a comparable runtime that reflects limitations in the SSDM package's parallelisation scheme (see below). This modelling phase necessitated multiple repetitions to test diverse setups and to resolve emergent issues throughout the workflow. It was particularly noted that the Random Forest algorithm alone accounted for over 90% of the computational time; however, given its superior performance in evaluation metrics, it was deemed the most reliable and thus retained. This outcome is attributable to the inherent limitations of the SSDM package, which only permits parallelization of either repetitions or algorithms. In the context of the present study, with eight algorithms set for five repetitions, the maximum number of cores effectively utilized by the machine was constrained by one of these parameters (i.e. 8 or 5), rendering the availability of additional cores practically redundant. While the species are currently modelled individually, a significant future improvement could involve parallelizing the modelling process across species, rather than just repetitions or algorithms. This would allow for the full utilization of available computational resources and considerably reduce the overall modelling time. While such an improvement in parallelization necessitates advanced computer coding

skills – and thus fell outside the scope of this particular study – it represents a potential improvement on the workflow.

A different consideration, however, applies to the availability of temporary computer memory (RAM). Particularly during the stacking of individual models and their subsequent projection into future scenarios, a minimum of 150 GB of RAM proved essential, a memory capacity not commonly available outside of dedicated HPC systems.

Uncertainty maps from SSDM outputs highlight greater disagreement among the algorithms at the margins of the high and medium suitability areas, suggesting cautious interpretation in these areas. Future sensitivity analyses should test (a) multiple thresholding rules, (b) alternative stacking algorithms (e.g., probabilistic stacking vs. binary stacking), and (c) explicit dispersal scenarios (no dispersal vs full dispersal vs species-specific dispersal kernels) to quantify projection spread. It is essential to emphasize that outputs represent hypotheses of potential suitability rather than deterministic forecasts, requiring validation and adaptive updating.

Key **uncertainty sources** included:

- 1) Data uncertainty from presence-only datasets. Forest Unit (Ufor) inventories may omit private lands. The Edmund Mach Foundation (FEM) and the iNaturalist data may be spatially clustered and biased toward accessible areas or subject to identification errors;
- 2) Model uncertainty from algorithmic variation and predictor collinearity decisions. While a collinearity test was considered, eventually a uniform predictor set across species was maintained for comparability;
- 3) Climate projection uncertainty – aggregating GCMs/RCMs into a mean scenario reduces variability but conceals range of plausible futures; downscaling errors also contribute.

Comparing the uncertainty patterns between the cold-adapted specialist, *Pinus cembra*, and the thermophilic generalist, *Quercus pubescens*, offers a powerful insight into the challenges of forecasting species' futures. For the warmth-loving downy oak, there is a strong consensus on the direction of its response to climate change: an upward expansion in altitude. The uncertainty, which is concentrated at the leading edge of this expansion and largely driven by the outlier behaviour of the GAM algorithm, is therefore primarily about the rate and ultimate limit of this advance.

In stark contrast, the future for the high-altitude Swiss stone pine is characterized by systemic and widespread uncertainty, but remains within moderate values (Figure 3.13).

As its climatic niche is projected to shrink and fragment, the models show broad disagreement, not just from a single outlier (Figure 3.12). This reflects a fundamental uncertainty about where, or even if, viable refugia will persist.

4.5 Study Limitations and Future Developments

This section outlines the primary limitations of the study and the strategies employed to mitigate their potential impact on the findings.

A comprehensive interpretation of this study's findings requires acknowledging its inherent limitations, which also pave the way for future research directions. These limitations span the ecological assumptions of the models, the nature of the input data, and the computational framework itself.

4.5.1 Latent Variables and Biotic Interactions

A primary consideration is that the habitat suitability maps represent a species' *potential climatic niche*, not its *realized niche* or a guaranteed future distribution. The models are a necessary simplification of complex ecological realities and do not account for numerous external factors that can mediate species presence, such as human interventions (e.g., forest management), stochastic events (e.g., fires, storms), and the impact of pests and diseases. While this simplification is a limitation, it is also an advantage for interpretability, as it provides a clear baseline for understanding the powerful influence of climate and topography. It isolates these drivers from other confounding factors, offering a crucial "tile" in the larger mosaic of ecosystem dynamics.

The models are based on climatic and topographic predictors but do not explicitly account for several latent variables that critically influence species distribution on the ground. These include:

- **Biotic Interactions:** Factors like competition, facilitation, and predation are not modelled. For example, the projected expansion of *Quercus pubescens* may be limited in reality by competition from established species like *Fagus sylvatica*.
- **Soil Properties:** While broad soil pH categories were included, more detailed factors like microbial communities, which enrich soil fertility, and specific soil characteristics were not considered. Regional-scale soil maps may lack the detail to capture the local variations that influence individual plant establishment and growth. Moreover, most soil maps are categorical in nature and exhibit numerous

soil type, rendering their incorporation into SDM frameworks challenging due to the requirement for binary encoding of categorical variables. However, alternative approaches using globally (Hengl et al., 2025) or regionally (Rota et al., 2024) available continuous datasets do exist.

The projections should thus be interpreted with caution, as they may present a more favourable scenario than the actual ecological changes that will transpire (Dyderski et al., 2025), with potential suitability further restrained by biotic interaction and unsuitable soil characteristics.

Integrating other ecologically and socio-economics significant variable such as the increasing demand for wood, the land cover changes and the demographic trends (Keenan, 2015) could enhance model robustness, always taking into account the risk of collinearity.

4.5.2 Occurrence Datasets and Human Influence

The accuracy of any SDM is fundamentally dependent on the quality of the occurrence data. This study faces three main limitations in this regard:

- **Managed vs. Primary Forests:** The occurrence data were collected almost exclusively from managed forests, as primary forests are not present in the province. The models, therefore, reflect species distributions as shaped by decades of human silvicultural practices, not just natural environmental filters.
- **Data Biases:** The use of citizen-science data (iNaturalist), while valuable for supplementing records, carries potential biases related to spatial clustering in accessible areas and potential identification and georeferencing errors (Estien et al., 2024; López-Guillén et al., 2024). For the purposes of this study, however, these limitations were not considered particularly significant, as the proportion of potentially erroneous data points (due to species misidentification or inaccurate location) was deemed insufficient to affect the ESDM models.
- **Niche truncation:** In this study, the use of local species data has produced a highly accurate model of current tree species distribution, which is invaluable for regional forest management. However, as demonstrated by Anselmetto et al. (2025), this fine-scale approach is susceptible to niche truncation when projecting into novel future climates. This limitation arises because the model is calibrated on only a partial segment of a species' full environmental tolerance, which can lead to an overestimation of the magnitude of future changes. Consequently, the model's

predictions are a good reflection of the potential climatic niche but may not capture the full realized niche. Specifically, the most thermophilus species, including *Q. ilex* and *Q. pubescens*, are not currently at their thermal tolerance threshold in any area in the study region. Consequently, the model fails to adequately constrain their future suitability. This likely results in the overestimation of their suitability at low elevations under the extreme warming scenarios of RCP 8.5 during the 2081-2100 period. Furthermore, the current climatic conditions in the study area lack the continental warm valley environments that constitute typical habitat for *Q. pubescens*, as documented in the central and western Alps (de Pasquale & Spinelli, 2022). This absence prevents the model from accurately identifying continental valleys as potentially suitable habitat for the downy oak under projected warming scenarios.

To create more robust and less biased input datasets, future studies could leverage more advanced data aggregation tools. For instance, the R package SPOCC (Owens et al., 2024) allows for the integration of multiple citizen science databases, which can help to cross-validate records and reduce sampling bias. Future research should also aim to mitigate the niche truncation bias by adopting a data pooling methodology, integrating detailed local data with broader inventories to create more robust and reliable future projections. Many frameworks for “nesting” whole-range and sub-range distribution models have been proposed, and summarized in Guisan et al. (2025). Despite this constraint for future scenarios, the current model's fine-scale precision remains essential. It uniquely captures local anthropogenic signals and provides the detailed habitat information necessary for effective, on-the-ground conservation and management planning (Bonannella et al., 2022).

Building on this work, future research should move toward more comprehensive ecosystem forecasts. The following steps are recommended:

- **Integrate Dynamic Processes:** Future models should incorporate species-specific dispersal capacities and dynamic vegetation models (DVMs) to simulate transient responses to climate change, moving from potential distribution to projected actual distribution.
- **Incorporate Biotic Interactions:** Explicitly modelling biotic factors, including competition among tree species and the influence of pests and pathogens (e.g., bark beetle dynamics for *Picea abies*), would significantly refine the accuracy of the projections.

- Address Niche Truncation: To mitigate the risk of niche truncation, a data-pooling methodology should be adopted, integrating the detailed local data from this study with broader, trans-regional inventories to capture a more complete representation of species' climatic tolerances. In addition, training models over a broader geographical extent – while retaining the same fine spatial resolution – and subsequently cropping them to the study area could help capture a wider portion of each species' ecological niche, thus improving the reliability of the models.

4.6 Management and Conservation Implications

There is rising interest and need in developing effective forest policies in all Europe (Nabuurs et al., 2019). Although continental and national policy frameworks are necessarily informed by coarse-resolution assessments, operational forest management is implemented at the local scale; therefore, high-resolution, management-relevant maps and models (here at 50 m) are needed (Anselmetto et al., 2025).

This work can help the policy makers to identify the best suitable locations for each species, with the aim of effectively implement reforestation and assisted migration programs. For instance, *Picea abies* – the most important species in the province in terms of surface area and multifunctionality (PAT, 2025a), and one of the most threatened by the climate change (Dyderski et al., 2025; Section 3.1) – in most areas will need a substitute in order to guarantee a stable forest cover, that can be selected according to its future projections. Human intervention should be applied only where necessary, always prioritising natural local regeneration when feasible. Some species, selected and authorized for the reforestations (Section 2.3.1), confirmed their suitability for the future climate (e.g. *Fagus sylvatica*, *Prunus avium*, and *Tilia cordata*), while others must be taken into consideration carefully, since the locations where they are planted today might not be suitable in the future (e.g. *Pinus sylvestris*, *Pinus cembra*, and *Fraxinus ornus*). For the “Losers” and the “Different behaviours” species (Section 3.1) a thorough evaluation of the present and future suitability is advised, in order to find the best locations. The habitat suitability maps created in this study at 50 m resolution can help these reforestations policies.

The implications of this research are threefold:

- For forestry practice, the high-resolution suitability maps offer a valuable tool for long-term strategic planning, enabling forest managers to identify vulnerable species,

locate potential climatic refugia, and evaluate the suitability of tree species for future reforestation and assisted migration efforts.

- For conservation policy, the findings provide a scientific basis for prioritizing conservation actions, particularly for "loser" species, and for designing resilient ecological networks.
- For future research, this work establishes a methodological benchmark for regional-scale ENM and highlights the critical importance of integrating high-resolution local data.

5 CONCLUSIONS

This thesis addressed a critical gap between broad-scale climate impact assessments and the operational needs of regional forest management in mountain ecosystems. The primary objective was to develop, apply, and validate a high-resolution (50 m) Ecological Niche Modelling framework to project the potential distribution of 23 dominant tree species in the Autonomous Province of Trento under future climate change scenarios. By employing a Stacked Species Distribution Model (SSDM) approach, the study successfully generated a replicable and computationally robust workflow, providing spatially explicit insights at a scale directly relevant to local conservation planning and silvicultural decision-making.

The ecological findings reveal a significant, climate-driven restructuring of the region's forest communities projected by the end of the 21st century. A clear divergence emerged between the future trajectories of thermophilous species, such as *Quercus pubescens*, which are anticipated to undergo substantial upward altitudinal expansion, and cold-adapted, high-elevation specialists, notably *Pinus cembra*, which face a severe contraction and high risk of local extinction. At the community level, this turnover is projected to drive an overall contained decline in mean tree species richness under the intermediate RCP4.5 scenario and a structural shift toward biotic homogenization and accelerated richness decline under the business-as-usual RCP8.5 scenario. Methodologically, the ensemble modelling approach proved to be a powerful tool for this regional application, with individual species models (ESDMs) achieving high predictive accuracy (mean AUC > 0.90), thereby validating the workflow's effectiveness for regional-scale ecological niche modelling. The stacking process (SSDM), on the other hand, requires careful thresholding, a finer tuning, and comprehensive uncertainty assessment, since the mean species richness errors were high for all the scenarios and time periods.

The projections represent hypotheses of potential climatic suitability and do not incorporate dynamic ecological processes. Key factors such as species-specific dispersal rates, complex biotic interactions (e.g., competition, pest and disease outbreaks), and the potential for local genetic adaptation were not explicitly modelled. Furthermore, the reliance on presence-only data from managed forests may introduce a bias reflecting anthropogenic influences rather than the species' full fundamental niche, potentially overestimating the magnitude of future changes.

The ESDM/SSDM analyses produced 50 m habitat suitability and species richness maps that can directly inform forest policy, guide site-level reforestation and assisted migration, and prioritise targeted conservation areas. Future works should focus on linking these correlative outputs with dynamic or dispersal models, combining broader-scale occurrence data to reduce niche truncation, improving fine-scale predictor layers, and optimising the computational workflow to enhance robustness and operational utility.

Supplementary Material

Reproducibility is a central requirement of modern science. All model outputs (maps and evaluation metrics), the R scripts used for data processing and modelling are publicly available in the EU research repository on Zenodo: <https://doi.org/10.5281/zenodo.16781155>.

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