



Future expansion of upper forest-grassland ecotone under land-use and climate change in the Eastern Alps

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Abstract

Context Across Alpine landscapes, a combination of land-use abandonment and climate change is driving forest expansion and promoting the upward migration of trees on grasslands. Yet, it remains unclear how rapidly the upper forest-grassland ecotone will shift and how tree species composition will change, both in terms of species proportions and along elevational gradients.

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Objectives Our aim is to investigate the future forest expansion in a landscape in the Eastern Alps under potential grassland abandonment, climate change, natural disturbances (wind and bark beetle), and forest management.

Methods We used the iLand forest landscape model to simulate long-term dynamics (2020–2200) under different scenarios. We coupled model outputs with the concave hull algorithm to identify potential changes in the forest-grassland ecotone, tracking tree species expansion and quantifying elevation and compositional shifts.

Results Under a potential abandonment of alpine grasslands, forest will likely expand rapidly within the twenty-first century regardless climate warming. This because the current upper forest-grassland ecotone is mainly constrained by land use rather than climate. Our simulations also showed that ecotone shifts will be more pronounced on S-facing slopes, while climate change will affect more future tree species composition and forest stocking at higher elevations.

Conclusions Our outcomes provide useful insights on future dynamics of the upper forest ecotone by using a forest landscape model and by integrating not only species migration and climate but also other factors such as disturbances and management. Our results could provide useful information for designing landscape management strategies in rapidly changing Alpine mountain valleys.

Keywords Climate change · Forest expansion · Forest-grassland ecotone · Forest landscape model · Land-use change · Alpine landscape

Introduction

In the European Alps, past land-use has deeply shaped the landscape throughout human history (Tasser et al. 2005; Plieninger et al. 2006). Historically, forests have been extensively used for timber extraction and to provide a broad variety of other ecosystem services, such as water regulation, soil stabilization, and protection from gravitational hazards (Conedera et al. 2017), still essential today (Blattert et al. 2017; Mina et al. 2017). Before the industrial revolution, the need for local food subsistence in mountain areas promoted mountain agriculture and pasture even at high elevation, drastically reducing the natural forest line (i.e., the elevation threshold above which forests do not occur due to the climatic limitation of tree growth) and moving down the upper forest edge at lower elevations across the entire Alpine region (Dirnböck et al. 2003; Körner and Hoch 2023). The socioeconomic shifts after the middle of the twentieth century led to structural changes of mountain landscapes (Tasser et al. 2024) and to the abandonment of mountain agriculture at higher elevations (Frei et al. 2023). This trend is still ongoing and it is expected to continue in the future (Dax et al. 2021). As a consequence, in the past 70 years, forest cover and tree density have been increasing in the Alps (Falcucci et al. 2007; Bebi et al. 2017; Stritih et al. 2021). In line with these changes, the upper edge of the forest has shifted upwards considerably in the past decades (between 0.43 and 1.9 m yr⁻¹) expanding into the grassland areas depending on climate and management (Díaz-Varela et al. 2010; Leonelli et al. 2016; Cudlín et al. 2017).

The forest-grassland ecotone is an important element in mountain landscapes, providing key cultural and regulating services, as well as offering habitat for multiple species dwelling in the subalpine altitudinal belt (Sarkki et al. 2016; Kyriazopoulos et al. 2017). The expansion of forests to higher elevations as a result of climate and land-use change is expected to have different effects on alpine

dynamics (Dirnböck et al. 2003; Greenwood and Jump 2014; Cudlín et al. 2017). Tree species growing rate at this altitudinal belt exhibit different responses to climate change effects (i.e., temperature increase and drought). Increasing temperatures, lengthening of the growing season, and altered precipitation regimes causing frequent drought periods have already been affecting tree growth at the uppermost elevations (Moser et al. 2010; Lévesque et al. 2013; Obojes et al. 2022; Oddi et al. 2022). For example, Swiss stone pine (*Pinus cembra* L.) has been showing increasing growth trends due to longer growing seasons and higher summer temperatures (Boden et al. 2010). Nevertheless, current low genetic variability of the juveniles of species with long generations at highest elevations is likely to lead to local disappearance under rapid future changes (Dauphin et al. 2021). Moreover, longer drought periods have already shown negative effects on the radial growth of subalpine tree species (see Obojes et al. (2022) for Swiss stone pine) favouring the expansion of more drought-resistant ones (Vittoz et al. 2008). Therefore, optimal climate conditions for species growing close to the timberline will be likely found at higher elevations in the next future, as a consequence of an increased risk of being outcompeted by more adapted species (Casalegno et al. 2010).

Disentangling the interacting effects of land use and climate on forest expansion and tree growth under changing climate and natural disturbance conditions is therefore of utmost importance. Depending on the scale of observation, past studies indicated that grassland abandonment mainly affects the pattern of forest cover (i.e., shrinkage vs expansion of forested surface) and tree establishment (Motta et al. 2006; Wallentin et al. 2008; Mietkiewicz et al. 2017; Anselmetto et al. 2024;), while climate has a stronger impact on ecological processes such as tree growth and mortality (Bolli et al. 2007; Frei et al. 2023). Nevertheless, climate change is expected to have a large impact on these ecosystems due to the high susceptibility of mountain areas (Nogués-Bravo et al. 2007) and the European Alps (Pepin et al. 2022) to warming. Moreover, natural disturbance events (i.e., windstorms, wildfires, pest outbreaks) are expected to become more intense and frequent in the future (Senf and Seidl 2018; Senf and Seidl 2021). This

is particularly the case for windstorms and bark beetle outbreaks, which are the main disturbance types across the Alps (Schelhaas et al. 2003; Seidl et al. 2014). Thus, both direct and indirect effects of climate change are expected to become the key driving factors in shaping forest dynamics including forest structure and composition.

Because of the limitations of experimental approaches when dealing with spatial (stand to landscape) and temporal (year to centuries) scales (Albrich et al. 2020a), modelling have been used to simulate the forest expansion dynamics at the upper forest edge under future changing conditions. Using a land-use/land-cover (LULC) statistical model, Tasser et al. (2017) and Fondevilla et al. (2016) found an increasing reforestation trend both under land-use abandonment and temperature increase. Similarly, using a wooded pasture process-based model, Peringer et al. (2022) observed an upslope migration of tree species with a high intermixing of tree species at different elevation belts, leading to a disruption of current vegetation belts. Scherrer et al. (2020) compared a species distribution model (SDM) with a dynamic forest model, with the latter projecting a much slower upslope migration of tree species due to tree demographic processes (e.g., establishment, growth, competition) that are not accounted for in SDM and LULC models. Rickebusch et al. (2007) combined a probabilistic land-use change model with a forest dynamic model in a mountain landscape in the Alps, but without exploring the effect of climate change. Although previous modelling studies investigated these dynamics using single factors or a combination of them, it remains unclear how the interacting effects of land-use abandonment, climate change and disturbances will drive forest expansion towards the upper limit of the forest-grassland ecotone in mountain regions.

A recent and comprehensive review on the topic highlighted the need for fine spatial and temporal data to capture heterogeneity of land-use legacies and patchiness of secondary forest succession, and at the same time advocated the application of process-based models able to upscale such spatially-explicit processes at landscape level (Anselmetto et al. 2024). Specifically, process-based forest landscape models (Shifley et al. 2017) are powerful tools allowing to

assess spatial changes in forest cover—thanks to their spatially explicit feature including seed dispersal—and temporal changes in ecological processes driving forest dynamics (Gustafson 2013; Albrich et al. 2020b). In particular, scalable forest landscape models that can simulate processes at the individual-tree level and that are able to capture the complex topography of mountain terrains are particularly suitable for exploring forest expansion at the forest-grassland ecotone. Additionally, such models allow for assessing the potential impacts of natural disturbances directly linked to climatic drivers (Seidl and Rammer 2017; Lucash et al. 2018), something that has not been done yet for the upper forest-grassland ecotone. Understanding potential shifts in forest ecotones and forest expansion patterns in a changing future would be helpful in guiding decision-making toward an improvement of the management of Alpine areas.

In this study, our objective was to investigate potential shifts in the upper forest-grassland ecotone under land-use abandonment and diverging climate changes scenarios in the European Alps. We applied the individual-based forest model *iLand*, with a spatially explicit approach, to simulate, for the first time to our knowledge, the upslope forest expansion in a mountain landscape in the Alps. We simulated forest successional dynamics for 180 years in the future (2020–2200), considering also current forest management and main natural disturbances (wind and bark beetle), letting the forest expand on alpine pastures and grasslands. To define and analyse changes in the upper forest-grassland ecotone, we coupled the model outputs with a machine learning algorithm to determine the area covered by the ecotone. We then focused our analysis on changes in tree species composition and their spatial distribution, as well as quantifying species-specific elevational shifts by aspect (i.e., topographic exposure) in response to climate change. We hypothesised that (H1) even under historical climate the upper forest-grassland ecotone would rapidly shift upward given that the current forest edge is likely much lower than its potential due to past land use, especially on S-facing slopes (Pecher et al. 2011; Tasser et al. 2017). Furthermore, we hypothesised that (H2) climate change would influence the velocity of the shift at the end of the simulation period, with drier

and hotter climate condition slowing the pace of tree species movement along the mountain slopes (Theurillat and Guisan 2001). Finally, (H3) we expected the future upper forest-grassland ecotone to shift more rapidly on S-facing slopes and to detect differences in future species composition in relation to the intensity of the climate change scenario, especially under more extreme conditions (Mietkiewicz et al. 2017).

Materials and methods

Study area

The Stubai valley is located in the eastern Central Alps, in the province of Tyrol, Austria (Fig. 1), and representative for mountain forest landscapes in the Eastern Alps (Seidl et al. 2019). The elevation ranges from 900 m a.s.l. in the valley bottom up to more

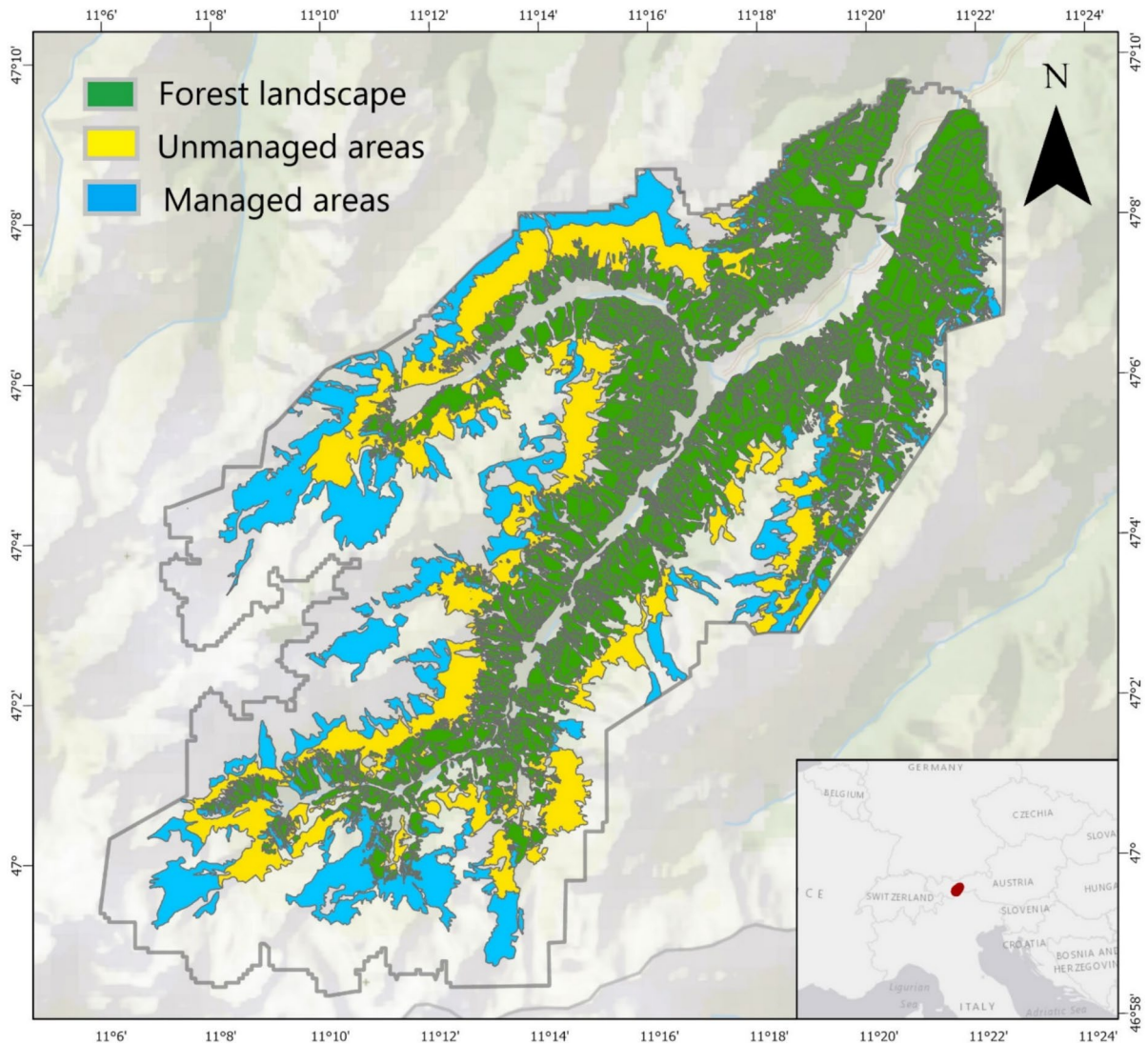


Fig. 1 The Stubai landscape, depicting differences in land use/land cover as a simplification of Tasser et al. (2024). The forest landscape (dark green) is the area used as starting conditions for the simulations (see Sect. “Simulation setup and analyses”). Blue and yellow areas are those assumed to become available

for forest expansion, representing managed and unmanaged non-forest land covers, respectively. The grey line shows our area of interest for parameterising climate and environmental model inputs (see Sect. “Model initialization and climate scenarios”)

than 3500 m a.s.l. in the highest peaks (Fig. S1). The whole valley covers a total area of 22,961 ha of which 4811 ha are covered by forest and 1834 ha by mountain pine (*Pinus mugo Turra, 1764*) shrubland, for a total of forested area of 6646 ha. The main tree species composing the forest are Norway spruce (*Picea abies (L) H. Karst.*), European larch (*Larix decidua Mill.*), and Swiss stone pine (*Pinus cembra L.*; hereafter stone pine). Norway spruce characterizes the montane belt, forming dense stands with closed canopies, while European larch and stone pine can be found throughout the sub-alpine belt up to the current upper forest edge, approximately around 2000 m a.s.l., often mixed with mountain pine communities. A minor population of Scots pine (*Pinus sylvestris L.*) is also present in the lowest westernmost part of the valley. Current forest composition largely corresponds to the potential natural vegetation, while the structure has been largely influenced by past human land use such as forest and grassland management (Tasser et al. 2017). Besides the forest and the mountain pine stands, other types of land use are present in the landscape (Fig. 1). In the valley bottom, managed areas such as arable farmlands and intensively used hay meadows are dominant. Extensively used summer pastures, unmanaged natural alpine grasslands and rocks dominate the higher elevations. In the landscape prevails an inner-Alpine temperate continental climate, influenced by the strong topographical and ecological gradients, with historic (1961–2014) mean annual temperatures of 6.8 °C and mean precipitations of 850 mm at the valley bottom, and 1.1 °C and 1170.2 mm at around 2000 m.

Simulation model

We conducted our simulation experiment with the individual-based forest landscape and disturbance model iLand (Seidl et al. 2012; Rammer et al. 2024). iLand is a spatially explicit process-based model that simulates regeneration, growth, and mortality of individual trees and their interactions with environmental conditions, as well as management and natural disturbances, at the landscape scale. Primary productivity at canopy level is calculated monthly using a resource use efficiency approach (Landsberg and Waring 1997), accounting for the effect of CO₂ concentration, climate and soil condition (effective soil depth, texture, and nitrogen availability). As

climate inputs, the model requires temperature, precipitation, solar radiation and vapor pressure deficit at daily resolution, allocated to homogenous climatic areas across the landscape. The allocation of carbohydrates is based on tree competition and allometric ratios (Duursma et al. 2007), depending on light availability. The model explicitly simulates regeneration accounting for seed availability (i.e., local availability of mature trees), seed dispersal, germination and establishment of seedling constrained by environmental filters such as light availability, temperature, and drought. Tree mortality probability is influenced by species-specific age and size but also by carbon starvation of individual trees as a proxy for stress-related mortality due to competition for light, or water and nutrient limitations (Seidl et al. 2012). A range of natural disturbances such as windthrows and bark beetle outbreaks can be simulated spatially explicitly with a mechanistic approach. Wind disturbances are driven by maximum wind gust wind speeds, wind direction and depend also on soil frost, forest structure, and composition (Seidl et al. 2014). Critical windspeed is calculated at the tree level as a function of canopy roughness (taking into account forest edges) and forest structure and is updated during the entire disturbance event; this means that the critical wind speed for breakage or uprooting is calculated iteratively (Seidl et al. 2014). Spruce bark beetle (*Ips typographus L.*) outbreaks are triggered either by windthrow or by a climate-dependent infestation probability. The bark beetle module simulates beetles' dispersal, colonization and overwintering using a phenological approach, with beetle's development and host susceptibility (i.e., reserve of non-structural carbohydrate) influenced by temperature and water stress (Seidl and Rammer 2017). Forest management is simulated with the dedicated Agent-Based Engine ABE integrated in the iLand framework (Rammer and Seidl 2015). Through ABE, forest management can be scheduled for each stand, and it can also be spatially–explicitly adapted to the area (i.e., by applying a slit cut reproducing cable cranes lines in relation to the topography). The model has been parametrized, evaluated and widely applied in Central European forests to study forest management (Rammer and Seidl 2015; Seidl et al. 2017, 2018; Dollinger et al. 2023), ecosystem services provisioning (Albrich et al. 2018; Seidl et al. 2019; Thom and Seidl 2022) and disturbance impacts

(Silva Pedro et al. 2015; Dobor et al. 2020; Hlásny et al. 2021; Albrich et al. 2022). It has been also tested and applied beyond the European borders to investigate wildfires in the United States (Seidl et al. 2014; Braziunas et al. 2021; Rammer et al. 2021) and ecosystem restoration in Japan (Kobayashi et al. 2022).

Model initialization and climate scenarios

The model was previously evaluated and applied in the Stubai landscape in the studies by Seidl et al. (2019) and Albrich et al. (2020a). However, the extent of the simulation area was delimited by the current forest cover (4811 ha from Seidl et al. 2019). To study changes in the upper forest-grassland ecotone, we extended the data to non-forest land-use sites (Fig. 1) and set them as potential stockable forest (i.e., area where trees can potentially establish and grow). For this reason, climate variables and soil data were extended to a larger landscape (22,961 ha), which included forest, mountain pine stands and both managed and unmanaged subalpine and alpine grasslands for a total of stockable area of 8131 ha. Soil data such as soil depth, texture and plant-available nitrogen for the area covered by forest was retrieved from Seidl et al. (2019), who derived it combining data from the Austrian Forest Soil Survey (Seidl et al. 2009) with local forest type maps (Hotter et al. 2013). Soil data for the non-forest land-use areas were derived by upscaling plot-level data on spatial units following the method proposed by Schirpke et al. (2020) (Fig. S3). A climatology representing historical climate (1961–2014) was downscaled at a resolution of 100 m using weather station in combination with gridded climate products of the Austrian weather service (Seidl et al. 2019) and reprojected to the extended landscape. Current vegetation structure and composition were obtained from angle count sample plots combined with wall-to-wall forest type information (Hotter et al. 2013) and a canopy height model derived from LIDAR (see details in Seidl et al. 2019). In the extended landscape, we also included mountain pine communities following the approach by Thom and Seidl (2022). Initialization of the current vegetation state was achieved via the legacy spin-up, a procedure that consists of running the model for a number of iterations until reaching the conditions that most closely resemble observational data and ensure

consistency with model logic (Thom et al. 2018). We ran the legacy spin-up procedure for 600 years under historic climate and past management until obtaining a vegetation composition that matched well observed values (further details in the Supplementary Information and Fig. S3). Current forest management system was implemented in the current forest stands following Seidl et al. (2019) to simulate small and irregular openings perpendicular to skyline track (slit-cuts) that are used to regenerate the forest in mountain terrains (Streit et al. 2009). Management interventions also include salvage logging for trees killed by bark beetle or wind.

Climate changes scenarios were determined by selecting four future climate trajectories from different combinations of GCM-RCM and RCPs (4.5 and 8.5): (1) moderate (+2.6 °C of temperature and no significant changes in precipitation in 2081–2100 compared to historic), (2) warm (+4.7 °C and no significant changes in precipitation), (3) warm and wet (+4.6 °C of temperature and +6.2% precipitation), and (4) hot-and-dry (+6.3 °C temperature and –18.3% annual precipitation). Further details are given in the Supplementary Information (Fig. S2, Table S1). Climate changes scenario covered a time interval of 80 years (2020–2100). To run simulations until 2200, a random sampling with replacement of the last 20 years of the twenty-first century (2080–2100) was applied after the first half of the simulation interval, assuming a stabilization of the condition during the twenty-second century. Whereas an historic climate scenario was assumed as reference and derived through a random sample (with replacement) of the records for the period 1990–2010. CO₂ concentrations under climate change increased from current conditions at the start of the simulations to reach the levels estimated for 2100 according to the RCPs (approximately 650 and 1370 ppm for 4.5 and 8.5, respectively). Climate change did not directly affect wind disturbances, for which time series of events were assigned by randomly sampling values from the historical distribution.

Simulation setup and analyses

Starting from the current vegetation conditions (year 2020), we simulated 180 years of forest development under the five climate scenarios, including also forest management and disturbances. As disturbance

agents, we simulated both wind and bark beetle (Seidl and Rammer 2017), which were implemented as described in Seidl et al. (2019). Both disturbances were dynamically simulated with iLand as the model includes direct interactions between climate and disturbance severity. We ran 10 replicates for each simulation to account for stochasticity from successional dynamics, seed dispersal, and disturbance events (total 50 model runs: 5 climate \times 1 management + disturbance \times 10 replicates). Model outputs saved on 20-years' time step were analysed at a spatial resolution of 100 \times 100 m.

We let the forest expand beyond its current borders assuming a general abandonment of agriculturally used semi-natural grassland areas in the subalpine-alpine belt and into unmanaged natural alpine grasslands (Tasser et al. 2017). We did not consider potential expansion on screen and rocky slopes as the model does not simulate dynamically the formation of new soil and cannot capture micro-site effects in the soil and climate data. Since we were interested in detecting upward shifts of the upper forest edge, we needed an approach to delineate it in our simulations. In accordance with Körner and Hoch (2023) we distinguish the climatic treeline from the current forest edge that is the object of this study in determining the *upper forest-grassland ecotone* as a belt connecting the uppermost 1-ha forest cells (i.e., including forest edge, krummholz or forest expansion zones as well), where trees reach their maximum elevational limit on soils capable of carrying forests as simulated by iLand within the available landscape in each time step. To that end, we applied a computational approach using the *concave hull* function, a machine learning algorithm that has been applied for map classification, pattern recognition and image processing (Lu and Pavlidis 2007; Zhou and Shi 2009). The concave hull algorithm was applied to extract the border or the surface of a set of points in a plane, generally a 2-dimensional space, using a *k*-nearest neighbours' approach (Park and Oh 2012). Compared to the more widely employed convex hull (Zhang et al. 2010), the concave hull approach can better capture the shape of a given set of data. To do this, we first transformed the 100 \times 100 m model outputs into points (i.e., converting the raster cells into spatial points). Successively, we applied the concave hull function, to obtain a delineation of the treeline in relation to the outermost points of the forest area for every simulated time interval (Fig. 2). Finally, we reconverted the delineated points into raster

cells in order to use the related data for further analysis. To restrict our analysis to the upper forest-grassland ecotone, we constrained the computation to the cells with an elevation higher than the 75th percentile of the overall forest landscape (i.e., 1700 m a.s.l.). Whereas, we defined as *forested area* the remaining vegetated portion of the landscape simulated by the model, located below what we identified as forest-grassland ecotone using the above-mentioned approach.

Once we differentiated our output in the forest-grassland ecotone and forested area, we analysed temporal and spatial changes of forest composition (i.e., species proportion of basal area) for both of them under the five climate scenarios. Moreover, we analysed these results also in relation to the topographic aspect (north vs south exposition), which was obtained by overlying the simulated study area with an exposure map derived from the DEM. Spatial changes were quantified as potential elevational shift of the tree species taking into account the slope aspect in both the forested area and the forest-grassland ecotone. Elevational shift was defined as change in the mean elevation across all the cells within the analysed category (i.e., forest-grassland ecotone and forested area), grouped by the different tree species per year and scenario. Compositional changes were analysed by computing the mean basal area for each species, for the same years, scenario, and topographical aspects. For the visualization of the results and their discussion we focused on two most diverging climate projections (moderate, hot-and-dry) compared to historical, whereas all other results can be found in the Supplementary Information. All analyses were conducted using R (R Development Core Team 2022). Specifically, we used the *concaveman* package (Gombin et al. 2017) for computing the concave hull function.

Results

Elevational shift of tree species by topographic aspect under climate change

The forest expanded throughout all available areas of the upper landscape under all climate scenarios (Figs. 3, S9). The average elevation of both the forested area and the forest-grassland ecotone shifted upwards regardless of climate warming (Table 1).

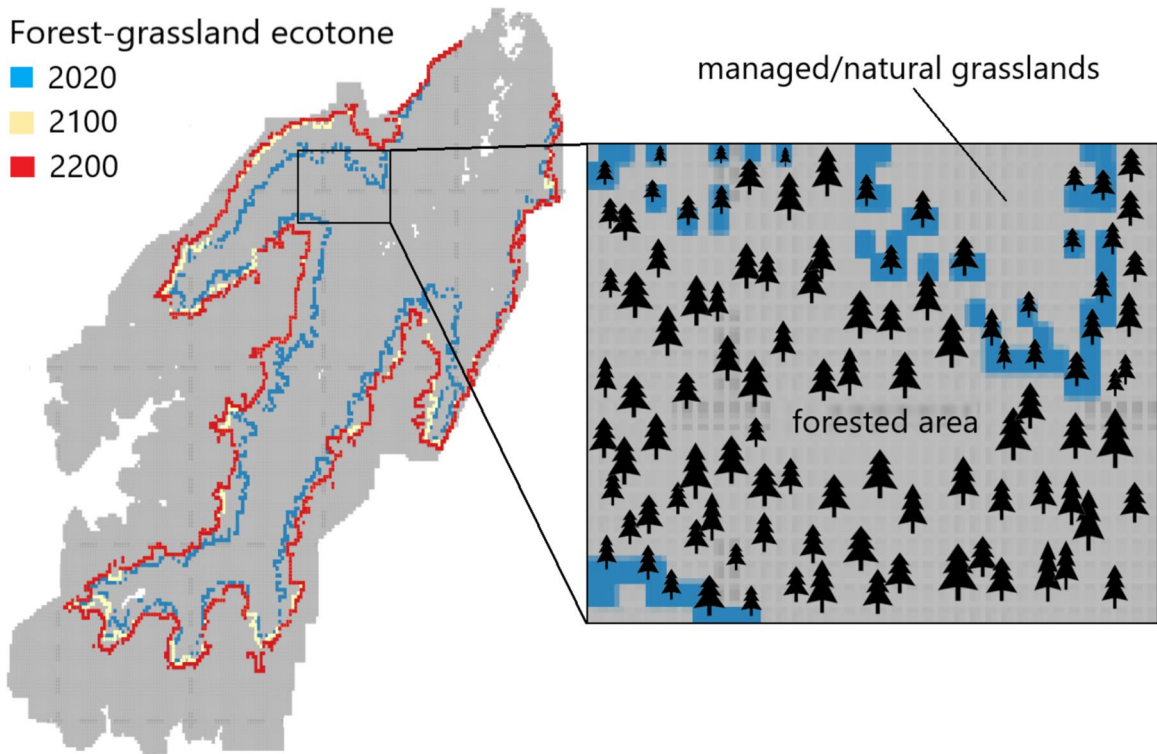


Fig. 2 Example of forest-grassland ecotone delineation using the concave hull function. Different colours represent the delimitation of the 1-ha upper forest-grassland ecotone for different simulation years. Cells containing tree species data

below the forest-grassland ecotone represent the forested area. Elevation details of the study areas can be observed using Fig. S1

For the forested area, the average elevation at the beginning of the simulation was 1504.9 m a.s.l. In 2100, the mean elevation increased by up to 140 m, with no visible difference between scenarios. Between year 2100 and 2200, the mean elevation of the forested area increased further only by 40 m. Similarly, in the upper forest-grassland ecotone, the initial mean elevation increased by 140–150 m in 2100 and by an additional 40–50 m in 2200, with slight differences among climate scenarios. The maximum elevation of the upper forest-grassland ecotone at year 2200 was about 2400 m a.s.l. under all scenarios (Fig. S7 in Supplementary Information). Overall, the upper forest-grassland ecotone showed a slightly more pronounced shift than the forested area, with a mean upward shift of 185.3 m compared to 175.7 m (average across scenarios). However, the mean elevation of both forested area and ecotone reached at the end of the simulation were similar with negligible differences across the scenarios (Table 1).

In terms of velocity, most of the elevational shift of the ecotone happened in the first 80 years, slowing down in the following years.

The velocity of the elevational shift showed species-specific trends by topographic aspect (Figs. 4, S5). In general, they were notably more rapid until 2100 and on S-facing slopes. Species distribution showed a clear divergence from the initial one for almost all species. In forested areas, mountain pine reached the highest elevation among all species on both N and S-facing slopes (Fig. 4a–b), while the species with the highest elevational shift was Scots pine (Fig. S6). Norway spruce showed a moderate shift, stabilizing after 2100 and reaching higher elevations only on S-facing slopes (Fig. 4b). On N-facing slopes, stone pine presented the sharpest upward shift (+118 m at 2100; see Fig. S6). Within the forested areas, differences between climate scenarios were almost negligible, with a minor variability respect to historical conditions under the warmer

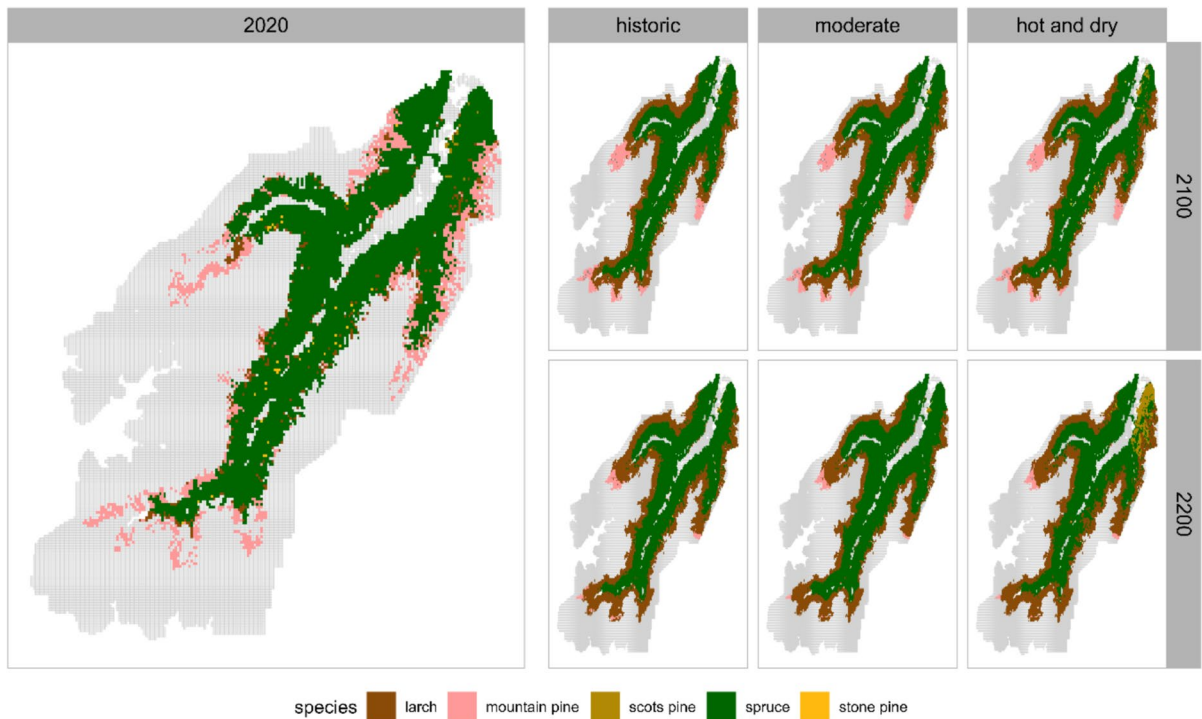


Fig. 3 Spatial distribution of the dominant tree species across the landscape at simulation start (left panel) and during the simulation period under the different climate scenarios (six

panels on the right). Pixels’ colours indicate the species with the highest portion of basal area within the ha cell. For the elevational range of the valley, see Fig. S1

Table 1 Mean elevation (m a.s.l.) of the pixels covering the forested area and the upper forest-grassland ecotone at the beginning of the simulation (2020) and at year 2100 and 2200 under all climate scenarios

Scenario	Forested area			Forest-grassland ecotone		
	Year					
	2020	2100	2200	2020	2100	2200
Historic	1504.9	1642.9	1678.8	1923.8	2067.1	2104.1
Moderate		1643.1	1680.0		2071.9	2110.4
Warm		1642.8	1681.4		2072.9	2111.5
Warm-and-wet		1643.0	1681.4		2072.6	2111.7
Hot-and-dry		1642.8	1681.1		2071.5	2109.0

climate scenarios (i.e., between 0 and 5 m of elevation change).

The most pronounced species shifts were observed at the ecotone level but not consistently for all species and topographic aspect. Within the upper forest-grassland ecotone, European larch was the species with the highest elevational shift among all climate scenarios, particularly on S-facing slopes (between +329 and +339 m at 2100; Figs. 4c–d and S6). European larch and stone pine distributions diverged clearly, with the former expanding

more towards higher elevations, especially on N-facing slopes. Stone pine, instead, presented two different trends depending on climate scenario and in relation to the aspect. On N-facing slopes, its mean elevation increased by approximately +50 m under historic and hot-and-dry conditions and only by +16 m under warm climate by 2100. Whereas, in the twenty-second century its elevation increased only slightly under historic and warm climate but decreased under hot-and-dry conditions (Figs. 4c and S5c). On S-facing slopes, the shift of

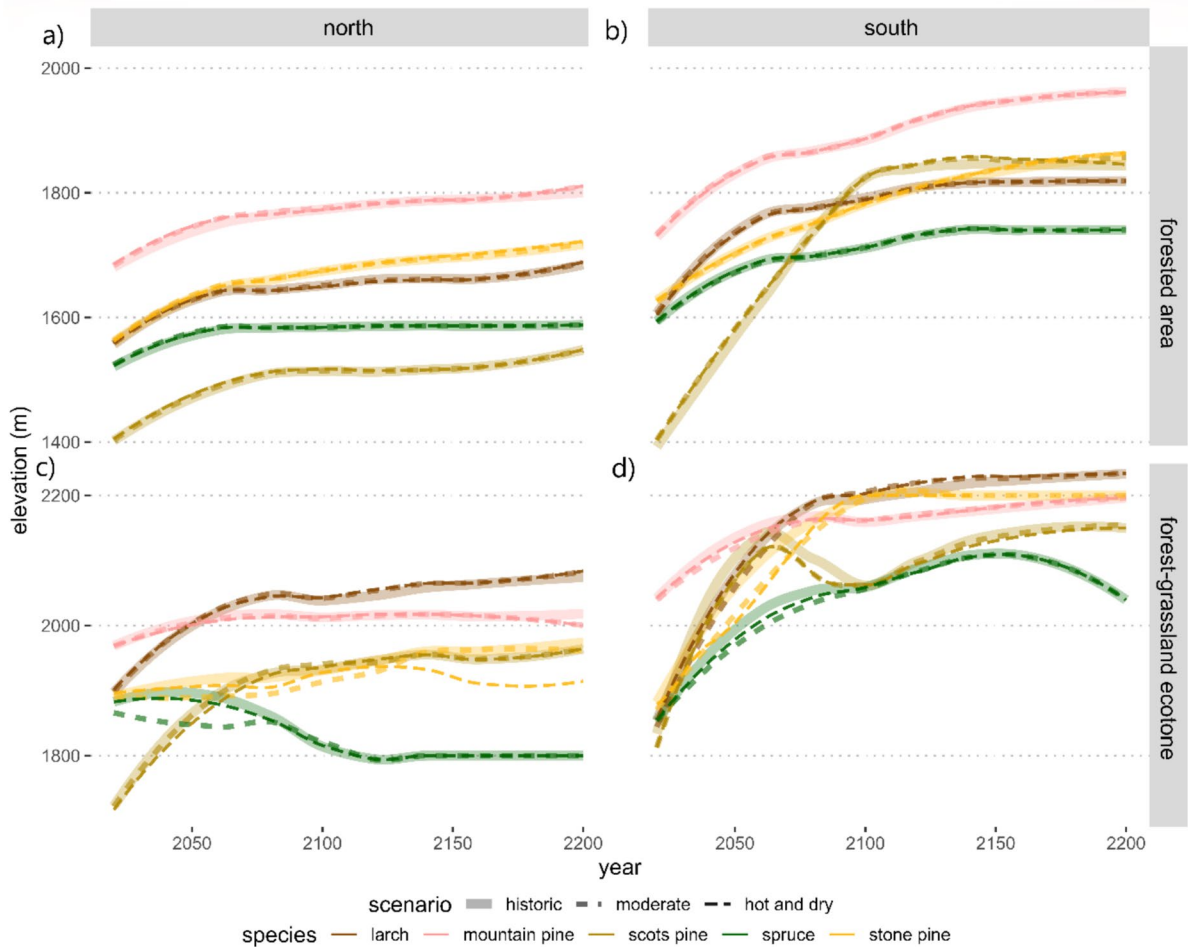


Fig. 4 Trends of tree species shift within the forested area and the upper forest-grassland ecotone in relation to the aspect and the climate scenario. Different scenarios are represented by dif-

ferent line types and shades. Note the different y-scale for the horizontal panels. Additional scenarios are shown in Fig. S5

stone pine was much larger at the upper forest-grassland ecotone (+321 m at 2100) compared to its shift in the forested area (+161 m at 2100). At the ecotone's S-facing slopes, stone pine's upshift followed a similar trend to that of N-facing slopes. However, under hot-and-dry conditions the species was not detected anymore at the upper forest-grassland ecotone from mid-twenty-second century (i.e., year 2140) until the end of the simulations (Fig. 4d). Norway spruce distribution trends at the upper forest-grassland ecotone showed very different trend in relation to aspect, respect those observed in the forested areas (+72 m overall in N-slopes and +158 m on S-slopes consistently across scenarios). On N-facing slopes, spruce's mean elevation decreased by -84 m in the first 80 simulation years, while on S-facing slopes

shifted rapidly upwards (+177 m at 2100) with a decline in mean elevation in the last 50 years of simulation. Also for this species, differences between climate scenarios were marginal.

The absolute maximum elevation reached in the forest-grassland ecotone was roughly the same under every scenario, at about 2400 m a.s.l., with only some slight differences in relation to the tree species. Further results showing the minimum and maximum elevation variation range of every species at different time steps are shown in Figs. S6 and S7 in the Supplementary Information.

Future species composition in the forested area and upper forest-grassland ecotone

Overall, we found an increase in the stocked forest area (in terms of basal area) for both the forested area and the upper forest-grassland ecotone. Differently from the elevational shifts, here the climate scenario induced clear changes in forest structure and composition (Fig. 5). Within the forested area, basal area increased more under climate change compared to historic climate, but only under those scenarios with temperature warming combined with increasing (or stable) precipitations (e.g., +52.9% under warm conditions; see Table 2, Figs. 4 and S8). Basal area increases were instead lower under

hot-and-dry climate scenario (+11.2%). At the forest-grassland ecotone, basal area increased by +68.6% under historic climate, while under climate change the increase was higher, with the largest increase under warm scenario (+368.4%). Differently from the forested area, here the hot-and-dry scenario showed higher increases in basal area compared to historic. Overall, before the end of the simulation period, tree density within the forest-grassland ecotone reached similar values of the forested areas.

When looking at temporal trends in species-specific basal area, differences in future species distribution were apparent among climate scenario and by topographic aspect (Fig. 5). Generally, the forested

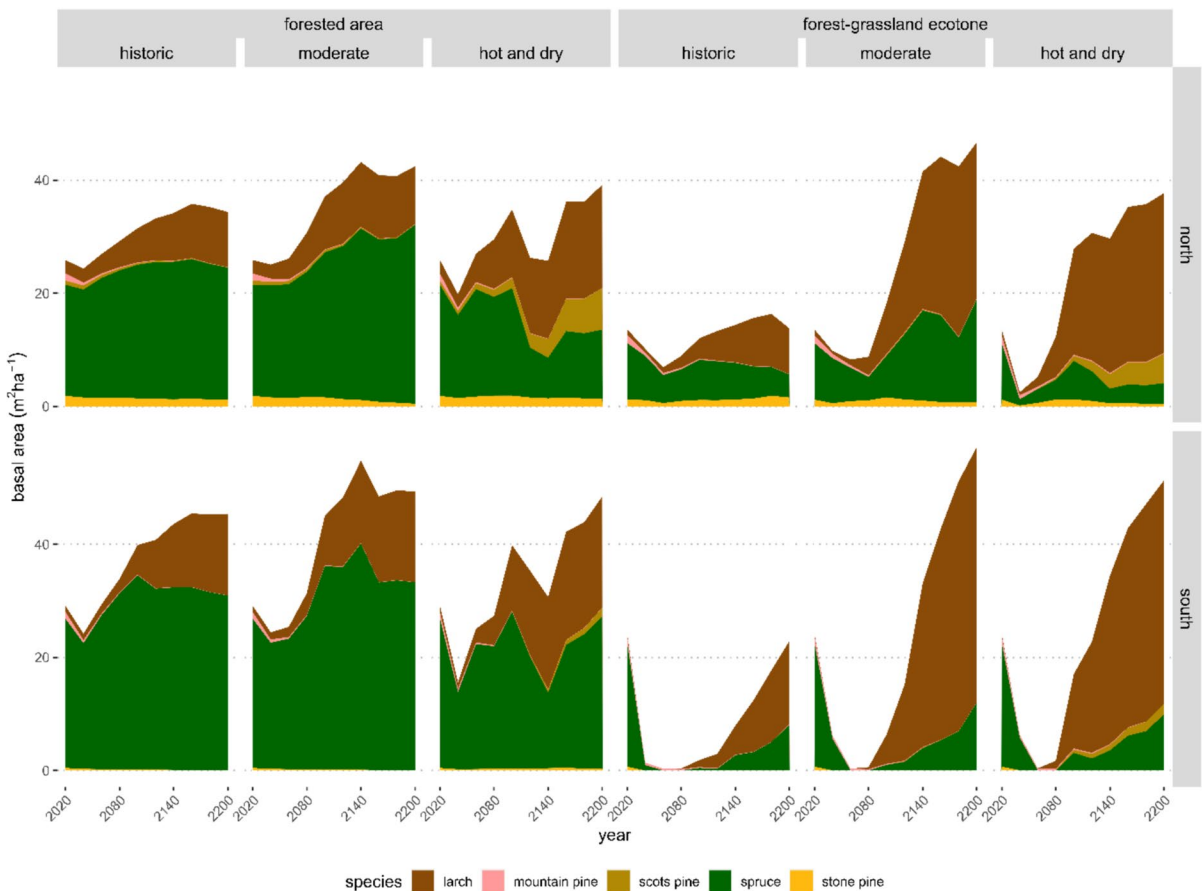


Fig. 5 Projected mean basal area ($m^2 ha^{-1}$) along the simulation for both the forested area and the upper forest-grassland ecotone by climate scenarios (vertical panels) and topographic aspect (horizontal panels). Values represent means across the ten model runs (see Table S2 for variations across repli-

cates). Additional climate scenarios are shown Fig. S8. It is worth noting that the area for which the values are calculated is dynamic (i.e., it moves differently in relation to the number of cells for each species within the forested area and the upper forest-grassland ecotone)

Table 2 Percentage of overall basal area ($\text{m}^2 \text{ha}^{-1}$) increase under historic and climate change scenarios for the forested area and the upper forest-grassland ecotone

Climate scenario	Basal area increase (%)	
	Forested area	Forest-grassland ecotone
Historic	+22.8	+55.1
Moderate	+37.2	+287.7
Warm	+52.9	+368.4
Warm and wet	+51.3	+321
Hot-and-dry	+11.2	+257

The values represent the difference in percent change between the beginning and the end of the simulations, calculated relatively to the number of hectares of the two categories in the different years

area remained characterized by a strong dominance of Norway spruce, whose basal area increased under moderate warming scenarios, with the exception of hot-and-dry conditions. With increasing warming and water-deficit stress (hot-and-dry), Norway spruce showed strong basal area decrease, mainly on N-facing slopes, with sharp variations throughout the simulation period (Fig. 5). Within the forested area, larch was the species that showed the highest increase of basal area in all the scenarios, augmenting on both N and S-facing slopes; this especially under hot-and-dry climate where larch became the most represented species in the north-exposed portion of the landscape.

At the upper forest-grassland ecotone, Norway spruce showed a general decrease in basal area during the first simulation years, which was particularly pronounced on S-facing slopes (Fig. 5). This sharp decline was related with the shift of the ecotone belt along the simulation interval. As observed in Fig. 4, tree species shifted quickly during in the first simulation years, with Norway spruce being less capable than the other species to keep up with the rapid upward shift, mainly distributing on lower elevations respect to the other species. This is highlighted in Fig. 5 by a sharp decrease of Norway spruce basal area on S-facing slope for the forest-grassland ecotone. Despite this, a moderate climate change induced a slight increase in spruce's basal area at the ecotone compared to historic climate, which was not observed under hot-and-dry conditions especially on N-facing slopes.

European larch, however, expanded rapidly and resulted in the most dominant species at the upper forest-grassland ecotone, particularly under moderate climate. Over time, larch replaced most of mountain pine stands, which however persisted at high elevations by 2100 but mostly converted into larch-dominated forests by 2200 (Fig. 3). Stone pine remained quite stable under historic climate (e.g., basal area remained constant in the forested area on N-facing slopes; Fig. 5) but it showed a decline under hot-and-dry climate in the second part of the simulation. Contrarily, Scots pine increased its share of basal area only under the hot-and-dry scenarios and became dominant in the northernmost part of the valley (i.e., at the entrance of the valley; see Fig. 3), at the expenses of Norway spruce. Under the most severe climate projection (hot-and-dry), this species also reached the upper forest-grassland ecotone (Fig. 5).

Discussion

In the Alps, the upper forest-grassland ecotone has been highly influenced by past and current land-use management (Vitali et al. 2019; Anselmetto et al. 2022; Frei et al. 2023) and it will be impacted in the future by climate change and other environmental factors (Cudlín et al. 2017). Despite several studies exploring future LULC changes in mountain valleys (Fondevilla et al. 2016; Tasser et al. 2017), an assessment including the synergic effect of multiple drivers (i.e., land use abandonment, regeneration dynamics, climate change, natural disturbances, forest management, competitive effects between tree species) of forest and ecotone dynamics at landscape scale was missing. Our results indicate that, under a likely abandonment of alpine grasslands, forest will rapidly expand upwards regardless of the magnitude of future climate change. Our outcomes therefore support our first hypothesis—and related studies—that the current forest edge is much lower than its potential edge (i.e., based on the fundamental niche of tree species) due to past land use, and that colonization of abandoned areas will be relatively quick, within the next 100 years already, with almost no limiting effects of climate conditions. However, they could not validate our second hypothesis about a deceleration of the upward expansion of trees

due to increasingly adverse climatic aspects, as differences in elevational shifts of the upper forest-grassland ecotone and for the individual tree species were almost negligible among different climate scenarios. Nevertheless, stronger differences among climate scenarios might arise giving the species more available surface at higher elevations, which, in our case, was topographically limited. In line with our third hypothesis about the future upslope forest expansion, we also found that ecotone shifts were much more pronounced on S-facing slopes and that differences in future climate will not only effect tree species composition but also forest stand density and stocking at the upper forest-grassland ecotone.

Upper forest-grassland ecotone shift under land-use abandonment and climate change

The expansion of the tree species stopped close to the upper borders of the available grassland land cover on higher elevations within the end of the simulation period under each scenario. The establishment of trees in new available sites happened quickly, within the first 100 years of the simulation, regardless the climate projection applied. This suggests a stronger effect of land use than climate change in driving reforestation dynamics in subalpine-alpine areas (Garbarino et al. 2020), which is something that is also in line with outcomes from other studies (Didier 2001; Bolli et al. 2007; Gehrig-Fasel et al. 2007; Ameztegui et al. 2016; Cudlín et al. 2017; Tasser et al. 2017). Once the species reached a certain elevational distribution, their upward movement decreased in both speed and elevation until the end of the simulation, regardless of the scenario. This slower increase compared to the first simulated decades might indicate still a decreasing effect of land use, and a positive effect of climate in nudging species distribution toward higher elevations. However, no differences in relation to increasing temperatures and changes in the precipitation regimes within the next two centuries were detected, similarly as observed in Holtmeier and Broll (2005). Moreover, lower soil depth at higher elevations likely concur to hamper trees' establishment, as well as a limitation in available surface between N and S-facing slopes. Interestingly, most of the species shifts of the upper forest-grassland ecotone were slightly more rapid under historic climate compared to other scenarios

before their stabilization after 2100, suggesting that increasing temperatures and drought might delay the speed of trees establishment on higher elevations where sun exposure already has a warming effect. This effect was evident for all species except European larch and mountain pine, which are both resistant to warmer and drier conditions. Stronger limiting effects on tree establishment due to harsher conditions might be clearly observable at even higher elevations, when climate becomes predominant in driving ecotonal dynamics, respect to land use.

Climate changes might induce trees' advance around the forest line ecotone as results of longer growing seasons and reduced winter temperatures (Grabherr et al. 2010). However, as observed in our results, this effect might slow down the pace of tree species movement toward higher elevations. Climate change effects might become more evident at higher elevations (i.e., at the climatic treeline level), where temperatures play a major role in determining trees' growth. Here, we found climate change to be predominant in driving structural and compositional changes of the upper forest-grassland ecotone instead of its shift dynamics. Similar results have been found also by Peringer et al. (2022), who simulated large-scale forest and treeline dynamics using a process-based model and found that the upward shift of trees within the upper forest-grassland ecotone is more constrained by the colonisation ability of tree species than by climate.

Species responses at the forest and forest-grassland ecotone level

Although we found that climate change is not the main driver of forest expansion at the upper forest-grassland ecotone, differences in the magnitude of climate warming will induce substantial changes in tree species' composition and growing stocks in upper subalpine forests (Mietkiewicz et al. 2017). Land abandonment allowed the establishment of trees at different elevations, but climate became the main driver in leading changes in the species share, as climate is expected to influence tree growth (due to longer growing seasons) but also regeneration and mortality (Grace 2002; Jochner et al. 2017; Cazzolla Gatti et al. 2019).

At the level of forested area in our target landscape, Norway spruce remained the dominant species

under every scenario. Its basal area increased across the entire valley under all climate scenarios except under the hot-and-dry one, reaching highest basal areas values under warmer and wetter conditions. Norway spruce has been observed to adapt to mild temperature increases (Hartl-Meier et al. 2014; Ponocná et al. 2016), and this can be seen when looking at its basal area increase under moderate warming. On the contrary, under warmer climates characterized by stable or reduced precipitation regimes, Norway spruce biomass trends showed a slight decrease with strong fluctuations. This can be explained by a low resistance of Norway spruce against severe droughts (Lévesque et al. 2013; Bottero et al. 2021), along with increased impact of bark beetle outbreaks at lower elevations, favoured by longer warm summers, and strong water-deficit stress (Seidl and Rammer 2017; Patacca et al. 2022; Thom and Seidl 2022). Also, Obojes et al. (2024) found a higher growth rate of Norway spruce only at higher elevations, indicating a stronger effect of reduced precipitations at lower elevations, that is expected to trigger pest susceptibility and the displacement of low-elevation conifers with more drought-resistant broadleaf species. Moreover, these adverse climatic conditions increase competition with pioneer species such as European larch and Scots pine, that can better establish on open gaps previously occupied by Norway spruce (Holeksa et al. 2016). Instead, at the forest-grassland ecotone level, Norway spruce behaved differently in relation mainly to the climate scenario. This specie's spread at the ecotone level is favoured by warm climates (Jevšenak et al. 2021), where temperature is less constraining than at lower elevations (Klopčič et al. 2017). Moreover, Norway spruce seems to be highly influenced by topography (Bałazy et al. 2019), as we found its share to increase generally more on N-facing slopes that present cooler conditions than S-facing ones. On the contrary, the expansion of Norway spruce's distribution towards higher elevations seemed to be favoured by warmer condition on S-facing slopes, as also observed by Winkler et al. (2016), where they found that species colonization on temperate mountain areas is more frequent on southern and warmer slopes than on N-facing ones. Nevertheless, high temperatures and reduced rainfalls are expected to limit its establishment at the edge of its distribution (Lévesque et al. 2013; Honkaniemi et al. 2020;

Hlásny et al. 2021). As shown in our results, the contraction of Norway spruce under the most extreme climate change scenario is often counterbalanced by an increase of Scots pine, although past studies demonstrated negative drought-induced effects on this species too, particularly at low elevations (Castagneri et al. 2015; Rebetz and Dobbertin 2004; Vacchiano et al. 2012). Therefore, Scots pine establishment at higher elevations might be enhanced by a reduction in drought risk, compared to the lower montane belt.

Overall, European larch showed the highest basal area increase. Within 100 years it established in all the available sites, dominating the upper belt but being constrained by Norway spruce at lower elevations. Similarly, Mietkiewicz et al. (2017) found a general forest expansion trend in the last century, with an increase of European larch at higher elevations, and Albert et al. (2008) found an expansion of European larch in subalpine grasslands, as being highly suitable for its establishment. Also, Frei et al. (2023) found a general and consistent advance of larch at the upper ecotone and mainly on S-facing slopes. However, under hot and dry conditions, its distribution amplified also toward lower elevations, penetrating into areas previously occupied by Norway spruce, likely due to creation of openings within the spruce stands due to increased disturbances and a lower resistance of spruce to extreme conditions. Moreover, on higher elevations and at the ecotone level, European larch expanded on sites occupied by mountain pine by almost replacing it completely by the end of the simulation time, especially on N-facing slopes. This might be related to a nursing effect of mountain pine or a reduction of its density due to light competition with taller trees, leaving open spaces for the establishment of larch (i.e., lower competitive strength of mountain pine) (Dullinger et al. 2005; Treml and Chuman 2015). Also, Moris et al. (2017) highlighted a dominance of larch on high elevation belts (i.e., pure larch forests) and a high resilience of the species along with elevation increase. As shown in our simulation experiment, the forest-grassland ecotone is likely to shift from an anthropogenically shaped composition to a more natural one that is mainly driven by abandonment and climate, dominated by larch (Leonelli et al. 2011), in a mixture with other species, and with a low share of stone pine.

Interestingly, Scots pine, which was initially present as a small population at the entrance of

the valley and mainly constrained on N-facing slopes, was capable of crossing the valley bottom and spreading on S-facing slopes. Here, the species showed to be not capable to establish in the dense Norway spruce stands, but it expanded quickly upwards on grasslands, thanks to more suitable climatic conditions (Holtmeier and Broll 2007; Rigling et al. 2013). Under extreme climate conditions, instead, the dominance of the Scots pine at the entrance of the valley was favoured, likely due to a decrease of competition with Norway spruce. However, after a few years, larch and stone pine pushed Scots pine to lower elevations, as these two typical subalpine species are better suited to environmental conditions on those elevations. Stone pine, instead, showed a decreasing basal area trend in every climate scenario at the landscape level, concentrating mainly on N-facing slopes. The distribution of this species shifted towards higher elevations, mainly establishing at the upper forest-grassland ecotone level, while almost disappearing on S-facing slopes. The quick upward shift might be also explained by the presence of Norway spruce at lower belts, outcompeting stone pine (F.-K. Holtmeier 1990). The fast and long upward movement of this species showed in our simulation experiment is consistent with studies highlighting a significant upshift of stone pine with an increase of temperature and growing season length (Casalegno et al. 2010; Pecchi et al. 2020). Nevertheless, despite that higher temperatures might foster seeds' germination and trees' growth (Motta and Nola 2001; Boden et al. 2010), we found a reduction of the share of stone pine, especially under hot and dry climate, where the species is not present anymore in the ecotone on S-facing slopes. Other studies also highlighted a high sensitivity of stone pine to higher temperatures and drier conditions (Oberhuber et al. 2020; Obojes et al. 2022), and difficulties in keeping up with changing climate conditions due to long generation times (Dauphin et al. 2021), as well as lower seed dispersal ability compared to other species sharing the same elevation belts, such as larch, that presents a different dissemination strategy (Leonelli et al. 2011). Similarly, Noce et al. (2023) found that under future climate projections the environmental suitability of stone pine is expected to decrease, especially in the northeastern Alps. Moreover, the low share of stone pine in the high ecotone areas could likely be related

to stronger competition from upshifting species. Different results might be observed if these species were allowed to expand further upward.

Methodological aspects

In this study we used a process-based forest landscape model (i.e. iLand) to explore forest expansion dynamics after land-use abandonment considering a multitude of drivers such as interactive effects of climate change and natural disturbances, seed dispersal, and tree demographic processes. As a novel approach, we also coupled the model output with a machine learning algorithm (i.e. concave hull) to identify changes of the potential upper forest-grassland ecotone, pioneering its use in investigating changes in this ecotone. However, we did not take into account browsing nor herbaceous competition, which are also important drivers of forest succession dynamics at both the forest stand and ecotone level (Thrippleton et al. 2018; Albrich et al. 2020b; Scherrer et al. 2020). Natural disturbances are also important factors affecting forest and ecotone dynamics. In our simulation experiment, we integrated forest management, wind, and bark beetles but we did not quantify their impact, nor did we modulate their frequency along the simulations as we did not want to introduce additional factors in our study that focused on the upper ecotone dynamics. Forest management was not adapted to changes in species composition and harvesting was not implemented in the newly colonized sites as we wanted to assess changes in the forest composition under natural dynamics only. Furthermore, the integration of mountain pine within the model framework presented some challenges due to lack of reliable data for its initialization and parameterization (see further discussion in the Supplementary Information). Moreover, forest expansion stopped before reaching the limits of the theoretically available landscape, regardless the scenario. This is most likely related to a limitation according to the available soil data (see Supplementary Information), specifically to the low values of soil depth due to extrapolation (between 0 and 20 cm, see Fig. S3) that, along with more critical climatic conditions at higher elevations (above 2400 m a.s.l.) typically marks the limits of natural alpine grasslands and thus prevents the establishment of the forest vegetation. However,

this does not invalidate our results since we mainly looked at the current forest-grassland ecotone up to around 2400 m and the data for which soil depth was uncertain was outside this core area. While it is plausible that not all areas currently occupied by grassland are suitable for tree establishment, there are uncertainties regarding the exact limitations and their implementation in the model. Further investigations are required to disentangle these dynamics, maybe related to species parameters or soil-related environmental constraints.

While forest succession dynamics are well reproduced in forest landscape models (Bugmann and Seidl 2022), simulating forest edge dynamics in iLand presented some challenges. At these elevations, where most of the environmental conditions are harsh, microclimate and microsite factors play an important role in determining species establishment and growth (Vittoz et al. 2008) since they may vary greatly in relation to the elevation and to the species composition (i.e., communities) present in the area (Smith et al. 2009). The current iLand version does not capture microclimate differences, and future studies could focus on using microclimate data, combining them with model outputs or implementing them into a dedicated module, to further investigate trees dynamics at their upper limits under environmental changes. However, looking at the wider scale and given its complexity, this model is a promising tool to explore ecotonal changes across mountain areas. Last but not least, the identification of the potential position of the upper forest-grassland ecotone performed at 1-ha resolution, could have been improved using a higher output resolution, which was not directly available in the current iLand version.

Conclusion

Our results confirm that, under a potential abandonment of alpine grasslands, the forested area of inner-Central Alpine valleys is expected to expand in the next decades, with a general upward movement of the forest-grassland ecotone that is projected to stabilize before 2200, regardless the magnitude of climate change. Every tree species will likely shift upward within the next 80 years, especially those adapted to higher elevations. In our landscape, past

land use—that caused the current treeline to be lower than the climatic one—shows to be the most significant trigger of these expansion dynamics, but changes in climate will affect the growth of tree species, their establishment and eventually forest composition, mainly in relation to the aspect. However, climate change effects on species shift might become predominant on longer time scale, playing a major role in influencing micro-climate/topography.

We believe that our simulations present a reliable picture of future forest and forest-grassland ecotone trends at the landscape level in alpine areas. The results presented here could be used to determine hypothetical future scenarios and to provide information for designing long-term management strategies in relation to environmental constraints and stakeholders needs. This study highlights also the need for embedding new processes within forest landscape models, such as the effect of microclimate on tree and vegetation dynamics, conditions characterizing important ecotones such as the border between forests and alpine grasslands.

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Author's contributions S.M. and M.M. conceptualised the study and wrote the final draft. S.M. curated all data, conducted the analysis, visualised the results and wrote the original draft. M.M. provided supervision, funding and supported in data analysis and visualization. K.A. and W.R. provided data and software support. E.T. and C.W. provided input data and support in conceptualization. All authors commented, reviewed and edited the manuscript.

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Data availability Data and code supplementary the analysis of this study are available in Zenodo at the following link: <https://doi.org/10.5281/zenodo.14617309>. The iLand model, including documentation and the full source code, is freely available at <https://iland-model.org/startpage> under the GNU General Public License.

Declarations

Conflict of interest The authors declare no competing interests.

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