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# Species distribution models built with local species data perform better for current time, but suffer from niche truncation



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#### ABSTRACT

To cope with climate change-induced alterations, forest ecosystems' conservation and restoration require models that are both capable to incorporate current local-scale dynamics but also to anticipate future changes. These requirements may be fulfilled by robust assessments of response (i.e., species data such as forest inventories) and predictor (e.g., climate) variables. The aim of this study is to predict current and future probability of occurrence for 22 tree species comparing inventory and climate data at different spatial scales and test for model performance, reliability, and niche truncation.

We built species distribution models (SDMs) for 22 tree species of Piedmont, an Alpine administrative region of north-western Italy. We compared (i) a fine-scale model calibrated with a local forest inventory with a 250-m spatial resolution at the extent of Piedmont and a regional climate model calibrated on the Italian extent versus (ii) coarse-scale model calibrated with a pan-European forest inventory (EU-Forest) at 1-km resolution and a global climate dataset (CHELSA v1.2). Moreover, (iii) we developed a data pooling method by combining the species data and using CHELSA. We evaluated models using spatial-block cross-validation and external validation through several metrics. We predicted the probability of occurrence for current and future under RCP4.5 and RCP8.5 climate scenarios.

Models built with local species data performed better for the future than those incorporating broad species data and their current predictions reflected the realized distribution of species but they suffered from niche truncation while extrapolated to the future. Indeed, models calibrated at the local scale predicted greater magnitude of changes for future scenarios compared to coarse-scale models. Integrating species data at different extents and resolutions is a valid approach when both are available.

### 1. Introduction

It is well known that forest ecosystems provide essential ecosystem services such as biodiversity conservation, food and timber production, water regulation, and carbon sequestration (Mori et al., 2017). However, these ecosystems are increasingly affected by climate and land-use changes, which are reshaping the distribution, abundance, and phenology of forest species across various scales (Vitasse et al., 2021). These alterations have significant implications for the resilience of the human communities that depend on forest services (Forzieri et al., 2022; Smith et al., 2022). To address these challenges, it is essential to understand the past, present, and future dynamics of forest ecosystems to monitor and anticipate their responses to global changes across diverse spatiotemporal scales (Guisan et al., 2013; Albrich et al., 2020; McDowell et al., 2020). In response to these pressures, global forest policies have increasingly focused on conserving forest systems as a vital strategy for mitigating climate change (Fagan et al., 2020; Begemann et al., 2021). However, global forest governance is characterized by a complex cross-scale interaction of institutions (e.g., from the United Nations [UN] to sub-national levels), actors (e.g., public and private

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stakeholders), targets (e.g., biodiversity, human rights, climate crisis), and norms (Begemann et al., 2021; Sharma et al., 2023). This intricate governance framework underscores the need for adaptive strategies that are informed by robust and predictive tools at different spatiotemporal scales. Predictive spatial modeling has emerged as a promising approach for guiding adaptive planning and management in forest ecosystems (Zurell et al., 2022). Quantitative predictions lie at the heart of informed decision-making and responsible management, predicting ecological shifts and preparing for necessary interventions such as assisted migration of animals and plants (Twardek et al., 2023; Xu and Prescott, 2024) and ecological restoration. To maximize their utility and cope with the multiscale policy framework, ecologists and forest managers require models that are reliable and applicable across broad scales (regional to continental) and fine scales (landscape to regional). Such models play a crucial role in prioritizing spatial reserves and guiding restoration efforts (Wan et al., 2017; Mateo et al., 2019; Buenafe et al., 2023), ensuring that conservation strategies are both targeted and effective.

Correlative species distribution models (SDMs) are the most common predictive tools for assessing potential range shifts of tree species under future scenarios (Franklin, 1995; Guisan et al., 2013; Zurell et al., 2020; 2022). They work by establishing a relationship between the presence or abundance of a species and a suite of several socio-ecological covariates. These covariates include, but are not limited to, climate data, soil features, topography, land use, and socioeconomic drivers (Franklin, 1995; Guisan et al., 2013). These models have been extensively used at several spatial and temporal scales to study the potential ecological impact of climate change on various plant and animal species worldwide (Newbold, 2018; Maréchaux et al., 2021; Chevalier et al., 2022; Zurell et al., 2022). Broad-extent and coarse-resolution models, primarily associated with climatic predictors, are more prevalent than local-extent and fine-resolution models, which however often reflect better the structure and characteristics of existing habitats (Araújo et al., 2019). However, regardless of the scale or resolution, the performance and reliability of predictions hinge on the source of response (i.e. species data such as ecological inventories) and predictor (e.g., climate) variables used in model calibration and validation (Bobrowski and Udo, 2017; Araújo et al., 2019; Zurell et al., 2020). Decisions regarding the spatial scales - both resolution and extent - of such variables in SDMs have significant ecological consequences. It is indeed a complex task to capture local habitat heterogeneity and detailed species-environment interactions while aiming for robust extrapolation across broad contexts and changing climates. Alternatives to correlative SDMs at a regional to global scales exist in the form of mechanistic or hybrid models that incorporate, for example, tree demography (Macfadyen and Kriticos, 2012), phenology (Chapman et al., 2017), and biophysics (Briscoe et al., 2023). These alternative models are based on deeper ecological realism and the capacity to simulate species responses under conditions beyond their observed range, their application is mostly concentrated at the stand and landscape scales. However, their application at broader, global scales - where one the main outputs of dynamic forest models are net primary production and carbon stock - is limited (Bugmann and Seidl, 2022). Despite the ecological reliability benefits resulting from the application of these models, their complexity often creates barriers for integration into policy and decision-making processes. Policymakers and foresters may struggle with their technical demands and data requirements, which contrasts with the simplicity and accessibility of correlative SDMs.

Among the main sources of species data, ecological inventories assume a pivotal role in understanding the status and trends of forest ecosystems and populations across different spatiotemporal scales (Tomppo et al., 2010; Tinkham et al., 2018). Their primary advantage lies in their statistical sampling scheme, which provides reliable information on true presences and absences at a specific extent and resolution (Pecchi et al., 2019; Ellis-Soto et al., 2021). Forest inventories, for instance, often include multiple stand attributes (e.g., basal area) that allow for a comprehensive assessment of ecosystem resources and services, and can inform decision-making for timber production, biodiversity conservation, and carbon sequestration (Tomppo et al., 2010). When it comes to climate predictors, limited-area high-resolution models (e.g., regional climate models, RCMs), serve as valuable tools for the dynamical downscaling of general circulation models (GCMs) to fine scales with very high resolution (VHR). This process offers detailed and reliable insights into the local variability of climate variables within specific local areas (Giorgi et al., 2009). Many studies have been so-called exploring RCMs at the convection-permitting, convection-resolving, convection-allowing, or kilometer-scale grid spacing (Kendon et al., 2014; Ban et al., 2014; Liu et al., 2017; Berthou et al., 2020; Fumière et al., 2020). The main characteristic of these types of simulations is the explicit resolution of deep convection at grid spacings below 4 km, without using any kind of parameterization. These studies demonstrate that kilometer-scale modeling offers significant advantages in representing climate, and the costs are justified when focusing on local to regional scales (Ban et al., 2021). The importance of VHR climate data has been recently increasing in several fields, including climate change research, environmental monitoring, agriculture, and water resource management (Crespi et al., 2018; Mauri et al., 2022).

Establishing robust standards for assessing the ecological reliability and statistical performance of species distribution models is essential, especially as the number of studies predicting current and future species distributions and habitat suitability continues to grow (Araújo et al., 2019; Zurell et al., 2020). The accuracy, reliability, and transferability of these models are strongly influenced by the spatial resolution and extent of both predictor and response variables, which play a critical role in the calibration and evaluation processes of SDMs (e.g., Betts et al. 2006, Elith and Leathwick 2009, Patiño et al. 2023). In parallel, advances in climate modeling have improved the reliability of environmental predictors. Indeed, the dynamical downscaling of GCMs to RCMs increase their reliability within the calibration area by pairing the broad synoptic scale of GCM fields and the mesoscale resolution fields simulated by RCMs (Fumière et al., 2020; Ban et al., 2021; Mauri et al., 2022). This coupling ensures a better representation of climatic variability at the regional level, offering more precise data for SDM development and evaluation. At the same time, many projections of future species distribution under climate change scenarios are based on SDMs that are built on a subset of species' ecological niches (i.e., niche truncation; Mateo et al., 2019; Chevalier et al., 2021; 2022). This phenomenon is caused by truncating the full range of conditions that a species can tolerate, leading to extrapolation to conditions that were not used to calibrate the models. Several studies have compared modeling algorithms (e.g., Valavi et al. 2022), response variables (e.g., Waldock et al. 2022), and predictors (e. g., Lembrechts et al. 2019a, Patiño et al. 2023) in SDMs. However, to our knowledge, very few (e.g., Simon et al. 2023) examine different combinations of predictors and response data at different scales to model current and future probability of occurrence of species at fine scales appropriate for regional and local planning and decision making and assess the impact of niche truncation.

Therefore, the aim of this paper was to predict current and future probability of occurrence for different tree species of Piedmont, an administrative region of the western Italian Alps, using different combinations of SDMs, from fine to coarse scale and data pooling methods. We defined fine scale as the combination of local species data (i.e., forest inventory for the Piedmont region) characterized by fine spatial resolution and local extent with an RCM characterized by a local calibration area and extent (i.e., Italian peninsula). In contrast, we defined coarse scale as the combination of continental species data (i.e., harmonized European forest inventory) characterized by coarse spatial resolution and broad extent with a GCM characterized by coarse area of calibration and global extent. Finally, the data pooling methods was obtained by integrating the two species data and using the GCM climate model (Fig. 1). Our main research question was: how does the spatial scale of



**Fig. 1.** Combinations of response (local versus broad species data) and climate (regional climate model, RCM, versus general circulation model, GCM) data according to the spatial resolution and spatial extent (for response) and area of calibration and spatial extent (for climate). We defined fine scale as the combination of local species data (fine resolution and local [Piedmont region] extent forest inventory) and a regional climate model (fine area of calibration and local [Italy] extent). We defined coarse scale as the combination of continental species data (coarse resolution and broad [European Alps] extent forest inventory) and a general circulation model (coarse area of calibration and broad [global] extent). We defined as hybrid scales the other combinations between response and climate data. In particular, Hybrid 1 is the combination of local species data and GCM, Hybrid 2 is the combination of broad species data and RCM, and Hybrid 3 is the combination of broad species data at the local extent and GCM. We defined a gradient from the fine to the coarse scale and placed the hybrid combinations along it.

response (i.e., species data) and predictor variables affect prediction success, reliability, and niche truncation in SDMs? To address this question, we compared SDM frameworks built using (i) a local forest inventory (250 m resolution at the extent of Piedmont, 25 387 km<sup>2</sup>) versus a broad European forest inventory (1 km resolution at the extent of the European Alp, 179 014 km<sup>2</sup>) and (ii) a local climate dataset based on an RCM versus a widely applied climate dataset based on GCM. Our final aim was to analyze future scenarios of climate change for the main tree species of Piedmont by comparing magnitude of change estimated from the different frameworks. We conclude by discussing the implications of local species data and predictors and their spatial scale within SDMs in ecology and forestry. The datasets produced by this study represent a comprehensive assessment of the current and future distribution of tree species in Piedmont region. To the best of our knowledge, this is the first dataset specifically developed for this region that integrates such fine-grained forest inventory data with RCM-based climate predictors.

#### 2. Materials and methods

#### 2.1. Study area

Piedmont is an administrative region of north-western Italy covering 25 387 km<sup>2</sup> (Fig. 2). Around 43 % of its area (11 000 km<sup>2</sup>) lies in the montane belt, with two mountain regions; the western Alps and the northern Apennines. Piedmont hosts more than 1 billion trees belonging to 52 different species; its forests cover 9 770 km<sup>2</sup> (38.5 % of the total surface area), but in mountain areas the forest cover increases to reach 57 % (6 631 km<sup>2</sup>) (Camerano et al., 2017). The main tree species in the region are the sweet chestnut (Castanea sativa Mill., 22 % of the total forest area), European beech (Fagus sylvatica L., 15 %), black locust (Robinia pseudoacacia L., 12%), and European larch (Larix decidua Mill., 10 %) (Camerano et al., 2017). Like many areas in Europe, the millennial history of human practices in the region (e.g., logging for timber and fuelwood, mining, and creation of semi-natural ecosystems) shaped the structure and composition of its forests since the Neolithic (Mietkiewicz et al., 2017; Zanon et al., 2018). For instance, in the subalpine elevation belt of the Alps, European larch has been favored over stone pine (Pinus cembra L.) and other competing species because of its suitability for wood pastures; indeed, its fast growth and timber quality make it a



Fig. 2. Maps of the (a) Alps and (b) Piedmont Region with occurrences of the local (Camerano et al., 2017) and broad inventory (EU-Forest; Mauri et al., 2017).

target species for timber production while its light canopy allows forage grass to grow underneath (Garbarino et al., 2011). At lower elevations, sweet chestnut cultivation was introduced by the Romans and then expanded in Medieval times (A.D. 100 to A.D. 600) in areas naturally occupied by oak stands (*Quercus* spp.) (Conedera et al., 2004). Due to socio-economic changes that led to land abandonment starting from the Industrial Revolution, forests are expanding to the detriment of former croplands, vineyards, and grasslands (Batzing et al., 1996; Plieninger et al., 2016; Anselmetto et al., 2024).

#### 2.2. SDM framework overview

Below we describe the SDM framework according to the ODMAP (Overview, Data, Model, Assessment, and Prediction) protocol for Species Distribution Models (Zurell et al., 2020; see Supplementary Material Table A.1 for further details). We assumed that the distribution of our 22 focal tree species is mostly driven by climate, topography, and soil characteristics. We know that human legacy has had a major role in current distribution, but we did not include those variables in our models due to a lack of spatially explicit data at a regional scale. We also assumed that (i) species are at (pseudo-) equilibrium with the environment (i.e., the species has reached all suitable habitats), (ii) inventory sampling is adequate and representative, with negligible detection errors, (iii) in forest inventories, tree individuals below a certain diameter at breast height are not recorded, and we assume that this procedure does not bias species identification, and (v) the current distribution's delimiting factors will also form the niche of the species in the future (i. e., niche conservatism).

All the analyses were conducted in R version 4.2.3 (R Core Team, 2023) (See Supplementary Table A.2 for R packages used in the analyses).

#### 2.3. Species occurrence data

For model calibration, we applied a local forest inventory led by IPLA (Istituto per le Piante da Legno e l'Ambiente; Camerano et al., 2017) in the early 2000s for the Piedmont region for management implications (informing forest plans known as Piani Forestali Territoriali, PFT; Camerano et al., 2017) and a broad inventory that comes from a

harmonization of national forest inventories at the European scale called EU-Forest (Mauri et al., 2017). We cropped EU-Forest to the rectangular extent (i.e., a rectangle defined by coordinate extremes of easting and northing) of the Alpine Convention Perimeter (PASC, 2020).

The local species data encompasses 36 species and 14 164 occurrence points at a spatial resolution of 250 m. The EU-Forest project emerged from a collaboration between JRC (Joint European Research Center) and 21 European Countries. This dataset is the result of merge and harmonization of National forest inventories and pre-existing European datasets, and it collects occurrence (presence/absence) data of 242 tree species and a total of 1 000 525 occurrence records. EU-Forest has a spatial resolution of 1 km and is aligned to the European INSPIREcompliant 1 km x 1 km grid (European Parliament, 2007). We also compared models trained with the broad species data clipped on the extent of the Piedmont Region (i.e., Hybrid 3) to the broad species data at the extent of the entire Alps to evaluate the utility of broad inventories in local contexts. We did this to account for different spatial (i.e., geographical range) and ecological (i.e., niche) extents for a coarse-resolution species dataset. Finally, we developed a data pooling method by integrating local and broad species data for model calibration. Our hypothesis was that coarse-resolution species data clipped to a smaller extent before model calibration will suffer of niche truncation even more than fine-scale models with species data characterized by finer spatial resolution. We selected 22 species that were common between the two datasets and with at least 150 occurrences (Table 1). Both datasets were re-projected to the coordinate reference system ETRS89 / LAEA Europe (EPSG: 3035). To address uneven sampling intensity and spatial clustering of points, we applied a spatial filter to the presence points using a custom function written in R. A minimum distance of 500 m was set between points to ensure a consistent sampling intensity between presence and absence data. We included the abundance (i.e., relative basal area) of species in each observation point as weights in the model algorithm for the local species data. This approach was not possible for the broad species data as the basal area is not available.

#### 2.4. Environmental predictors for SDMs

#### 2.4.1. Climate data

We tested two different climate datasets in the calibration of the

#### Table 1

List of the 22 tree forest species assessed in this study and their prevalence (presence/total number of occurrences) according to the local and broad inventories for both the local (Piedmont) and broad (Alpine) extent.

species nametypeLocal Local appected spec.Broad spec. dataBroad spec. dataBroad spec. dataBroad spec. dataBroad spec. dataBroad cata dataSilver fir Black alderAbies alba Almus glutinosa pseudoplatanusConifer Broadleaf0.056 0.016 0.0570.010 0.02010.0201 0.086Field maple Luropean birchAcer BroadleafBroadleaf 0.0340.046 0.0410.044 0.039European birchBetula pendula BroadleafBroadleaf 0.0340.016 0.0590.059 0.039Sweet chestnutCastanea sativa excelsiorBroadleaf 0.0540.040 0.0400.011 0.025European ash chestnutFraxinus excelsiorBroadleaf 0.0540.040 0.0400.011 0.024European brows beechFraxinus ornus exclasiorBroadleaf 0.0540.040 0.0400.011 0.024European brows chestnutFraxinus ornus exclasiorBroadleaf 0.0540.040 0.0400.011 0.024European brows beechLarix decidua conifer0.064 0.0640.011 0.0120.024 0.025Swiss stone pinePinus sigra Conifer0.064 0.0640.011 0.0140.124 0.022Swiss stone pinus sigra Conifer0.066 0.0660.011 0.0020.001 0.002Black pine pineFinus sylvestris Conifer0.068 0.0680.011 0.0020.002Pedunculate Quercus robur pubescensBro	Common	Scientific species name	Forest type	Prevalence		
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Sessile oak Quercus petraea Broadleaf 0.130 0.016 0.006 Black locust Robinia Broadleaf 0.197 0.019 0.002 pseudoacacia Rowan Sorbus Broadleaf 0.042 0.002 0.000	Downy oak	Quercus	Broadleaf	0.070	0.002	0.017
Black locust Robinia Broadleaf 0.100 0.010 0.000   pseudoacacia Broadleaf 0.197 0.019 0.002   Rowan Sorbus Broadleaf 0.042 0.002 0.000	Sessile oak	Quercus petraea	Broadleaf	0.130	0.016	0.006
Rowan Sorbus Broadleaf 0.042 0.002 0.000	Black locust	Robinia	Broadleaf	0.197	0.019	0.002
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	Rowan	Sorbus	Broadleaf	0.042	0.002	0.000
adcuparta		aucuparia				

SDMs (Table 2). First, we applied VHR (Very High Resolution) climate data from the Euro-Mediterranean Center on Climate Change (CMCC) for the Piedmont region available from the Highlander project (https://highlanderproject.eu/). The dataset was based on a dynamic downscaling of current (1989-2013) ERA5 reanalysis (Hersbach et al., 2020), originally available at  $\sim$ 31 km spatial resolution, to obtain a final resolution of ~2.2 km through a regional climate model called COSMO (Raffa et al., 2021). We identified this climate dataset as the local climate dataset. For the future period (2041-2060) we utilized another climate dataset developed within the Highlander project through a dynamic downscaling of CMCC-CM global model to  $0.02^{\circ}$  (~2.2 km) spatial resolution according to IPCC scenarios RCP8.5 (Raffa et al., 2023) and RCP4.5 (Raffa and Mercogliano, 2022). The dynamical downscaling makes use of the same RCM (COSMO-CLM) used for ERA5. Pre-processing on this dataset consisted of a bias-correction procedure to remove overestimation or underestimation of the model in comparison to the observed data, for every timestep (every day) and every grid point, due to systematic errors originated (Watanabe et al., 2012). We applied a simple pixel-based additive bias correction method for temperatures and a multiplicative one for precipitation. Climate data are part of the project Highlander and are available at https://dds-dev. highlander.cineca.it/app/datasets. We used the local climate data for the calibration of the fine-scale framework and the model "Hybrid 2".

The second dataset derived from CHELSA (Climate at high resolution

#### Table 2

Environmental predictors resulting from the variable pre-selection based on the correlation between variables and the variance inflation factor (VIF) used for SDMs calibration. Information about all the variables (comprising those excluded by the variable selection), and the resampling strategies can be found in Table A4.

Group	Variable	Data source	Native spatial resolution	Refs.
Topography	Elevation (median)	MERIT DEM	3'' (~90 m)	Yamazaki et al. (2017)
	Slope (median, standard	MERIT DEM	3'' (~90 m)	Ct al. (2017)
	Heat load index (median, standard deviation)	MERIT DEM	3'' (~90 m)	
	Topographic position index (median, standard deviation)	MERIT DEM	3'' (~90 m)	
Climate	Monthly precipitation (Jan, Mar, Apr, May,	CHELSA timeseries	1 km	Karger et al. (2017, 2018)
	Jun, Sep, Oct)	COSMO	0.02° (~2.2 km)	Raffa et al. (2021, 2023)
	Mean diurnal range	CHELSA timeseries	1 km	
		COSMO	$0.02^{\circ}$	
			(~2.2 km)	
	Isothermality	CHELSA timeseries	1 km	
		COSMO	$0.02^{\circ}$	
			(~2.2 km)	
	Temperature seasonality	CHELSA timeseries	1 km	
		COSMO	0.02° (∼2.2 km)	
	Temperature	CHELSA	1 km	
	annual range	timeseries		
		COSMO	0.02°	
		011771.01	(~2.2 km)	
	Mean temperature	CHELSA	1 km	
	of wettest quarter	COSMO	0.02°	
		Gobino	$(\sim 2.2 \text{ km})$	
	Mean temperature of driest quarter	CHELSA timeseries	1 km	
	·· ····· 4·····	COSMO	$0.02^{\circ}$	
			(~2.2 km)	
	Precipitation of wettest month	CHELSA timeseries	1 km	
		COSMO	$0.02^{\circ}$	
			(~2.2 km)	
	Precipitation of	CHELSA	1 km	
	driest month	timeseries		
		COSMO	0.02° (~2.2 km)	
	Precipitation	CHELSA	1 km	
	seasonality	timeseries		
		COSMO	0.02°	
Cail	-U (0, 15)	0.010.01000	(~2.2 km)	Tional -t -1
5011	pri (0–15 cm) Soil organic Carbon (0–15 cm)	SoilGrid250m	250 m 250 m	(2017)

for the Earth's land surface areas) v1.2 (Karger et al., 2017, 2018). CHELSA consists of downscaled general circulation models output temperature and precipitation estimates at a horizontal resolution of 30 arc *sec* ( $\sim$ 1 km at the Alps latitude). The temperature downscaling algorithm is based on statistical downscaling of atmospheric temperatures from ERA-Interim using a temperature lapse rate based on elevation. The precipitation downscaling algorithm includes orographic predictors such as wind, valley exposition, and boundary layer height.

Final data consist of monthly temperature and precipitation and derived parameters. We cropped the gridded variables at the extent of the Alps, and we identified this dataset as broad climate dataset. The future climate data were derived from downscaled CMIP5 climatologies (Karger et al., 2017, 2018, 2020). We selected six different models (CESM1-CAM5, CMCC—CM, CNRM-CM5, CSIRO-Mk3.6.0, GISS-E2-H, HadGEM2-AO) based on the quality of current prediction on the Alps and Europe (Zubler et al., 2016) but also considering dissimilarities between models to capture uncertainties in modeling future climate scenarios (Knutti et al., 2013; Sanderson et al., 2015). We used the broad climate data for the calibration of the fine-scale framework and the models "Hybrid 1", "Hybrid 3" and the data pooling method.

For each of the two climate datasets, we calculated monthly average values for the current (1989-2013) and future (2041-2060) periods and the 19 bioclimatic predictors (Hijmans et al., 2005; Table A.3). We considered 1989–2013 as the current since it was the common temporal extent of both local and broad climate datasets. We assessed two different future IPCC RCPs (RCP4.5 and RCP8.5) for the 2041-2060 period. The RCPs – acronym for Representative Concentration Pathways - are four scenarios developed by IPCC and included in the IPCC fifth assessment report (AR5; IPCC, 2014). The numbers in the RCP names indicate the increase in the radiative forcing  $[W m^{-2}]$  expected at the end of the 21st century relative to pre-industrial conditions. Among those four scenarios, RCP4.5 is considered an intermediate scenario, with peak of emissions in 2040 and then a decrease, while RCP8.5 is considered the worst-case scenario, with emissions increasing throughout the century. Climate data were resampled through a nearest neighbor method to 250 m. That means that they operated at the native resolution (1 km and ~2.2 km for the broad and the local dataset, respectively). To test for correlation between the variables of the two climate data sets, the centroids of every cell were extracted and examined using Pearson's correlation. To visualize geographical discordance between the two climate data sets, variables were intersected performing cell by cell subtraction of broad climate minus local climate. We also tested current (1989-2013) seasonal trends and spatial patterns with a regional gridded dataset derived from weather stations and available at ~16-km resolution (https://www.arpa.piemonte.it/scheda-informativa /dataset-griglia-nwioi).

#### 2.4.2. Other environmental predictors

We derived topography from the Multi-Error Removed Improved-Terrain (MERIT) digital elevation model (DEM; Table 2). The MERIT DEM is available at 3 sec spatial resolution ( $\sim$ 90 m at the equator). This dataset derives from multiple satellite data and several filtering techniques used for the bias correction of height error components from previous spaceborne DEMs (Yamazaki et al., 2017). We derived the median and standard deviation of five topographic metrics from MERIT DEM resampled at 250 m. We calculated the elevation, slope, heat load index (HLI) or the incident radiation of the sun according to the aspect (McCune et al., 2002), topographic position index (TPI), indicating the position of a cell according to its 8 surrounding cells neighbors, and terrain ruggedness index (TRI), that expresses the amount of elevation difference between adjacent cells of a DEM (Riley et al., 1999) (Table 2). Topographic predictors do not directly represent resource variables for plants, but they have an indirect impact on plant distribution through altering the distribution of temperature, moisture, nutrients and light (Mod et al., 2016). Moreover, incorporating these topographic predictors in SDMs proved to improve model reliability and performance as they refine macroclimate conditions, which are decoupled from mesoscale terrain variations (Slavich et al., 2014). We included soil pH and organic carbon content (OCC) for the 0-15 cm depth at 250-m spatial resolution derived from SoilGrids250 m (Table 2; Hengl et al., 2017).

#### 2.5. SDMs architecture, assessment, and predictions

#### 2.5.1. SDM architecture

We built species distribution models using Bayesian additive regression trees (BART) through the embarcadero R package v1.2.0 (Carlson, 2020). BART is a machine learning modeling procedure based on an ensemble of trees, similar to boosted regression trees and random forest. In addition, BART employs a sum-of-trees model within a Bayesian framework; trees are first constrained as weak learners by priors, then updated through an iterative Bayesian backfitting Markov Chain Monte Carlo (MCMC) algorithm which generates a posteriori distribution of predicted classification probabilities instead of a single estimate (Chipman et al., 2010; Carlson, 2020). Overfitting results are lower than other similar methods, and several studies showed the better predictive power of this model compared to ensemble models with multiple algorithms (e.g., Baquero et al. 2021, Konowalik and Nosol 2021). We used BART's default settings (Table A.1).

We reduced the number of initial variables through a variable preselection based on the correlation between variables and the variance inflation factor (VIF) through the function vifcor of the usdm package (Naimi et al., 2014; Figs. B.3–B.5). The function first pairs variables with a linear correlation higher than a pre-selected threshold and excludes the one with a greater VIF. The procedure is iterated until no pair of variables with a high correlation remains. We used a Pearson's correlation of 0.9 as the threshold at which one of a correlated pair was excluded. Our aim was to avoid highly correlated variables and speed-up the computation time even if BART is considered to be robust against multicollinearity. We performed this variable selection once, therefore all the species were trained with the same 25 variables described in Table 2. We assessed spatial autocorrelation using automatic variograms through the R package automap (Hiemstra et al., 2009).

#### 2.5.2. SDMs assessment

We assessed models performance, calibration, and realism. The former was statistically tested through internal (5-fold spatial block cross-validation) and external validation on a fully independent dataset (GBIF + LUCAS; Mauri et al., 2022). We determined the block-size dimension by constructing empirical variograms for measuring spatial autocorrelation. When the mean range of spatial autocorrelation was > 15 000 m, we used 10 000 m as block-size dimension. We retrieved several performance metrics such as the Area Under the receiving operator Curve (AUC), True Skill Statistic (TSS), Sensitivity, Specificity, and the F1 score. The AUC is a threshold-independent metric that shows the relationship between false-positive and true-positive rates. The TSS and F1 score are threshold-dependent metrics that depend on the sensitivity and specificity of the models. TSS values > 0.6 are considered to be useful to excellent, AUC scores > 0.8 are considered to be good to excellent. We assessed the calibration (i.e., the agreement between predicted probabilities of occurrence and observation of presence and absence) and generalizability of the models through Pearson's correlation coefficient (COR). We calculated the correlation between the observation (presence/absence dichotomous variable) and the predictions (range of probabilities). COR is therefore а threshold-independent metric similar to AUC, but it accounts for the distance between the prediction and the observation (Elith et al., 2006). Realism was assessed from an ecological point of view through variable importance (vimp) and a visual comparison of the spatial predictions for the current time to the European geographic range of different species developed by the Joint Research Center (JRC) of the European Union (Caudullo et al., 2017) and the EU-Trees4F dataset (Mauri et al., 2022). We ran generalized linear mixed models (GLMMs) on performance (AUC, TSS, F1) and calibration (COR) results to test for significant differences among species data (i.e., local species data, broad species data, or a combination of the two), climate (i.e., local dataset or global dataset), and frameworks (i.e., the six combinations showed in Fig. 1) using the species as a random effect. We transformed the variables to

meet normality, checked among different families of distributions, and inspected model residuals. More information on the transformation and families can be found in Table B.1.

#### 2.5.3. SDMs predictions

The main output of the modeling consisted of predictions of relative probability of occurrence. To obtain future predictions of occurrence, we averaged climate conditions from the six models according to the two climate scenarios (i.e., RCP4.5 and RCP8.5) using the so-called climate ensemble (e.g., Mauri et al. 2022). This approach speeds up the computation but may average out climate extremes coming from different climate models. We also derived the uncertainty based on the 5th and 95th percentile of the probability distribution obtained through the Bayesian approach. We converted continuous probability maps into binary maps for ecological assessment and quantification of species range shifts. The threshold selection for binary maps is a crucial step in species distribution mapping (Hintze et al., 2021). Therefore, we tested three different widely applied thresholds; minimum training presence (MTP, sometimes also called lowest presence threshold), 10th percentile of the predicted values (P10), and maximum of TSS (maxTSS). We chose the latter since it was the most conservative approach.

#### 2.5.4. Post-processing analysis

We post-processed models output using Corine Land Cover (CLC; European Commission, 1994) to mask out unvegetated areas (i.e., urban areas, rocks, and water). We assessed changes in terms of probability of occurrence of the different tree species between each one of the two future climate scenarios (RCP4.5 and RCP8.5 for 2041–2060) and the current. Finally, we created probability-based richness (i.e., the sum of the predicted probability for each species) maps for the current and future scenarios according to the different modeling frameworks. We chose this approach over the threshold-based (i.e., sum of the binary maps) as it proved to better predict the observed species richness of an area whatever levels of habitat saturation (Grenié et al., 2020).

#### 3. Results

#### 3.1. Climate data comparison

We compared the spatial distribution and seasonal trends of mean temperature (Fig. 3a, c) and precipitation (Fig. 3b, d) to characterize differences among the two climate datasets. The broad climate dataset was colder than the local one for all months except for the winter ones



**Fig. 3.** Spatial (a, b) and temporal (c, d) distribution of mean temperature (a, c) and precipitation (b, d) of the two climate datasets (local climate = COSMO—CLM and broad climate = CHELSA v1.2) for the period 1989–2013. The broad climate dataset was consistently cooler than the local, but with similar seasonal trends. Differences in precipitation patterns seemed to be more related to continentality.

(min difference = -5.76 °C, mean difference = -0.78 °C, max difference = 5.47 °C; Fig. 3a, c). Compared to the regional climate grid produced by an Optimal Interpolation (OI; Gandin, 1963) of the existing weather stations of the regional weather agency (ARPA), both datasets showed higher summer mean temperatures and lower winter mean temperatures, but the seasonal trend was well represented (Fig. A.1). Values showed similar left-skewed distributions, with lower values associated with upper elevations (Fig. 3c). Spatial differences in temperature were scattered, especially in mountain areas with complex terrains, while in the Po Valley the average difference was  $-0.82\pm0.69$  °C and the local climate dataset was consistently hotter than the broad one (Fig. 3a). Differences in precipitation patterns decreased with elevation ( $R^2$  = 0.53, slope = -3 mm every 100 m of elevation gain), with the broad climate dataset showing lower values in the mountains (>800 m), with average differences of  $-45.5\pm30.9$  (mean  $\pm$  standard deviation) and  $8.6 \pm 22.6$  in the flat areas of the Po Valley (Fig. 3b). Patterns of differences in precipitation appeared to be also related to continentality; dry continental sectors, like the inner Alps (e.g., upper Susa Valley) and Po Valley, exhibited higher values in the broad dataset, while wetter sectors such as Cuneoprovince (South of Piedmont) and Ossola (the Northern extremity of Piedmont) showed higher values in the local climate dataset. The seasonal trends of precipitation was well depicted by both datasets (Fig. A.1), but spatially the local climate dataset performed better in representing observed climate conditions of the region (Fig. A.2).

We assessed spatial and temporal trends for the two future scenarios (Fig. B.1 for RCP4.5 and Fig. B.2 for RCP8.5). We derived average values of monthly temperatures and precipitation between the six CMIP5 models included within the broad climate dataset. We observed a higher degree of similarity in temperature spatial patterns and seasonal trends (monthly local ~ monthly broad with intercept = -0.42, slope = 1.13, and R<sup>2</sup> = 0.99 for RCP4.5; intercept = -0.74, slope = 1.12, and R<sup>2</sup> = 0.99 for RCP4.5; intercept = -0.74, slope = 1.12, and R<sup>2</sup> = -33.2, slope = 1.88, and R<sup>2</sup> = 0.34 for RCP4.5; intercept = -34.9, slope = 1.77, and R<sup>2</sup> = 0.65 for RCP8.5). Similarly to the current time, also for future scenarios the local climate dataset was hotter than the broad one during summer, but colder than or equal to in winter. Seasonal trends of precipitation showed differences between the two RCPs,

especially for the local climate data.

#### 3.2. Model performance and predictions

We compared model performance in terms of performance and calibration for different frameworks based on different responses (local species data versus broad species data) and predictors (local climate versus broad climate). From the spatial cross-validation procedure, models trained with local inventories showed significantly better performance of those calibrated with broad species data in terms of AUC, F1, and COR (Fig. 4a). No significance emerged for the independent validation but for AUC metrics related to species data, with local data having slightly better performance (p = 0.02) than broad species data and data pooling (Fig. 4b and Table B.1). Most models trained with local species data had an AUC >0.8 and a TSS >0.6, showing good model performance; the fine-scale model had an average AUC of 0.84  $\pm$  0.09. Similar values were observed for the Hybrid 1 model (local species data and broad climate dataset) and for the data pooling model. The COR metric of these three models was on average  $\sim$  0.40, showing good calibration. The only significant difference we observed when validating against an external dataset (i.e., GBIF, LUCAS) was in terms of the AUC between models calibrated with different species data (Fig. 4b). We did not observe significant differences in performance between models based on different sets of climate datasets.

The 5th and 95th percentiles were 0.63 and 0.95 for AUC (mean = 0.81, median = 0.82), 0.24 and 0.84 for TSS (mean = 0.54, median = 0.57), 0.05 and 0.68 for F1 (mean = 0.31, median = 0.31), and 0.04 and 0.64 for COR (mean = 0.32, median = 0.31). On average across the frameworks, we observed the best model performances for Swiss stone pine (AUC = 0.98, COR = 0.48), European larch (AUC = 0.92, COR = 0.67), and manna ash (AUC = 0.92, COR = 0.40), while the worst were European aspen (AUC = 0.58, 0.05), sycamore (AUC = 0.71, COR = 0.20), and field maple (AUC = 0.72, COR = 0.13), despite large differences can be observed relatively to the modeling framework. When comparing AUC (accuracy) and COR (calibration), local-scale models performed better than coarse-scale ones especially for sessile oak ( $\Delta$  AUC = 0.27 and  $\Delta$  COR = 0.34), European aspen ( $\Delta$  AUC = 0.21), and silver fir ( $\Delta$  AUC = 0.18 and  $\Delta$  COR = 0.24). Details and *p-values* of



**Fig. 4.** Validation results from (a) internal 5-fold spatial block cross-validation and (b) external validation on a fully independent dataset for performance (AUC, TSS, and F1 score) and calibration (COR). Letters represent the results of significant generalized linear mixed models (Table B1). Decreasing the scale detail (from fine to coarse with all the combinations in between) leads to a decrease in model performance for some metrics. Hybrid1 refers to the combination of local species data and GCM, Hybrid2 is the combination of broad species data and RCM, and Hybrid3 is the combination of broad species data at the local extent and GCM.

generalized models for performance and calibration can be found in Table B1.

We assessed the ecological reliability of model outputs, and we observed individualistic patterns in terms of spatial predictions (Figs. 5, B.6–B.8), variable importance (Figs. B.9–B.11), and correlation between spatial predictions (Table B.2). Coarse-scale models for sweet chestnut overestimated the current occurrence of the species and was more related to potential climate distribution (Fig. 5). Patterns of over- and underestimation for European beech (Fig. B.6), European larch (Fig. B.7), and Scots pine (Fig. B.8) were more difficult to decipher. Variable importance was similar among models for species such as black alder, sweet chestnut, European larch, black pine, and downy oak (Figs. B.9–B.11). Correlation between spatial predictions ranged between -0.01 (sessile oak, RCP8.5) and 0.88 (European larch) with a mean value of 0.47, a median value of 0.49, and a standard deviation of 0.22 (Table B.2).

# 3.3. Current and future probability of occurrence of tree species and species richness

The species showed individualistic responses between the fine-scale and coarse-scale models for current and future (2041–2060) both in spatial predictions (Figs. 6, B.12–B.14) and estimated changes in probability of occurrence (Fig. 7, B.15 and B.16, Tables B.3 and B.4). Coarsescale models generally exhibited changes in the probability of occurrence closer to zero (median = 0.002), while models calibrated with local species data (i.e., fine-scale, hybrid 1, and partially also data pooling models) showed more significant positive or negative values (Fig. 7). For several species, the data pooling models had a response that was somewhere between the fine- and the coarse-scale models but closer to the former (e.g., see Fig. B.18 for overall trends).

Sweet chestnut (Figs. 5, 6a), oaks (Fig. B.14), and silver fir (Fig. B.12a) showed discrepancies in terms of spatial prediction patterns between the models, while European beech (Fig. 6b), European larch (Fig. 6c), and Scots pine (Fig. 6d) displayed consistency. In terms of absolute changes in probability of occurrence, models consistently indicated decreasing probabilities for sweet chestnut, Scots pine and black locust (except for the hybrid 2 model in all cases) and increasing probabilities for four broadleaf species such as black alder, European hornbeam, and European birch.

European beech showed differing predictions, increasing in models calibrated with the local species data and remaining stable according to the other models (Figs. 6b, 7). Norway spruce and pedunculate oak followed an inverse pattern, with the fine-scale, hybrid 1, and data pooling models predicting a median net loss and the others predicting stability or slight increase. The probability of occurrence of European larch was predicted to decrease according to all the models but the coarse scale and the data pooling (Figs. 6c, 7).

Among the fine-scale models, we observed the highest expected gain for European beech (median = +0.18 and +0.22 for RCP4.5 and RCP8.5, respectively) and sessile oak (median = +0.14 and +0.17 for RCP4.5 and RCP8.5, respectively) and the highest loss for black locust (median = -0.18 and -0.14 for RCP4.5 and RCP8.5, respectively) and sweet chestnut (median = -0.14 and -0.08 for RCP4.5 and RCP8.5, respectively).

Species richness exhibited a general increase according to models calibrated with local species data such as the fine-scale and hybrid 1 models and models calibrated at the extent of the Piedmont Region (Figs. 8, B.17, Table B.5). Models calibrated at the extent of the Alps had changes in species richness below (i.e., data pooling model) or close to



**Fig. 5.** Comparison between the current potential suitable range of sweet chestnut *Castanea sativa* expressed by the two scales (Fine = local species data + local climate in blue and coarse scale = broad species data + broad climate at the extent of the Alpine region in pink). The two outputs were compared to the Piedmont Forest Map of 2016 (filtered only for the selected forest type, in orange) and the geographic range for Europe (light blue polygons) derived from Caudullo et al. (2017). Panel (a) shows an overview of the entire administrative area, panels (b) and (c) show two closeups corresponding to the Northern (b) and Southern Piedmont (c). Coarse-scale models seemed to overpredict the distribution of sweet chestnut, especially compared to the main stands of the species within Piedmont.



**Fig. 6.** Probability of occurrence of four species (sweet chestnut, European beech, European larch, and Scots pine) for current and future (RCP4.5 and RCP8.5) scenarios for fine-scale (local species data + local climate, upper rows) and coarse-scale (broad species data + broad climate at the alpine extent, lower rows) models. Very different patterns emerged between species in terms of current and future probability of occurrence.

(i.e., coarse-scale model) zero, with the data pooling showing greater variation. The hybrid 1 model was the only one with a different response to climate scenarios, while the hybrid 2 was the one with a higher increase in species richness, which was spatially distributed across the region (Fig. 8d and k). The fine-scale model foresaw increases in species richness in the low mountain areas, while the data pooling model showed different patterns of changes in species richness in the mountain areas of Piedmont (Figs. 8g and n, B.17). Species richness was more stable in lowland and alpine areas according to the fine-scale, coarse-scale, and data pooling models, while the largest variations were observed at medium altitudes. A different pattern was observed for the hybrid models, where richness change was inversely related to elevation.

## 4. Discussion

Species Distribution Models (SDMs) along with future scenarios of climate and land use have the potential to be a fundamental part of spatially explicit landscape conservation and restoration for numerous species (Guisan et al., 2013; Mateo et al., 2019; Zurell et al., 2022). However, most predictive SDMs are typically conducted at coarse spatial scales (i.e., continental to global extent and kilometers resolution), which is hardly useful for reserve selection at fine scales, or in

considering where to move organisms in assisted migration. On the other hand, locally calibrated models suffer of niche truncation, overlooking environmental conditions that a species may withstand and are therefore potentially incorrect when extrapolated to new conditions such as changing climates. Therefore, the aim of this study was to evaluate the role of spatial scales in local planning and management and the ecological consequences of modeling decisions.

#### 4.1. The role of spatial scale in SDMs

Our study demonstrates that SDMs built at different scales yield different spatial predictions and performance. Models trained with local species data (i.e., fine-scale, hybrid1, and data pooling models) performed better than coarse-scale and hybrid-scale models based on a broad European species data for current times (EU-Forest inventory; Mauri et al., 2017). This performance was especially evident in the internal spatial-block cross-validation. In the independent validation, models trained with local data only showed a better AUC than the others, and the patterns of performance were more complex. Our results highlight the distinctive characteristics of different scales of response and predictor variables (Anderson and Raza, 2010; Mateo et al., 2019). Fine-scale models can better capture local conditions, benefiting from dynamically downscaled RCM climate data and finer spatial resolution



**Fig. 7.** Boxplots representing the change in probability of occurrence of thirteen species according to the two climate scenarios (RCP4.5 and RCP8.5) and the input dataset (fine = local species data + local climate, coarse = broad species data + broad climate at the extent of the Alps). Delta between -0.05 and 0.05 were removed to enhance differences between the frameworks. Models calibrated at the broad extent generally predicted fewer changes.

and higher density of points of species data (i.e., inventories). Nevertheless, models fitted with species data from a partial section of a species' ecological niche suffer from niche truncation and express truncated response curves (Sánchez-Fernández et al., 2011; Chevalier et al., 2021; 2022). Conversely, coarse-scale models, while encompassing a broader portion of the species niche, can lead to higher commission errors due to increased false positives (see for instance sweet chestnut within our study; Fig. 5), but are less sensitive to extrapolation problems to new conditions, as revealed by the results of species richness for future times. These behaviors were evident also when comparing future expected changes in probability of occurrence and species richness (Figs. 6, 7, B.12–17 Supplementary Materials), where coarse-scale models predicted a magnitude of changes in probability closer to zero and fine-scale models predicted higher negative values. Hybrid and data pooling models showed more individualistic responses. The latter predicted changes in the probability of occurrence of different species that were closer to fine-scale models, but changes in species richness that were closer to coarse-scale models.

While our study found that climate data did not significantly affect model performance, spatial patterns and expected changes in species richness were affected by the type of climate dataset. Indeed, the characteristics of climate data can impact spatial outcomes in terms of probability of occurrence and binary maps (Bobrowski and Udo, 2017; Patiño et al., 2023). Patiño et al. (2023) showed the potential of



Difference in species richness

**Fig. 8.** Expected changes in probability-based species richness according to the different climate scenarios (a-g = RCP4.5, h-n = RCP8.5) and modeling frameworks both in terms of values (a, h) and spatial patterns across Piedmont Region (b–g and i–n). Models calibrated at the broad extent had changes in species richness closer to zero than models calibrated at the local extent.

finer-resolution climate data in detecting warming trends and mesorefugia by comparing CHELSA with its downscaling version for Canary Islands (~100 m) even if their performance did not show significant difference. For this reason, it is recommended to account for climate uncertainty by using ensembles of multiple dissimilar regional climate models when projecting into the future (Knutti et al., 2013). For instance, a recent pan-European study on tree species distributions applied 11 different RCMs at ~10 km resolution to project future change scenarios (Mauri et al., 2022). However, in our study, we used data from a single climate model for future local climate, which may be a limitation.

The choice of scale in SDMs is a critical factor, and in our study finescale models performed better in capturing local conditions and the current distribution of species. Nevertheless, when fine-scale response data are not accessible, coarse-scale data can still offer valuable insights, especially for certain species. Given the absence of consistent improvement patterns across different extents of broad inventories, we recommend that researchers opt for broader extents to mitigate the risk of niche truncation in such cases, especially when predicting future conditions. Data pooling can partially address this issue by including broad species data encompassing, which cover a large part of the niche, but also local species data, which reflect the peculiar conditions at the local scale. Furthermore, hierarchical approaches integrating variables at different scales have been proposed as a solution to address spatial mismatches in SDMs predictions (Pearson et al., 2004; Mateo et al., 2019; Simon et al., 2023). However, it is worth mentioning that hierarchical modeling has not shown consistent predictions improvement compared to common approaches, especially because of challenges in their validation (El-Gabbas and Dormann, 2018; Simon et al., 2023).

Our choice of using Bayesian Additive Regression Trees (BART) was supported by preliminary tests, which demonstrated comparable performance to ensemble models, as highlighted by previous studies (e.g., Baquero et al. 2021, Konowalik and Nosol 2021). We also experimented with different subsets of predictor variables (no filtering, principal components, VIF and correlation filter) and chose a variable reduction approach based on variable importance, as it offered faster computation and facilitated ecological assessment.

# 4.2. Current and future probability of occurrence of the main tree species and species richness: insights on niche truncation

Our study provides insights into the reliability of different tree species' predictions under various frameworks. Comparisons with local forest maps, European geographic range (Caudullo et al., 2017), EU-Trees4F (Mauri et al., 2022), and literature revealed both consistent and divergent results (Fig. B.18). Our results corroborated existing literature (Hanewinkel et al., 2013; Dyderski et al., 2018; Mauri et al., 2022; Noce et al., 2023), indicating probability increases for silver fir, particularly under the fine-scale RCP4.5 scenario, and European beech in fine-scale models. Conversely, decreases in probability were observed for European larch, especially in the fine-scale model, as well as for Scots pine and Norway spruce, the latter being more pronounced in the fine-scale model. Notably, many of the studies we used as references did not mask unvegetated areas at high elevations or in urban regions (e.g., Hanewinkel et al. 2013, Dyderski et al. 2018, Noce et al., 2023). In doing so, they included as suitable areas that we did not expect to be suitable in the next 50-100 years, such as unvegetatated areas and rocks at high elevations. This consideration is particularly important for montane and subalpine species such as the European larch.

Overall, many species showed different responses to the spatial scales of the predictors. We discuss two examples of tree species with an important history of use in Piedmont: sweet chestnut and European larch. Our analysis of sweet chestnut showed significantly different spatial predictions between fine-scale and coarse-scale models, yet the magnitude of the probability of occurrence loss remained similar. In the current scenario, the fine-scale model showed greater ecological reliability, identifying hilly and low mountain regions as the most suitable habitats for the species. This aligns with local traditional silvicultural practices that have historically favored sweet chestnut in these areas due to its value for fruit, timber, and fuelwood production, a practice also observed in other Alpine regions such as Canton Ticino, Switzerland (Conedera et al., 2004; Camerano et al., 2017). Conversely, coarse-scale models emphasized lowland areas (i.e., the Po Valley) as climatically suitable regions, but these models may overlook the influence of traditional land use and only reflect the potential distribution of the species in the region. The data pooling model, when applied to sweet chestnut, revealed spatial patterns more similar to the fine-scale model. This highlights the importance of the spatial scale and the inclusion of basal area information retained in this dataset. In terms of future scenarios, the expected future decline in the probability of occurrence of sweet chestnut is likely due to its expansion into areas of lower climatic suitability, such as regions potentially dominated by stands of sessile and downy oak (Conedera et al., 2004; Camerano et al., 2017).

When comparing models for a different species, such as the European larch, we observed a different outcome. Current probability of occurrence was relatively consistent between the modeling frameworks (r =0.88), but the fine-scale model displayed greater suitability at lower elevations, particularly in the Southern and Northern sectors of the study area. In spatial predictions more than in model performance, the effect of climate data emerged. Therefore, we attributed this discrepancy to differences in climate scenarios but also to possible niche truncation. Additionally, the relative variable importance exhibited similar patterns between the frameworks, with a slightly greater emphasis on temperature in the coarse-scale model. In terms of future scenarios, both models projected a decline in the probability of occurrence at lower elevations, but the fine-scale model predicted a more substantial loss compared to the coarse-scale model. The fine-scale result is in line with results from the literature (Dyderski et al., 2018; Mauri et al., 2022), likely due to the comprehensive representation of European larch in Piedmont region, encompassing a wide array of the environmental conditions across its entire geographic range because of the historical use of the species across several altitudinal and ecological gradients (Garbarino et al., 2011).

While this study provides valuable insights into the impactof spatial

scale and modeling decisions on SDM performance and reliability, it does not come without limitations. First, the models do not account for genetic variation or provenance, which can significantly influence species' adaptive capacity and response to environmental change (e.g., Marchelli et al. 2017, Marchi 2024). Second, population dynamics were not explicitly included, as we focused on pure correlative models: This approach potentially overlooks key processes such as dispersal, recruitment, and competition, which are essential for understanding future species distributions (e.g., Mauri et al. 2022). We should also note again that the modeling choice of a climate-ensemble modeling over the ensemble of predictions for singular climate models may reduce the extent and the magnitude of extreme climate conditions. Finally, forest management practices, which can influence habitat availability and species persistence, were not incorporated. Nevertheless, the dataset developed in this study may have the potential for applications in regional forestry and conservation planning. By providing fine-scale models that are accurate for the present, but also coarse-scale and data pooling methods that are more sound for future climate change scenarios, this dataset allows for the identification of habitat suitability at a resolution that aligns with the management practices and conservation priorities of the Piedmont region while limiting niche truncation for the future.

### 4.3. SDMs as tools for local forest management

As previously discussed, SDMs can be particularly important for implementing assisted migration and ecological restoration within local reforestation plans (Wan et al., 2017; Begemann et al., 2021; Twardek et al., 2023). Advancements in forest planning should therefore account for spatial scales of response and predictive variables within predictive models, especially given the growing body of research on microclimate variation based on fine-scale topography and canopy cover (Lembrechts et al., 2019; De Frenne, et al., 2021; Haesen et al., 2023).

We advocate for adequate testing of species data (i.e., forest inventories) and predictor variables within SDMs for forest planning and management. Fine-scale models are valuable for current predictions, particularly when local data sources and response data align with the scale of application. Moreover, in our study area, fine-scale models appeared to amplify local anthropogenic signals associated with the traditional use of sweet chestnut. This result underscores the difficulty of aligning meaningful spatial scales of ecological processes with available climate data, a major challenge especially in long-lasting humandominated mountain systems such as the Alps, where human activities have profoundly altered ecosystem spatial patterns (Batzing et al., 1996; Plieninger et al., 2016; Zanon et al., 2018). Coarse-scale models or data pooling approaches, on the other hand, can be trained over broader geographic extents, covering a larger portion of a species' niche (Anderson and Raza, 2010; Sánchez-Fernández et al., 2011). We should still note that SDMs usually refer to the species level, but many adaptation strategies take place at the level of genotypes and populations, which are defined at local spatial scales. A multi-scale approach can be particularly useful in complex forest policy frameworks, where various model scales correspond to different policy levels. Indeed, multi-scale approaches can enhance the discussion with stakeholders and increase the robustness of predictions (Begemann et al., 2021; Sharma et al., 2023).

#### 5. Conclusion

In this study, we explored the importance of spatial scales in Species Distribution Models (SDMs), shedding light on their core relevance in ecological research and forest management within the context of climate change. Our results stress the trade-off between reliability and performance for current times and the problem of niche truncation when extrapolating to changing climates that fine-scale models suffer from. Models built upon local species data (i.e., forest inventory) performed better than their coarser counterparts for current times, while highresolution regional climate models allowed for precision in capturing local conditions, making them indispensable for current predictions, ecological assessments, and localized forest management.

Fine-scale models also magnified local anthropogenic influences by emphasizing the profound impact of local traditional practices like sweet chestnut and European larch silvicultural systems. In contrast, coarse-scale models may miss these nuances, favoring climatic suitability over intricate local practices. Therefore, incorporating fine-scale data is essential when it aligns with the study's scale of application.

However, we demonstrated how fine-scale models do not come without problems. Niche truncation can occur when response data encompasses only a portion of a species' ecological niche, potentially affecting future predictive performance. This result emerged from the comparison of fine-scale, coarse-scale and data pooling models predictions. Therefore, ecologists and forest practitioners should carefully choose the scale of response data based on the study's scope and the species under investigation. In terms of climate data, while they did not significantly affect model performance, their resolution can impact the spatial outcomes of probability of occurrence and binary maps.

In the light of the ongoing climate and land use changes, SDMs have an increasingly important role in forest planning and management. Considering differences in spatial scales, integrating fine-scale models and microclimate data, and using data pooling by integrating species data with different spatial scales can enhance the performance and reliability of species distribution models for ecologists, policymakers, and forest practitioners.

#### CRediT authorship contribution statement

Nicolò Anselmetto: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Conceptualization. Donato Morresi: Writing – review & editing, Methodology, Formal analysis. Simona Barbarino: Writing – review & editing, Methodology, Formal analysis. Nicola Loglisci: Writing – review & editing, Methodology, Formal analysis. Matthew G. Betts: Writing – review & editing. Matteo Garbarino: Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence this paper.

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#### Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2024.110361.

## Data availability

Code and processed data supporting this study are publicly available at 10.6084/m9.figshare.26232551.

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