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ORIGINAL PAPER

A modeling approach to determine substitutive tree species for sweet chestnut in stands affected by ink disease

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Abstract Biological invasions, driven mainly by human activities, pose significant threats to global ecosystems and economies, with fungi and fungal-like oomycetes playing a pivotal role. Ink disease, caused by *Phytophthora cinnamomi* and *P.* × *cambivora*, is a growing concern for sweet chestnut stands (*Castanea sativa*) in Europe. Since both pathogens are thermophilic organisms, ongoing climate change will likely exacerbate their impact. In this study, we applied species distribution modeling techniques to identify potential substitutive species for sweet chestnut in the light of future climate scenarios SSP126 and SSP370 in southern Switzerland. Using the presence-only machine learning algorithm MaxEnt and leveraging occurrence data from the global dataset GBIF, we delineated the current and projected (2070–2100) distribution of 28 tree species. Several exotic species emerged as valuable alternatives to sweet chestnut, although careful consideration of all potential ecological consequences is required. We also identified several native tree species as promising substitutes, offering ecological benefits and potential adaptability to climatic conditions. Since species diversification fosters forest resilience, we also determined communities of alternative species that can be grown together. Our findings represent a valuable decision tool for forest managers confronted with the challenges posed by ink disease and climate change. Given that, even in absence of disease, sweet chestnut is not a future-proof tree species in the study region, the identified species could offer a pathway toward resilient and sustainable forests within the entire chestnut belt.

Keywords Invasive pathogens · Tree distribution modeling · Climate change · Forest area

Introduction

Biological invasions resulting from the unintentional or deliberate anthropogenic introduction of species are a major consequence of globalization and constitute a significant component of global environmental change (Vitousek et al. 1996; Simberloff et al. 2013). Consequences of introductions for native ecosystems may be dramatic, including alteration of their fundamental structure, loss of biodiversity, and subsequent threat of functioning (Ehrenfeld 2010). Biological invasions also impact world economies, with annual costs estimated at about 10 billion Euros in Europe and at over 21 billion US dollars in the United States (Hulme et al. 2009; Fantle-Lepczyk et al. 2022).

Forests are particularly prone to biological invasions all around the world (Liebhold et al. 2017) and fungi and fungal-like oomycetes play a significant role among invasive

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organisms (Desprez-Loustau et al. 2007; Wingfield et al. 2017). Global movement of live plants and plant material has been recognized as an important invasion pathway for exotic pests and pathogens (Liebhold et al. 2012). In some cases, invasive forest pathogens have caused large-scale changes of native ecosystems and modified the ecological dynamics through local and regional extinction of key host species. A well-known example is *Cryphonectria parasitica*, the causal agent of chestnut blight, which dramatically reduced populations of American chestnut (*Castanea dentata*) in North America (Anagnostakis 1987). Within a few decades, a keystone native species in local forest ecosystems experienced a strong niche contraction and significant changes in its ecological role (Paillet 2002; Burke 2012), with a cascade of consequences for wildlife and people. The fungus *Ophiostoma ulmi*, which causes Dutch elm disease, is another famous invasive pathogen that in the last century killed hundreds of millions of elms (*Ulmus* spp.) trees in Europe and North America (Gibbs 1978). Starting in the Netherlands in the late 1910s, the pathogen rapidly spread through much of Europe, and in the late 1920s, it was introduced to North America. The second epidemic of Dutch elm disease started around the 1940s, but was caused by *Ophiostoma novo-ulmi*, a much more aggressive pathogen. By the 1990s, very few mature elms were left in Britain and much of continental Europe. In North America, the impact of Dutch elm disease on American elms has been almost as severe as chestnut blight on American chestnut (Loo 2009).

Sweet chestnut (*Castanea sativa* Mill.; family Fagaceae) is an iconic tree species in southern Europe where it has been cultivated for centuries for its valuable wood and nuts (Conedera et al. 2004). Its extensive current distribution, covering over 2.5 million ha due to active management, has pushed the species to the limits of its ecological niche, making it difficult to determine its original range (Conedera et al. 2004). Despite being widely distributed, sweet chestnut is a poor competitor and requires active forest management to maintain its populations (Clark et al. 2023). It is also threatened by a few invasive and destructive diseases, in particular chestnut blight and ink disease.

Already known in southern Europe in the eighteenth century, ink disease causes root and collar rot of adult trees and of seedlings in nurseries, plantations, and forests (Vannini et al. 2001). The two main causal agents of this disease are

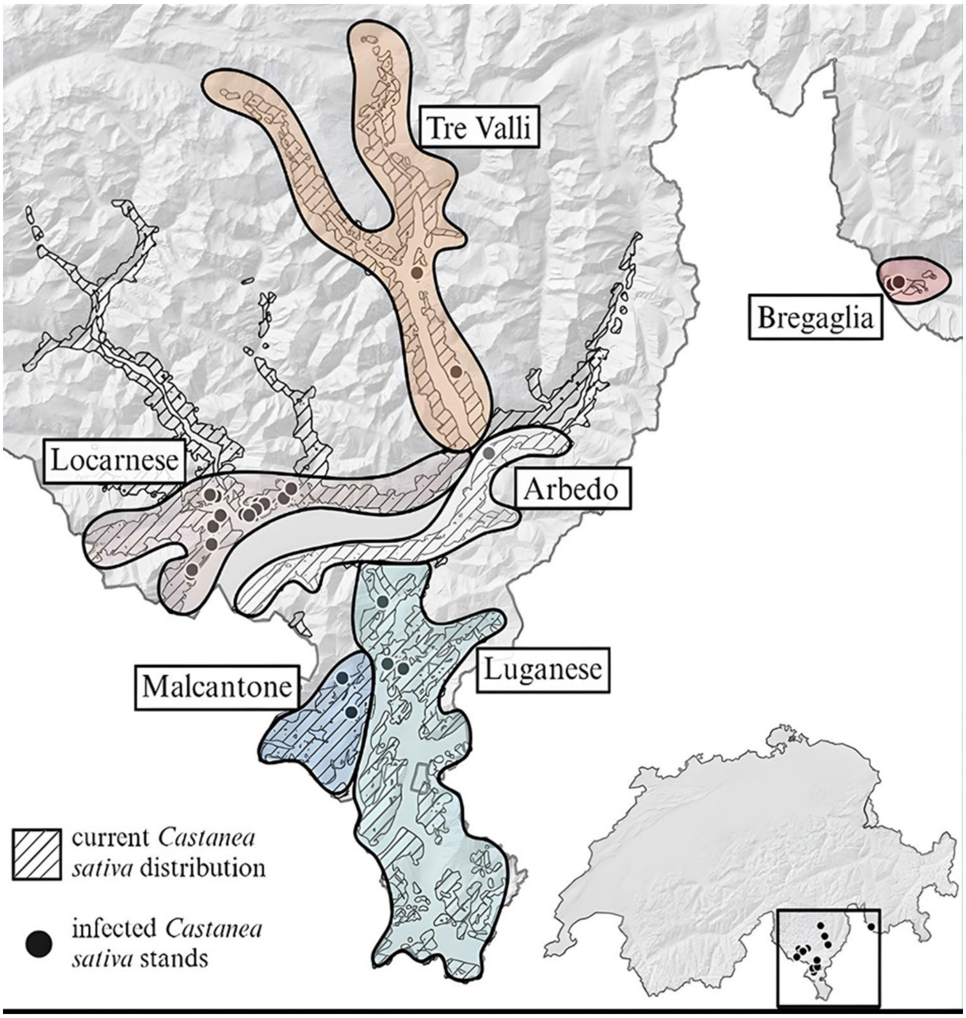


Fig. 1 Locations of currently known outbreaks of ink disease (*Phytophthora cinnamomi* and *P.* × *cambivora*) of sweet chestnut (*Castanea sativa*) in southern Switzerland (Prospero et al. 2023) and the six regions delimitated to account for local microclimatic and topographic variability. Background: digital elevation model (©Federal Office of Topography swisstopo, https://www.swisstopo.admin.ch/en/height-model-swissalti3d)

Phytophthora × *cambivora* (Petri) Buism and *P. cinnamomi* Rand, two oomycetes originating from Asia. Since the end of the last century, a resurgence of ink disease has been noted in chestnut stands in several European countries, including Italy, France, and Switzerland (Vettraino et al. 2001; Turchetti and Maresi 2006; Prospero et al. 2023). At the same time, the pathogens are spreading northward; cases have been reported, for example, in Germany and England (Vannini et al. 2001; Peters et al. 2019). Since both *Phytophthora*-species have a thermophilic character (Zentmyer 1981), the re-emergence of ink disease may be driven by global temperature increases (especially during the winter) and will most likely continue in the future. Unfortunately, to

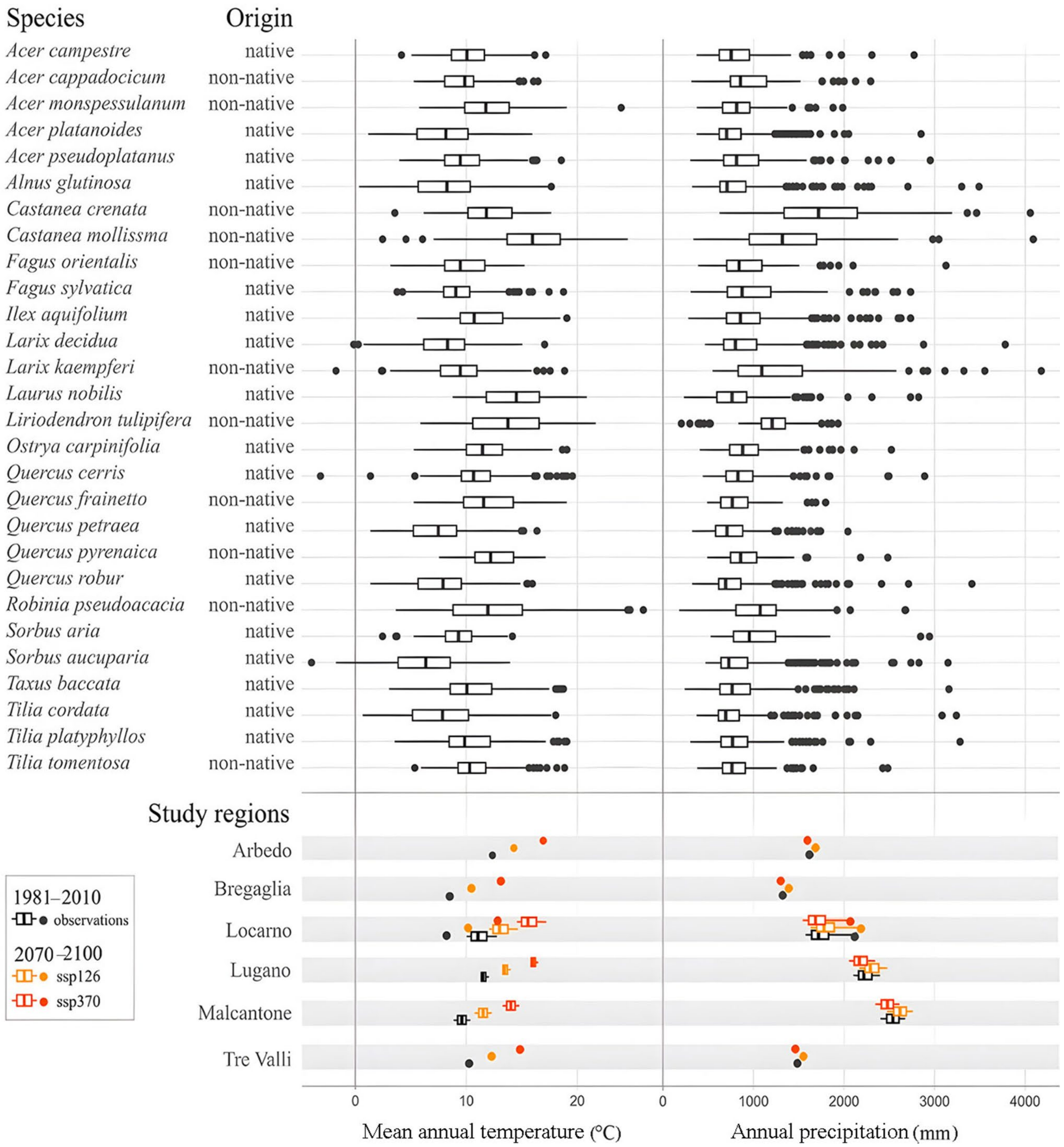


Fig. 2 Selected tree species (native and non-native to southern Switzerland) and study regions with their annual temperature and precipitation ranges (based on data by Karger et al. 2017)

Table 1 MaxEnt model output for each region and species for the future period 2070–2100 under the two scenarios SSP126 and SSP370. Bold indicates where the species-specific threshold was reached (indicating potential presence of the species)

Species	Family	Status	Occ	AUC diff	CBI	Region												SST
						Bregaglia		Locarnese		Luganese		Malcantone		Tre Valli		Arbedo		
						SSP 126	SSP 370	SSP 126	SSP 370	SSP 126	SSP 370	SSP 126	SSP 370	SSP 126	SSP 370	SSP 126	SSP 370	
Acer campestre	Sapindaceae	N	255	0.01	0.73	**0.51**	**0.52**	**0.60**	**0.56**	**0.62**	**0.57**	**0.61**	**0.62**	**0.58**	**0.57**	**0.53**	**0.51**	0.48
Acer cappadocicum	Sapindaceae	E	66	0.08	0.83	**0.38**	**0.36**	**0.54**	**0.39**	**0.49**	**0.37**	**0.53**	**0.42**	**0.52**	**0.44**	**0.43**	0.33	0.35
Acer monspessulanum	Sapindaceae	E	181	–0.02	0.83	0.33	**0.50**	**0.57**	**0.70**	**0.34**	**0.47**	0.30	**0.42**	**0.43**	**0.60**	**0.52**	**0.69**	0.33
Acer platanoides	Sapindaceae	N	349	0.03	0.84	**0.56**	**0.57**	**0.65**	**0.65**	**0.69**	**0.69**	**0.69**	**0.69**	**0.66**	**0.66**	**0.63**	**0.64**	0.43
Acer pseudoplatanus	Sapindaceae	N	241	0.03	0.64	0.32	0.34	**0.43**	0.37	**0.41**	0.33	**0.44**	0.35	**0.44**	**0.42**	0.38	0.33	0.41
Alnus glutinosa	Betulaceae	N	332	0.06	0.80	0.36	0.36	0.41	0.39	0.42	0.37	0.47	0.40	0.40	0.39	0.38	0.36	0.48
Castanea crenata	Fagaceae	E	69	–0.01	0.61	0.24	**0.29**	**0.74**	**0.70**	**0.69**	**0.63**	**0.64**	**0.66**	**0.66**	**0.74**	**0.67**	**0.58**	0.27
Castanea mollissima	Fagaceae	E	143	0.04	0.55	**0.32**	**0.32**	**0.28**	**0.27**	0.16	0.14	0.09	0.08	**0.38**	**0.37**	**0.34**	**0.30**	0.22
Fagus orientalis	Fagaceae	E	62	–0.08	0.76	**0.87**	**0.84**	**0.94**	**0.92**	**0.97**	**0.95**	**0.97**	**0.96**	**0.95**	**0.93**	**0.92**	**0.89**	0.51
Fagus sylvatica	Fagaceae	N	220	0.00	0.66	**0.56**	**0.51**	**0.66**	**0.65**	0.31	**0.39**	0.27	0.37	**0.66**	**0.60**	**0.65**	**0.60**	0.38
Ilex aquifolium	Aquifoliaceae	N	225	0.00	0.71	**0.65**	**0.49**	**0.79**	**0.53**	**0.62**	**0.44**	**0.86**	**0.65**	**0.75**	**0.63**	**0.47**	**0.37**	0.24
Larix decidua	Pinaceae	N	259	0.05	0.74	0.02	0.02	0.02	0.03	0.01	0.01	0.01	0.01	0.02	0.03	0.02	0.02	0.38
Larix kaempferi	Pinaceae	E	163	0.01	0.90	**0.70**	**0.55**	**0.66**	**0.45**	**0.63**	**0.42**	**0.80**	**0.61**	**0.77**	**0.59**	**0.54**	0.33	0.37
Laurus nobilis	Lauraceae	N	229	0.00	0.81	0.22	**0.44**	**0.50**	**0.63**	**0.50**	**0.64**	**0.35**	**0.50**	**0.37**	**0.55**	**0.56**	**0.69**	0.23
Liriodendron tulipifera	Magnoliaceae	E	487	–0.01	0.94	0.42	**0.45**	**0.47**	**0.49**	**0.48**	**0.50**	**0.48**	**0.50**	**0.48**	**0.51**	**0.45**	**0.47**	0.45
Ostrya carpinifolia	Betulaceae	N	136	0.00	0.81	**0.52**	**0.37**	**0.47**	**0.35**	**0.37**	0.26	**0.36**	0.26	**0.45**	**0.39**	**0.48**	**0.35**	0.34
Quercus cerris	Fagaceae	N	201	0.03	0.64	**0.64**	**0.71**	**0.76**	**0.82**	**0.77**	**0.85**	**0.71**	**0.81**	**0.70**	**0.75**	**0.80**	**0.84**	0.48
Quercus frainetto	Fagaceae	E	65	0.10	0.88	**0.78**	**0.92**	**0.97**	**0.99**	**0.96**	**0.99**	**0.86**	**0.94**	**0.79**	**0.94**	**0.99**	**1.00**	0.38

Table 1 (continued)

Species	Family	Status	Occ	AUC diff	CBI	Region												SST
						Bregaglia		Locarnese		Luganese		Malcantone		Tre Valli		Arbedo		
						SSP 126	SSP 370	SSP 126	SSP 370	SSP 126	SSP 370	SSP 126	SSP 370	SSP 126	SSP 370	SSP 126	SSP 370	
Quercus petraea	Fagaceae	N	200	0.01	0.64	**0.56**	**0.53**	**0.80**	**0.71**	**0.83**	**0.72**	**0.84**	**0.82**	**0.75**	**0.68**	**0.71**	**0.56**	0.24
Quercus pyrenaica	Fagaceae	E	79	0.03	0.78	**0.57**	**0.77**	**0.84**	**0.92**	**0.82**	**0.91**	**0.66**	**0.80**	**0.47**	**0.55**	**0.89**	**0.95**	0.34
Quercus robur	Fagaceae	N	293	0.02	0.77	**0.54**	**0.54**	**0.55**	**0.54**	**0.48**	**0.46**	**0.44**	0.42	**0.62**	**0.61**	**0.56**	**0.55**	0.43
Robinia pseudoacacia	Fabaceae	E	292	0.02	0.90	**0.55**	**0.58**	**0.61**	**0.60**	**0.61**	**0.59**	**0.61**	**0.61**	**0.63**	**0.64**	**0.61**	**0.58**	0.44
Sorbus aria	Rosaceae	N	101	–0.01	0.89	**0.53**	**0.39**	**0.78**	**0.66**	**0.90**	**0.76**	**0.96**	**0.89**	**0.74**	**0.59**	**0.73**	**0.59**	0.38
Sorbus aucuparia	Rosaceae	N	338	0.03	0.87	**0.57**	**0.55**	**0.64**	**0.62**	**0.61**	**0.62**	**0.58**	**0.61**	**0.66**	**0.64**	**0.63**	**0.61**	0.49
Taxus baccata	Taxaceae	N	299	0.00	0.85	**0.43**	**0.40**	**0.48**	**0.46**	**0.50**	**0.48**	**0.52**	**0.50**	**0.48**	**0.45**	**0.47**	**0.44**	0.38
Tilia cordata	Malvaceae	N	360	0.06	0.79	0.40	0.38	0.43	0.40	0.43	0.39	0.44	0.40	0.41	0.39	0.39	0.37	0.45
Tilia platyphyllos	Malvaceae	N	258	0.00	0.70	0.37	0.41	**0.50**	**0.53**	**0.52**	**0.56**	**0.51**	**0.55**	**0.49**	**0.52**	**0.49**	**0.52**	0.45
Tilia tomentosa	Malvaceae	E	121	0.05	0.76	**0.43**	**0.42**	**0.55**	**0.57**	**0.55**	**0.58**	**0.48**	**0.52**	**0.54**	**0.52**	**0.53**	**0.51**	0.34
Means			215.1	0.02	0.77													

N, native in southern Switzerland; E, exotic in southern Switzerland; Occ, number of occurrence points; AUC diff, difference between area under [receiver operator] curve of testing and training data and CBI (continuous Boyce index); SST, species specific threshold

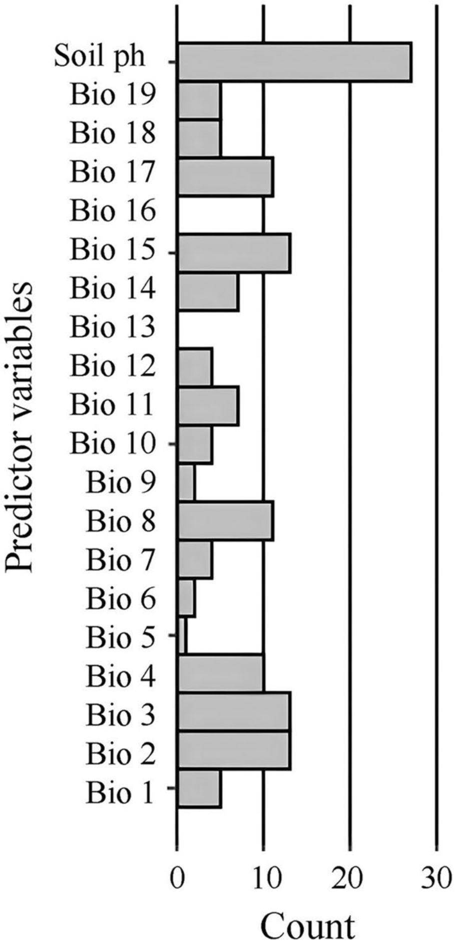


Fig. 3 Importance of the 20 predictor variables based on the frequency with which they were used overall in all species distribution models

date no effective measures can control the disease; preventing the spread of the two pathogens is a key strategy.

Although a recent study conducted by Marzocchi et al. (2024) in Italy suggests that sweet chestnut may be able to coexist in a dynamic equilibrium with ink disease, damage can be locally severe. Such is the case in southern Switzerland, where ink disease of chestnut is mainly caused by *P. cinnamomi* and has become a problem since the 1990s (Prospero et al. 2023). Many chestnut stands are on steep slopes and protect human infrastructure against natural hazards like rock falls and landslides, so the death of chestnut trees can have severe impacts, at least temporarily. Thus, to assure permanent forest cover, besides conserving existing chestnut stands, forest management needs to include active replacement of chestnuts killed by ink disease with other tree species. In this study, we selected potential tree species that can provide the same services as sweet chestnut, then modeled which ones can climatically adapt to two future scenarios of climate change. Since species diversification is a well-known strategy to reduce biotic and abiotic risks, we also determined possible communities of replacement species.

Materials and methods

Study area

In the study area, the southern slopes of the Swiss Alps in the cantons Ticino and Grisons (Fig. 1), sweet chestnut is the most frequent broadleaf tree species between 300 and 900 m a.s.l., and forms an almost continuous forest belt of about 30,000 ha. To account for local microclimatic and topographic variability, we divided the area into six regions, from north to south: Tre Valli (one known outbreak), Arbedo (one known outbreak), Locarnese (15 known outbreaks), Luganese (three known outbreaks), and Malcantone (two known outbreaks) in the canton Ticino, and Bregaglia (two known outbreaks) in the canton Grisons (Fig. 1).

Tree species selection

Potential tree species to replace sweet chestnut were selected among species already present in the study area and species present in European regions with a climate (temperatures and precipitations) like that expected in southern Switzerland in the mid-twenty-first century (replacing time by space). Evergreen conifers were excluded from the selection (except for native *Taxus baccata* as an accessory species) because their introduction would fundamentally alter the appearance of the chestnut-dominated landscape, which carries significant cultural implications in the area. Species preferring basic soils were also excluded, given the dominance of acidic soils in the study area. The selected species also had to be able to provide the same services as sweet chestnut for erosion control and slope stabilization because most chestnut stands with ink disease are on slopes and heavy precipitation is common in the study region (MeteoSwiss 2019). Species enhancing biodiversity by providing shelter and forage for wildlife or soil improvement were preferred. Finally, the selected species should not be highly susceptible to *P. cinnamomi* and *P.* × *cambivora* or other invasive pathogens (in particular, *Hymenoscyphus fraxineus*, which causes ash dieback, and *O. ulmi* and *O. novo-ulmi*) or harmed by game browsing. For exotic (non-native) tree species, the ability to become invasive in the study region was a criterion for exclusion.

Maps on the present potential distribution of several species were obtained using the national forest inventory (Wüest et al. 2021) and the online-tool TreeApp (https://tree-app.ch/), developed by the Federal Office for the Environment (FOEN) and the Swiss Federal Institute for

Table 2 Tested tree species grouped by their model results and origin (native vs. exotic)

Species origin	Group I	Group II	Group III	Group IV
Native	*Acer platanoides* *Quercus robur* *Sorbus. aucuparia*	*Acer pseudoplatanus* *Fagus sylvatica* *Ostrya carpinifolia* *Taxus baccata*	*Acer campestre* *Ilex aquifolium* *Sorbus aria*	*Laurus nobilis* *Quercus cerris* *Quercus petraea* *Tilia platyphyllos*
Exotic	*Fagus orientalis* *Robinia pseudoacacia*		*Acer cappadocicum* *Castanea crenata* *Castanea mollissima* *Tilia tomentosa* *Larix kaempferi*	*Acer monspessulanum* *Liriodendron tulipifera* *Quercus frainetto* *Quercus pyrenaica*
Total (N)	5	4	8	8

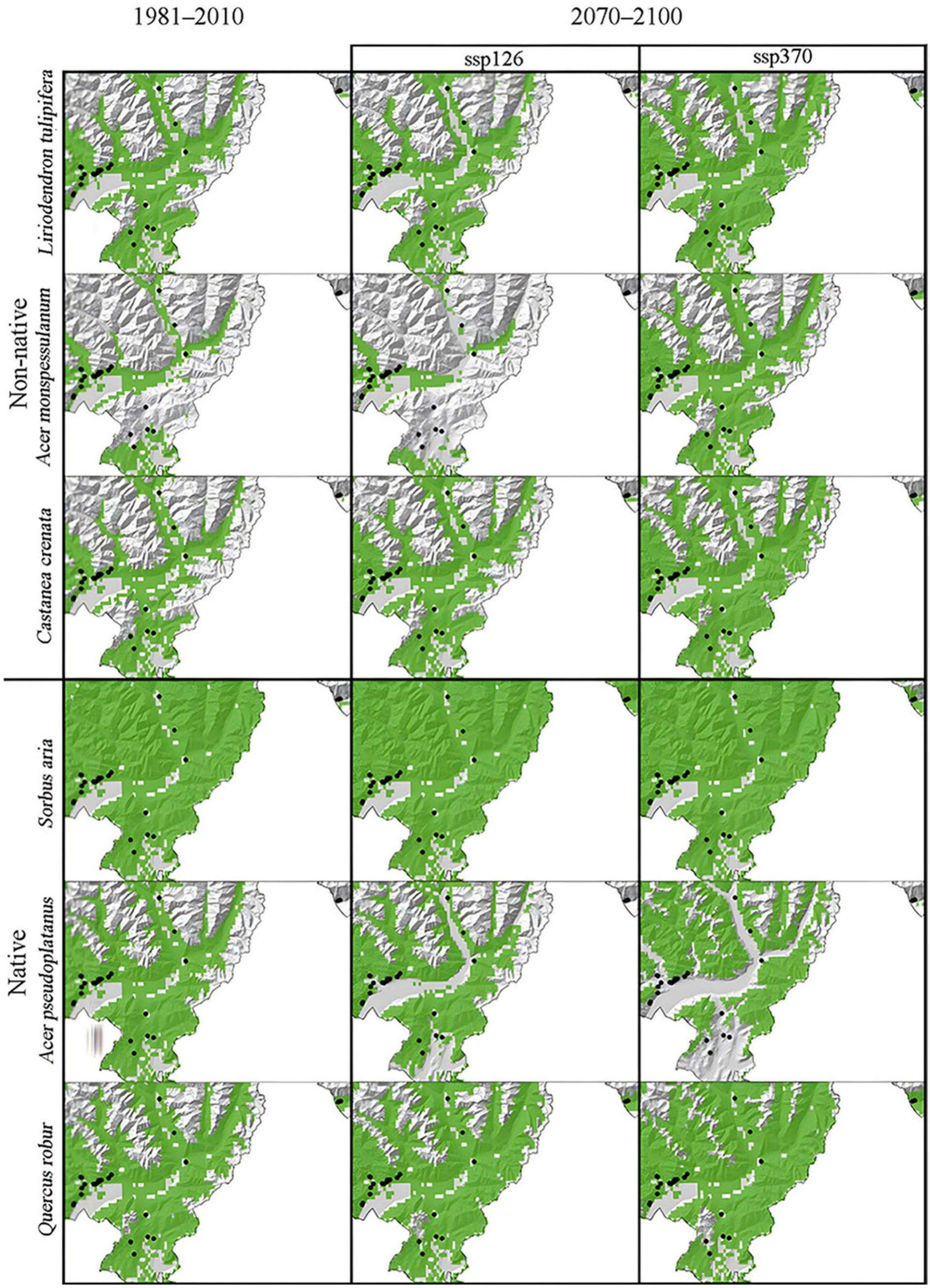
Group, (I) Probability values do not (or barely) differ between today and the two future scenarios (SSP126 and SSP370). (II) Values are highest in the reference period (1981–2010) and decrease in the future. (III) Values are highest in the future under scenario SSP126. (IV) Values are highest in the future under scenario SSP370 (see Material and Methods for details)

Forest Snow and Landscape Research (WSL). These tools give spatial tree species recommendations under different climate change trajectories and were therefore used to identify promising species that are already prevalent in the study area.

To identify well-adapted communities, we combined possible replacement species based on an extensive literature review and by ensuring that each species examined was included in at least one community. We then created a chord diagram in R (version 4.1.0, R Core Team 2021) to visually represent the associations between tree species, indicating which species can act as companion species for other ones and how these connections form distinct communities. Species were excluded if they were not reported to be companion species to any of our listed promising species or we could not find information on them. Subsequently, we documented every identified community. For each region of the study area, a possible species composition was given for the two future scenarios (see below).

Modelling settings

Climatic suitability of the tree species at the selected sites under the future climate scenarios was modeled using the presence-only species distribution model MaxEnt (Phillips et al. 2006), a maximum-entropy based machine learning algorithm (El-Gabbas and Dormann 2018; Manzoor et al. 2018) implemented in the R package dismo (Hijmans et al. 2015). This model is one of the most used and highly accurate algorithms (Yackulic et al. 2013; Booth 2018; Hosni et al. 2020; Zhang et al. 2021). Maximum entropy describes the state at which a system is closest to reality under the known conditions. The MaxEnt model finds the probability distribution with the greatest dispersion or uniformity (= maximum entropy) that is subject to constraints representing incomplete information about the target distribution. This incomplete information results from the environmental conditions (known to us) that determine where a species occurs (Li et al. 2020). Presence-only models take points with a confirmed presence of a species into account, but not points with a confirmed absence. Instead of using absence or pseudo-absence points, MaxEnt integrates "background" points, which are randomly selected from the area of the presence points. Thus, the distribution of presence points can be compared to the distribution of background points along environmental gradients. In our case, 1000 background points provided the most robust results for most species (except for *Castanea mollissima* and *Ilex aquifolium*, for which 10,000 points were chosen). The presence points were obtained via the R package rgbif (Chamberlain et al. 2022) from GBIF (Global Diversity Information Facility; https://www.gbif.org/), an open-source database derived from both historical observations and identification applications such as PlantNet. The DOI of the derived datasets for each species can be found in Table S1 (ordered as in Fig. 2). To account for any sampling bias and autocorrelation, the occurrence data was thinned, using the function thin.algorithm from the R package spThin (Aiello-Lammens et al. 2015; Thurm et al. 2018). We selected a minimum distance of 100 km between each occurrence point, as this distance gave the most robust results in trial runs (data not shown). We used georeferenced data only and deleted any duplicate values.


1981–2010
2070–2100
ssp126
ssp370
Non-native
Liriodendron tulipifera
Acer monspessulanum
Castanea crenata
Native
Sorbus aria
Acer pseudoplatanus
Quercus robur

◂**Fig. 4** Example of the modeled distribution of three native and three non-native species in southern Switzerland. Green area shows the potential occurrence of the species; black dots indicate the current outbreaks of ink disease. Background: Digital elevation model (©Federal Office of Topography swisstopo; https://www.swisstopo.admin.ch/en/height-model-swissalti3d)

The model output was defined as probability of presence between 0 and 1.

Predictor variables

As predictor variables, we used the 19 bioclimatic variables from the CHELSA V2.1 dataset (Karger et al. 2017), which represent annual and seasonal temperature and precipitation trends based on the ERA5 (Hersbach et al. 2020) and CMIP6 datasets (O'Neill et al. 2016) (Table S2). The data are available at a resolution of 30 arc seconds (approximately 1 km) for different time periods, model chains and scenarios. To account for model uncertainty, MaxEnt was run with all five available model chains (GFDL-ESM4, National Oceanic and Atmospheric Administration, USA; UKESM1-0-LL, Met Office Hadley Centre, UK; MPI-ESM1-2-HR, Max Planck Institute for Meteorology, Germany; IPSL-CM6A-LR, Institut Pierre-Simon Laplace, France; MRI-ESM2-0, Meteorological Research Institute, Japan), and the ensemble mean was calculated.

To model possible future scenarios for the period 2070–2100, we selected the SSP126 and the SSP370 shared socioeconomic pathways (SSP). The first scenario describes a sustainable pathway with an increase of radiative forcing by 2.6 W m^{-2} in 2100, and the second is dominated by regional rivalry, leading to higher damage and an increased radiative forcing of 7 W/m^2 in 2100 (Böttinger and Kasang 2021). Mean pH for soil at 30–60 cm depth from ISRIC SoilGrids (Poggio et al. 2021) was included as a further predictor. ISRIC provides global interpolated estimates of different chemical soil properties (Booth 2018), which are used in species distribution modeling studies (Amaral et al. 2017; Lyam et al. 2018). The soil pH grid was transformed to match the resolution and extent of the bioclimatic variables.

The inclusion of many predictor variables can lead to more complex, but also overfitted models (Brun et al. 2020; Li et al. 2020). To reduce the number of predictors, we ran the model for the reference period and analyzed the percentage contribution of each predictor to select the most important ones. Since the objective was to describe the ecological niche as precisely as possible, only mostly uncorrelated variables should be used (Li et al. 2020). Thus, we calculated a correlation tree and selected the variables with the highest contribution of each branch above an absolute Pearson correlation threshold of 0.7. According to Brun et al. (2020), this process helps to avoid collinearity-related effects in the projection of species ranges.

Model evaluation

For cross-validation, the model data were split into 75% training and 25% testing data using the kfold function in dismo. For each species, two evaluation metrics were calculated, namely the model AUCdiff, the difference between the AUC (area under the [receiver operator] curve) of the testing and training data, and continuous Boyce index (CBI). The AUC is a commonly used metric for overall model discriminatory ability (Heller et al. 2017), but there are conflicting reports on whether it should be used in presence-only models (e.g., Yackulic et al. 2013; Low et al. 2021). Hence, here we only considered AUCdiff to quantify model performance (Bosso et al. 2016; Heller et al. 2017). A high AUCdiff would indicate overfitting, i.e., fitting too closely to the training data. In this case, a high AUC (and thus theoretically good performance) would be achieved with the training data, but a low AUC with the test data; consequently, AUCdiff values close to 0 (no difference between training and testing AUC) are desirable (Heller et al. 2017; Fois et al. 2018). The CBI measures how much the model predictions deviate from the distribution of observed presence. Values closer to 1 indicate that the predictions match the actual presence points (Manzoor et al. 2018).

Binary distribution maps

To create binary maps for the presence/absence of a tree species, we determined a species-specific threshold using the threshold function in dismo. The threshold was set to maximize the sum of sensitivity (true positive rate) and specificity (true negative rate). This approach was described by Liu et al. (2005) as one of the most appropriate because a fixed threshold such as the commonly used 0.5 does not consider the different prevalence of each species.

Most promising species per site

The species-specific threshold was used to determine the most promising species for each region and scenario. We here define "promising" as those species for which model results exceed their threshold by 50%.

Table 3 Simulated area of occurrence of each tree species in the reference period (1981–2010) and in the future period 2070–2100 under the two scenarios SSP126 and SSP370 based on the extent of the maps in Fig. S1

Species	1981–2010 Reference	2070–2100 SSP126		2070–2100 SSP370	
	Area (km^2)	Area (km^2)	ΔHist (%)	Area (km^2)	ΔHist (%)
Acer campestre	1075	1492	+38.8	2234	+107.8
Acer cappadocicum	1980	2296	+15.9	2730	+37.9
Acer monspessulanum	682	499	−26.8	1806	+164.8
Acer platanoides	2231	3064	+37.3	4312	+93.3
Acer pseudoplatanus	2000	1916	−4.2	2545	+27.3
Castanea crenata	1193	1685	+41.2	3001	+151.6
Castanea mollissima	0	718	n.a	752	n.a
Fagus orientalis	5220	5473	+4.8	5482	+5.0
Fagus sylvatica	2042	1965	−3.8	2662	+30.4
Ilex aquifolium	4993	5481	+9.8	5481	+9.8
Larix kaempferi	2422	3573	+47.5	4543	+87.6
Laurus nobilis	605	1080	+78.5	1706	+182.0
Liriodendron tulipifera	1536	1572	+2.3	2505	+63.1
Ostrya carpinifolia	4157	3980	−4.3	1467	−64.7
Quercus cerris	234	1479	+532.1	2128	+809.4
Quercus frainetto	1028	1559	+51.7	2185	+112.5
Quercus petraea	1903	2597	+36.5	3458	+81.7
Quercus pyrenaica	810	1250	+54.3	1807	+123.1
Quercus robur	2214	2627	+18.7	3226	+45.7
Robinia pseudoacacia	2407	3164	+31.4	4306	+78.9
Sorbus aria	4345	5435	+25.1	5086	+17.1
Sorbus aucuparia	5428	5429	+0.02	5473	+0.8
Taxus baccata	5424	5403	−0.4	5251	−3.2
Tilia platyphyllos	140	1194	+752.9	1665	+1089.3
Tilia tomentosa	673	1664	+147.3	2200	+226.9

ΔHist, change (in %) compared to the reference period; n.a., not applicable

Results

Selected species

A total of 28 tree species (25 broadleaf and three conifers) belonging to 11 families and 14 genera were tested as possible substitutes for sweet chestnut in the study region (Table 1, Fig. 2). Seventeen species are native to southern Switzerland, and 11 species are native to southern Europe, Asia, or North America. Even though black locust (*Robinia pseudoacacia*) is an invasive species in Switzerland, we included it in the analyses. It is already widespread in parts of the study area (e.g., region Locarnese), where it frequently invades chestnut coppice stands after sylvicultural interventions (thinning, clearcutting). This species strongly contributes to slope stabilization and improves soil through nitrogen fixation.

Model evaluation

The summary results of the species-specific model performances and outputs per region are shown in

Table 4 Groups of tree species, in which each species in a group is a companion species to all species in that group. Each species is included in at least one group. Complete species names are given in Table 3

Group	Species composition
1	*A. platanoides*, *T. platyphyllos*, *I. aquifolium*
2	*Q. pyrenaica*, *Q. petraea*, *Q. robur*
3	*Q. frainetto*, *A. campestre*, *Q. robur*
4	*S. aria*, *A. campestre*, *Q. cerris*
5	*T. tomentosa*, *S. aria*, *Q. petraea*
6	*A. monespessulanum*, *S. aria*, *Q. cerris*
7	*L. nobilis*, *Q. petraea*, *I. aquifolium*
8	*A. cappadocicum*, *Q. cerris*
9	*F. orientalis*, *L. kaempferi*
10	*R. pseudoacacia*, *A. campestre*
11	*L. tulipifera*, *Q. robur*

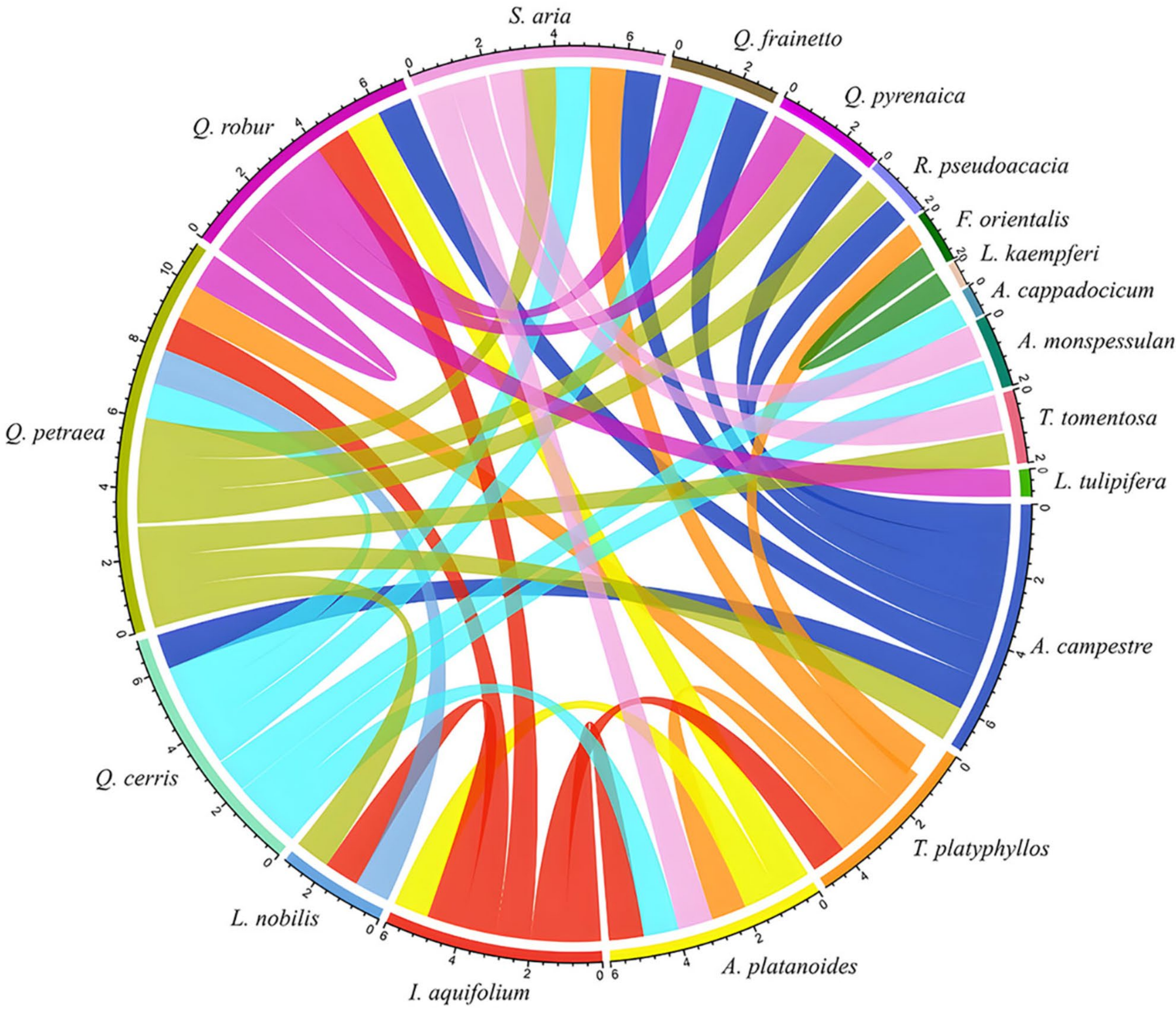


Fig. 5 Chord diagram showing how substitutive species for sweet chestnut could be combined to form mixed forest stands. *Castanea crenata* and *C. mollissima* were not included because we could not find information on known companion species within our list of species

Table 1. The MaxEnt model performed well (average AUCdiff = 0.02 ± 0.03; average CBI = 0.8 ± 0.1), but with a few exceptions. The AUCdiff for *Q. frainetto*, *A. cappadocicum*, and *F. orientalis* were relatively high, indicating a slight overfitting of the model. On the other hand, the CBI for *C. mollissima* especially, but also for *C. crenata*, *A. pseudoplatanus*, *Q. petraea*, and *Q. cerris* was relatively low, indicating rather mediocre applicability of the model to regions outside the study area for these species.

Importance of predictor variables

Five predictor variables on average (range: 3 to 7) were used for each model. While many of the bioclimatic variables were closely correlated, soil pH was nearly independent and was therefore used as a predictor variable for each species. The predictor variables Bio2 (mean monthly diurnal range of temperatures), Bio3 (isothermality = ratio of diurnal to annual range of temperatures) and Bio15 (precipitation seasonality) were used for 48% of the models, Bio8 (mean temperature of the wettest quarter) and Bio17 (mean precipitation of driest quarter) in 40%, and Bio4 (temperature seasonality) in 37% of the models (Fig. 3). In general, seasonality of precipitation and temperature seemed to be the most important factors for the distribution of most species (Fig. 3).

Model results

Before applying the species-specific threshold to create binary maps, we examined the raw results for each species and region (probability of presence between 0 and 1,

Table 1). The analysis revealed that in 56.5% of instances (28 species × 6 regions = 168 instances) the values obtained with SSP126 were higher than those with SSP370. In 35.7% of cases, the opposite situation was observed, whereas in 13 cases the same value was observed for both scenarios. When considering the six regions separately, for most species, the highest probability of presence was reached under SSP126 for all regions but Bregaglia, which is the coolest of all regions. When comparing the raw results (probability of presence) with the species-specific threshold, most species can be considered as present in all or most regions. However, under both future scenarios, the model output for *A. glutinosa*, *L. decidua*, and *T. cordata* did not exceed the species-specific threshold for any region (Table 1). Thus, according to our model results, these three species would not occur under the investigated conditions and were excluded from further analyses.

Based on the results in Table 1, the tested tree species could be assigned to one of four groups (Table 2): (I) Values do not (or hardly) differ between the reference period (1981–2010) and the two future scenarios. (II) Values are highest in the reference period and decrease in the future. (III) Values are highest in the future period under the scenario SSP126. (IV) Values are highest in the future period under the scenario SSP370. The five tree species in group I were projected to be suitable in all regions, today and in the future in both scenarios. The only exception was *Q. robur*, which did not reach the threshold value in Malcantone under SSP370. Group II consists of four native species that are better adapted to the current climate than to the future scenarios. On the contrary, the species in groups III and IV are particularly adapted for future climate conditions. Regarding the spatial distribution of the tested species under the two climate scenarios (Fig. 4; Fig. S1), two main patterns emerged: (1) an expansion or a contraction of the area of occurrence or (2) a shift toward higher altitudes. The area of potential occurrence of most species increased under the two future climate scenarios (19 of 25 species under SSP126 and 23 of 25 species under SSP370; Table 3), with increments ranging from + 0.02% of the historic (1981–2010) occurrence (*Sorbus aucuparia*, SSP126) to + 1089.3% (*Tilia platyphyllos*, SSP370). For most species (18 of 20), the area expansion was larger under SSP370 than SSP126, for one species (*I. aquifolium*) the same under both scenarios (+ 9.8%), and for one species (*Sorbus aria*) larger under SSP126 (+ 25.1%) than SSP370 (+ 17.1%). The area of potential distribution of three species (*Acer monspessulanum*, *A. pseudoplatanus*, *Fagus sylvatica*) decreased under SSP126, but increased under SSP370 (Table 3). Finally, two species (*Ostrya carpinifolia*, *T. baccata*) showed an area contraction under both climate scenarios, with that of *O. carpinifolia* particularly important (–64.7% compared to the historic period) under SSP370.

Species composition

From literature data, we identified 11 combinations of tree species (Table 4, Fig. 5), each containing two to three species. From this analysis, we excluded the four species from group II (Table 3) that performed better in the reference period than in the future under SSP126 and SSP370. Each of the six regions of the study area could harbor most combination of tree species (Table 5), with Bregaglia being the most selective region (8 tree combinations under SSP126 and 8 under SSP370). Within regions, differences in the number of tree combinations between the two scenarios were minimal (same number, plus or minus one), as were differences in the composition of the most promising species (Table 3, Fig. S1). We could not find any documentation of *C. crenata* or *C. mollissima* as companion species of any of our evaluated replacement species, so they were excluded from the analysis of tree species composition.

Discussion

The future distribution of tree species will be influenced not only by climate change but also by biotic disturbances that can severely reduce tree vitality and health (e.g., Vacek et al. 2023). Ink disease caused by the soil-borne oomycetes *Phytophthora cinnamomi* and *P.* × *cambivora* is one of the most severe diseases of sweet chestnut in Europe (Vannini et al. 2001; Robin and Marchand 2022). Its importance is likely to increase because the two pathogens are thermophilic and can persist in the soil over years. In this regard, Gustafson et al. (2022) in a simulation experiment showed that root rot caused by *P. cinnamomi* has the potential to seriously hamper restoration efforts of American chestnut (*C. dentata*) in the eastern United States under warming climate. In our study, we selected 28 tree species and used a modeling approach (model MaxEnt) to test their suitability to replace sweet chestnut in stands affected by ink disease in southern Switzerland in the two climate scenarios.

For most species, the model MaxEnt performed well, as shown by the formal evaluation criteria (AUCdiff and CBI), but also by a logical evaluation of the results. In general, the seasonality of precipitation and temperature seem to be the most important factors for the distribution of most species, as observed in previous studies (e.g., Dyderski et al. 2018). Since we only used one modelling algorithm due to time constraints, we were able to handle a larger number of species. Although the algorithm was adapted to each species, the raw model outcomes of the different species cannot be compared because the different amount of reference data available for each species would influence the species-specific threshold. For this reason, we calculated species-specific threshold to derive binary results for presence/absence.

Table 5 Recommendation per region for individual tree species and species composition for both future climate scenarios SSP126 and SSP370. The most promising species for each region are highlighted in bold. Complete species names are given in Table 3

Region	Scenario	Groups (see Table 4)	Tree species
Bregaglia	SSP126	2,3,4,5,6,8,9,10	*A. campestre, A. cappadocicum, A. platanoides, C. mollissima,* ***F. orientalis, I. aquifolium***, ***L. kaempferi***, *Q. cerris,* ***Q. frainetto, Q. petraea, Q. pyrenaica***, *Q. robur, R. pseudoacacia, S. aria, S. aucuparia, T. tomentosa*
	SSP370	2,3,4,5,7,8,9,10,11	*A. campestre, A. cappadocicum, A. platanoides, C. crenata, C. mollissima,* ***F. orientalis, I. aquifolium, L. nobilis***, *L. kaempferi, L. tulipifera,* ***Q. cerris, Q. frainetto, Q. petraea, P. pyrenaica***, *Q. robur, R. pseudoacacia, S. aria, S. aucuparia, T. tomentosa*
Locarnese	SSP126	2,3,4,5,6,7,8,9,10,11	*A. campestre, A. cappadocicum,* ***A. monspessulanum, A. platanoides, C. crenata***, *C. mollissima,* ***F. orientalis, I. aquifolium***, *L. nobilis,* ***L. kaempferi***, *L. tulipifera,* ***Q. cerris, Q. frainetto, Q. petraea, Q. pyrenaica,*** *Q. robur, R. pseudoacacia,* ***S. aria***, *S. aucuparia, T. platyphyllos,* ***T. tomentosa***
	SSP370	1,2,3,4,5,6,7,8,9,10, 11	*A. campestre, A. cappadocicum, A. monspessulanum,* ***A. platanoides***, ***C. crenata, C. mollissima, F. orientalis, I. aquifolium, L. nobilis***, *L. kaempferi, L. tulipifera, Q. cerris, Q. frainetto, Q. petraea, Q. pyrenaica, Q. robur, R. pseudoacacia, S. aria, S. aucuparia, T. platyphyllos,* ***T. tomentosa***
Luganese	SSP126	1,2,3,4,5,6,7,8,9,10,11	*A. campestre, A. cappadocicum, A. monspessulanum,* ***A. platanoides, C. crenata, F. orientalis, I. aquifolium, L. nobilis***, ***L. kaempferi***, *L. tulipifera,* ***Q. cerris, Q. frainetto, Q. petraea, Q. pyrenaica***, *Q. robur, R. pseudoacacia,* ***S. aria***, *S. aucuparia, T. platyphyllos,* ***T. tomentosa***
	SSP370	1,2,3,4,5,6,7,8,9,10,11	*A. campestre, A. cappadocicum, A. monspessulanum,* ***A. platanoides, C. crenata, F. orientalis, I. aquifolium, L. nobilis***, *L. kaempferi, L. tulipifera,* ***Q. cerris, Q. frainetto, Q. petraea, Q. pyrenaica***, *Q. robur, R. pseudoacacia,* ***S. aria***, *S. aucuparia, T. platyphyllos,* ***T. tomentosa***
Malcantone	SSP126	1,2,3,4,5,7,8,9,10,11	*A. campestre****, A. cappadocicum, A. platanoides, C. crenata, F. orientalis, I. aquifolium, L. nobilis***, *L. tulipifera,* ***L. kaempferi***, *Q. cerris,* ***Q. frainetto, Q. petraea, Q. pyrenaica***, *Q. robur, R. pseudoacacia,* ***S. aria***, *S. aucuparia, T. platyphyllos,* ***T. tomentosa***
	SSP370	1,4,5,6,7,8,9,10,11	*A. campestre, A. cappadocicum, A. monspessulanum,* ***A. platanoides, C. crenata, F. orientalis, I. aquifolium, L. nobilis***, ***L. kaempferi***, *L. tulipifera,* ***Q. cerris, Q. frainetto, Q. petraea, Q. pyrenaica***, *R. pseudoacacia****, S. aria***, *S. aucuparia, T platyphyllos,* ***T. tomentosa***
Tre Valli	SSP126	1,2,3,4,5,6,7,8,9,10,11	*A. campestre, A. cappadocicum, A. monspessulanum,* ***A. platanoides, C. crenata, C. mollissima, F. orientalis, I. aquifolium***, *L. nobilis,* ***L. kaempferi***, *L. tulipifera, Q. cerris,* ***Q. frainetto, Q. petraea***, *Q. pyrenaica, Q. robur, R. pseudoacacia,* ***S. aria***, *S. aucuparia, T. platyphyllos,* ***T. tomentosa***
	SSP370	1,2,3,4,5,6,7,8,9,10,11	*A. campestre, A. cappadocicum****, A. monspessulanum, A. platanoides, C. crenata, C. mollissima, F. orientalis, I. aquifolium, L. nobilis***, ***L. kaempferi***, *L. tulipifera,* ***Q. cerris, Q. frainetto, Q. petraea, Q. pyrenaica***, *Q. robur, R. pseudoacacia,* ***S. aria***, *S. aucuparia, T. platyphyllos,* ***T. tomentosa***
Arbedo	SSP126	1,2,3,4,5,6,7,8,9,10,11	*A. campestre, A. cappadocicum,* ***A. monspessulanum***, *A. platanoides****, C. crenata, C. mollissima, F. orientalis, I. aquifolium, L. nobilis***, *L. tulipifera,* ***Q. cerris, Q. frainetto, Q. petraea, Q. pyrenaica***, *Q. robur, R. pseudoacacia,* ***S. aria***, *S. aucuparia, T. platyphyllos,* ***T. tomentosa***
	SSP370	1,2,3,4,5,6,7,8,10,11	*A. campestre,* ***A. monspessulanum***, *A. platanoides,* ***C. crenata***, *C. mollissima,* ***F. orientalis, I. aquifolium, L. nobilis,*** *L. tulipifera****, Q. cerris, Q. frainetto, Q. petraea, Q. pyrenaica***, *Q. robur, R. pseudoacacia****, S. aria***, *S. aucuparia, T. platyphyllos,* ***T. tomentosa***

This approach has a limitation because some species can be marked as absent even if they might be present. For example, *A. glutinosa* and *T. cordata* currently occur in the study area, but the model projected their absence, even in the reference period. To account for these uncertainties derived from the modeling approach chosen, we could use additional modeling algorithms and pool their results. However, a study by Booth (2018), which elaborated on the species distribution modeling tools and databases that can assist in managing forests under climate change, recommended, among others, exactly the tools and databases used in our study and, thus, confirmed our approach. The authors mentioned MaxEnt as one of the most used algorithms, the CHELSA dataset for climate predictor variables, ISRIC SoilGrids as a source for soil predictor variables, and the use of the GBIF database for occurrence data.

Although the assessment of the future potential extent of the forest area in the study region was not the main objective of this study, our results show an increase of the overall potential range in which the tested tree species can occur in the future. Noteworthy, this increase is expected to be stronger under the more extreme climate scenario SSP370 than under the milder SSP126 scenario. Since the study region is characterized by altitudes ranging from about 200 m to more than 3000 m a.s.l., and deep alpine valleys, an increase in temperature will most likely open large amounts of newly suitable land at higher altitudes, with an upward shift of the tree line. Interestingly, Noce et al. (2023), using species distribution models, showed that in the Italian Alps and Apennines, most major tree species are expected to experience a future contraction in their altitudinal distribution, although some of them may spread beyond the current tree line. However, the authors specify that it is generally difficult to clearly define successful or unsuccessful species.

In our study, some of the tested tree species show different trends in their site-specific and spatial results, which underlines the heterogeneity, mainly due to altitude, within the study area. Based on our modeling, four tree species (*A. pseudoplatanus*, *F. sylvatica*, *O. carpinifolia*, *T. baccata*) performed better in the reference period (1981–2010) than in the future, which suggests they would not be a good alternative to sweet chestnut under climate change. All these species are native to southern Switzerland and already present in the study area, either as main species (e.g., *F. sylvatica*) or accessory species (e.g., *O. carpinifolia*, *T. baccata*). Five other tree species (*A. platanoides*, *Q. robur*, *S. aucuparia*, *F. orientalis*, *R. pseudoacacia)* are not expected to change in performance under the two future climate scenarios tested. Noteworthy, two of these five species— oriental beech (*F. orientalis*) and black locust (*R. pseudoacacia*)—are not native to the study area. Oriental beech is occasionally grown as an urban tree, but is not present in local forests, and black locust has become invasive in many parts of Europe, including southern Switzerland since its introduction from North America (e.g., Vítková et al. 2017). Given the difficulty in its eradication and its unchanged performance in the future, this neophyte may contribute to maintaining the forest cover in already invaded chestnut stands, especially on steep slopes or dry sites.

Finally, nine of the 16 tree species that seem to perform better in the future than today are exotic: *A. cappadocicum*, *A. monspessulanum*, *C. crenata*, *C. mollissima*, *L. kaempferi*, *L. tulipifera*, *Q. frainetto*, *Q. pyrenaica*, *T. tomentosa*. Among these species are two Asian chestnut species (*C. crenata* and *C. mollissima*), which could be introduced in chestnut stands affected by ink disease where the preservation of *Castanea* species is desired, e.g., for landscape reasons (e.g., region Bregaglia). Despite their low value as timber and fruit producers, Asian chestnut species are resistant to the pathogens causing ink disease (Crandall et al. 1945). Similarly, the other seven exotic species, present only sporadically in the study area, could be introduced or further promoted as an alternative to sweet chestnut. However, non-native tree species pose ecological risks that one should not underestimate (Vacek et al. 2023), for example, by becoming invasive in the new area or leading to considerable changes in the native biodiversity such as shifts in the soil microbial communities (Peterken 2001; Kjær et al. 2014; Byers et al 2020). When introduced in forests as seeds or seedlings/saplings, exotic species could also accidentally contribute to the spread of dangerous pests and pathogens (e.g., Wingfield et al. 2001; Franić et al. 2024). Finally, exotic species may hybridize with closely related native species (e.g., Asian chestnuts with sweet chestnut; Alcaide et al. 2022) and pollute their genetic background. Among the native tree species tested, *A. campestre*, *I. aquifolium*, *S. aria*, *L. nobilis*, *Q. cerris*, *Q. petraea*, and *T. platyphyllos* are expected to perform better under the future climate scenarios than today, and they are already sometimes present in sweet chestnut stands. Hence, they could be good alternatives to sweet chestnut in stands affected by ink disease. However, given the regular occurrence of forest fires in southern Switzerland (Tinner et al. 1999), the two evergreen species, *I. aquifolium* and *L. nobilis*, may not be the best choice (Dimitrakopoulos and Papaioannou 2001; Conedera et al. 2017).

Mixing tree species in a forest stand has numerous ecological advantages, including greater stability and resilience against biotic disturbance agents (Bauhus et al. 2017). For this reason, for each region of the study area, we determined a mixture of species that are potentially suited to replace sweet chestnut in the two future climate scenarios. Some tree species have a limited number of potential companion species, while others appear to be less selective. Since we based our species selection on the literature review, the results may be partially biased by data availability. Hence, for less common species, their presence in a small community does not necessarily imply that they cannot be companion species for many others. Despite the limited size of the study area (current forest area: approx. 1470 km^2), differences in the selected species communities are visible among regions and between climate scenarios within the same region. These differences may result from the small-scale environmental heterogeneity (climate, topography, soil) that characterizes the southern slope of the Swiss Alps.

Conclusion

Invasive soil-borne pathogens are of particular concern because once established in a forest stand, they are almost impossible to eradicate and thus have the potential to damage several generations of trees. In this study, we identified candidate tree species to replace sweet chestnut in stands affected by ink disease in southern Switzerland under the shared socioeconomic pathways SSP126 and SSP370. Even though the whole range of potential species could not be included in the analyses, we were able to provide lists of native and exotic tree combinations that could help forest managers to ensure the future forest cover in areas with ink disease. Because sweet chestnut is not a future-proof tree species in southern Switzerland (Conedera et al. 2021), the identified tree species could be useful for the whole chestnut belt.

Author contributions Both authors contributed to the study conception and design and wrote the first and final manuscript drafts. MH prepared materials and collected and analyzed data. Both authors read and approved the submitted version of the manuscript.

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