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Evidence for 40 Years of Treeline Shift in a Central Alpine Valley

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Abstract: Alpine treeline ecosystems are generally expected to advance with increasing temperatures and after land-use abandonment. Multiple interacting factors modify this trend. Understanding the long-term processes underlying treeline advance is essential to predict future changes in structure and function of mountain ecosystems. In a valley in the Central Swiss Alps, we re-assessed a 40-year-old survey of all treeline trees (>0.5 m height) and disentangled climate, topographical, biotic, and disturbance (land use and avalanche risk) factors that have led to treeline advance with a combination of ground-based mapping, decision tree, and dendroecological analyses. Between the first ground survey in 1972/73 and the resurvey in 2012, treeline advanced on average by 10 meters per decade with a maximum local advance of 42 meters per decade. Larch consistently advanced more on south-facing slopes, while pine advance was greater on north-facing slopes. Newly established spruce mostly represented infilling below the previous treeline. The forefront of treeline advance above 2330 m a.s.l. occurred mainly on favorable microsites without competing dwarf shrub vegetation. At slightly lower elevations, treeline advanced mainly on sites that were used for agriculture at the beginning of the 20th century. This study indicates that although treeline advances under the effect of climate warming, a combination of additional ecological factors controls this advance at regional and local scales.

Keywords: dendrochronology; forest infilling; land-use change; *Larix decidua*; UNESCO Man and the Biosphere Programme (MAB); *Picea abies*; *Pinus cembra*; treeline advance

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1. Introduction

Global surface temperature has risen by 0.95 °C to 1.20 °C during the last century, and climate projections predict further substantial warming that will be most pronounced in alpine and Arctic regions [1]. Climate change has induced changes in the composition and distribution of species worldwide [2,3]. With increasing temperatures, treeline, i.e., the transition zones between subalpine forests and treeless alpine tundra ecosystems, are expected to move upward or poleward because this boundary is defined by the thermal distributional limit of trees [4,5]. Although there is growing evidence for treeline advance over the past few decades [6–10], many treelines have not changed their geographical positions [8,11]. This variability in treeline responses suggests that the movement of treelines not only depends on climate but also on several other factors [12–14].

While temperature is considered to govern treeline at large scales [4], other factors, such as wind exposure, solar radiation, snow cover, soil properties, topographical features, or disturbances, may override or interact with temperature effects at regional and local scales [11,14–16]. Biotic factors, such as tree spatial patterns, snow fungi, or ungulate browsing, are also important factors that can slow down or impede treeline advance [17–20]. Land use is another important factor governing treeline at a regional scale in mountain areas that have a long history of intense anthropogenic influence, such as the European mountains. There, the climatically driven establishment of trees is modified by land-use change, leading to irregular treeline patterns and complex responses to environmental change [21–24].

In the European Alps, treelines have likely been modified by farming practices for more than 5000 years [25]. However, socioeconomic shifts in the past century, largely triggered by the industrial revolution in the late 19th century, have led to intensification of agriculture in fertile and more accessible areas at lower elevations and widespread abandonment of agricultural land at higher elevations over the past century. As a consequence, forest cover has substantially increased [26–28]. The expansion of woody species into open habitats potentially results in treeline advance, but it mainly represents an expansion of forested land into abandoned grasslands and a closing of open forest areas [29,30]. These processes may be exacerbated by the impacts of climate change, particularly near the treeline [11]. An increase in forested area may provide enhanced protection against natural hazards [27,31,32]. However, an increase in woody plant cover in species-rich, extensively managed dry alpine grasslands will ultimately lead to a decline in biodiversity [28,33,34]. While the importance of land-use changes and woody encroachment are widely acknowledged, the extent and location of those changes remain unknown [35].

Long-term changes of treeline positions are difficult to monitor as few forest inventory plots are found at the treeline. Furthermore, remote sensing techniques, e.g., high-resolution aerial photographs and LiDAR data, have rapidly developed in recent decades. While they are powerful tools to analyze treeline changes at large scales [22] and in remote areas [36,37], existing methods are still unable to accurately identify tree species and age or to capture the small stature of treeline trees. A better understanding of treeline dynamics is key to assessing disturbance regimes and climate feedbacks, which are essential for evaluating ecosystem services within the treeline ecotone. Moreover, while changes in climate, land use, and disturbances have been studied separately, only few studies have investigated how interactions among these factors affect treeline dynamics (but see [38]). However, examining how small-scale variations in environmental conditions, such as differences in topography, vegetation, climatic variables, disturbances, as well as former and current land use influence changes in treeline structure remains a major challenge. While it is expected that treeline advances will be greatest on warm, south-facing aspects, the additional influences of previous land use and microsite are unclear.

Here, we present a comprehensive assessment of regional treeline dynamics in the Central Swiss Alps based on detailed ground-based mapping. We combined field surveys and dendrochronological analyses to describe the dynamics of colonizing alpine tree species at their elevational limits. Sampling on opposing north- and south-facing slopes with differing temperatures, growing seasons lengths, and soil moisture regimes allowed us to make inferences regarding the importance of topography, vegetation, land use, and tree-related factors in the treeline ecotone. We expected establishment to vary between species, with cembran pine (*Pinus cembra* L.) and European larch (*Larix decidua* Mill.) colonizing higher elevations, and Norway spruce (*Picea abies* (L.) H. Karst.) largely representing an infilling at lower elevations. Specifically, we asked the following questions: (i) How did the treeline on the north- and south-facing slopes in the study area change over a period of 40 years? (ii) How much of the observed densification of the treeline ecotone can be attributed to treeline advance and infilling, respectively and how does this vary according to different site factors and tree species? (iii) What is the impact of land use on treeline advances and how does this relate to other environmental driving forces?

2. Methods

2.1. Study Area

The study area is located in the Dischma valley near Davos in the Central Swiss Alps (46°47′ N, 09°52′ E; Figure 1). The valley is 13 km long and stretches from southeast to northwest. The study area has a size of approx. 10 km^2 and encompasses an elevation gradient of approx. 1200 m ranging between 1600 and 2800 m a.s.l., with forested areas partly covering elevations up to ~2100 m on north-facing slopes and up to ~2200 m on south-facing slopes (Figure 1). Both aspects exhibit podzol soils from gneiss parent material [39], and relief is a key factor for differences in soil depth, texture, and biological activity. Situated in the eastern Swiss Alps, the climate of the study area is influenced by the humid climate of the Northern Alps and the continental climate of the Central Alps. Mean annual air temperature in Davos (1594 m a.s.l.) was 3.5 °C for the reference period 1981–2010 (MeteoSwiss, 2022). Average temperatures have increased over the last 100 years by about 1.5 °C, with accelerated warming since the late 1980s (MeteoSwiss, 2022; Figure 2). Average annual precipitation sum in the Dischma valley (1700 m a.s.l) was 1033 mm for the same period, with precipitation maxima during the summer months (MeteoSwiss, 2022). In contrast to temperature, annual precipitation sums have not significantly changed over the past century (MeteoSwiss, 2022).

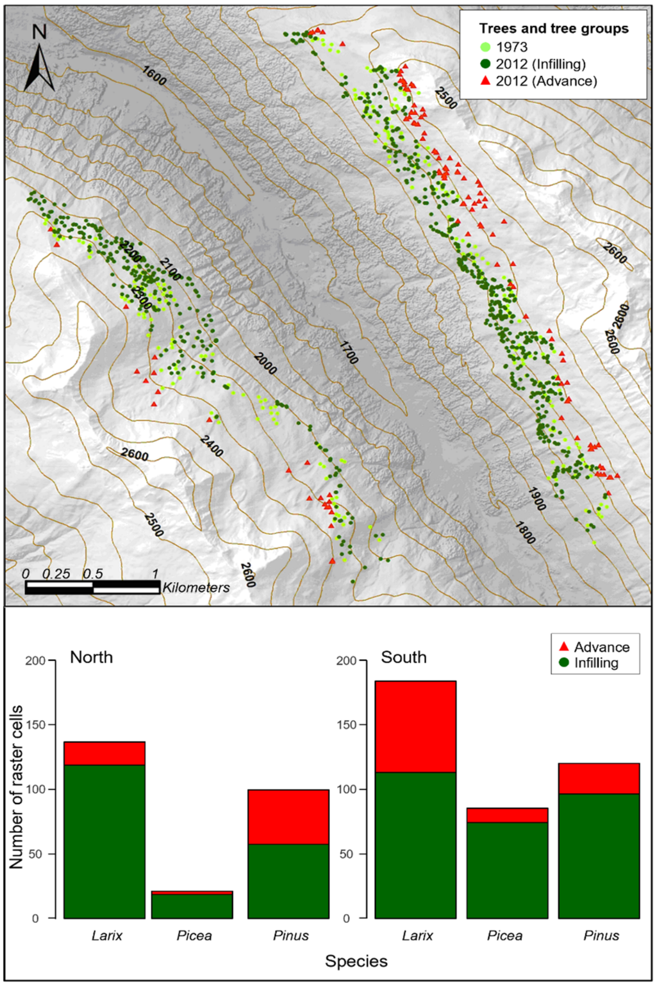

Figure 1. Upper panel: forest change in the study region derived from terrestrial mapping of trees and tree groups at treeline. A moving window analysis was used to discriminate between treeline advance and infilling below treeline. Light green circles represent trees or tree groups that were already present in the treeline ecotone in the 1972 survey. Red triangles represent individual trees and tree groups classified as advance, and dark green circles are trees and tree groups classified as infilling. Classification was calculated at a 50 m pixel resolution using a neighborhood elevation analysis comparing position of trees and tree groups in 2012 (dark green and red symbols) to 1972 (light green circles). Lower panel: classification of the trees and tree groups that established in the time interval between the two surveys (1972–2012). Bars represent the number of raster cells with trees classified as advance or infilling on the two valley slopes separated by species.

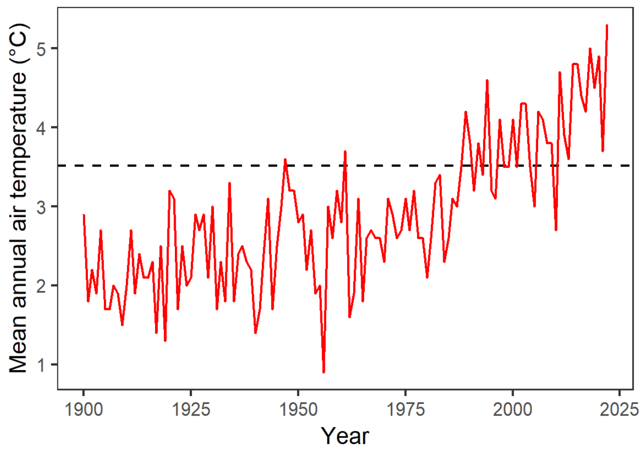

Figure 2. Mean annual air temperature at 2 m height (1900–2022) at the MeteoSwiss weather station in Davos at 1594 m a.s.l. The dashed horizontal line represents the corresponding value for the climate norm period 1981–2010 (source: MeteoSwiss).

Land use in the community of Davos, where the study area is located, is shaped by agriculture, but the number of farms has halved during the 20th century, leading to a reduction in the total agricultural area [40]. The slopes above the non-forested valley bottom are characterized by coniferous subalpine forests. The main tree species is the shade-tolerant, wind-dispersed Norway spruce. At higher elevations, it is mixed with the wind-dispersed colonizer European larch and near treeline with cembran pine. Cembran pine is dispersed by the Eurasian nutcracker (*Nucifraga caryocatactes*). Above treeline, alpine meadows and rock outcroppings dominate the landscape. Snow avalanches are the most important disturbance for the forests in the study area.

2.2. Field Surveys

Field surveys were conducted in the summers of 1972 and 1973 [41], hereafter referred to as 1972 survey. In summer 2012, these surveys were repeated by recording all trees and tree groups with heights >0.5 m growing in the treeline ecotone of the study area. Small tree groups consisted of 2–5 individuals and large groups consisted of >5 individual trees. In the 1972 survey, geographic positions of individual trees and tree groups were manually recorded on a topographic map (source: Swisstopo, 1983) using a barometric altimeter up to 6000 m (Thommen AG, Waldenburg, Switzerland). In 2012, all positions were recorded using a Garmin eTrex GPS device (Garmin Ltd., Lenexa, KS, USA). In addition, tree species, the presence of browsing, and the presence of infections caused by the snow fungus *Phacidium infestans* (only for pines) were recorded for each tree. For the subsequent spatial analysis, the data from 1972 was digitized. A binary value for tree presence or absence was assigned to each cell of a 50 m grid. First, the choice of grid resolution was based on the fact that the explanatory variables, obtained from the UNESCO Man and the Biosphere Programme (MAB) Project 6, were available as GIS raster data with a resolution of 50 m [42]. Second, a comparison of 1972 data points that were clearly identifiable in 2012 showed that errors due to mapping and the positions of symbols on the map were mostly <25 m. Thus, this justifies a grid resolution of 50 m and allows for consistent spatial analysis between environmental variables available in a gridded format and field surveys.

2.3. Data Analysis

2.3.1. Spatial Analysis

We adapted the moving window algorithm developed by Gehrig-Fasel, Guisan, and Zimmermann [22] to identify the treeline position in the two surveys (1972 and 2012) as well as treeline changes in this time interval. We assigned the local elevation from a digital elevation model to each forested grid cell. By considering quadratic neighborhoods, we assigned the maximum elevation of all forested cells in the search window to the central cell of this search window. The analysis was run with windows of varying size (30, 90, 120, 150, 250, and 350 m; windows <150 m were computed with a 10 m raster). Finally, a window size of 3 × 3 pixels (150 m × 150 m) was selected as it was large enough to include a sufficient number of trees and small enough to capture elevation differences from local topography. For windows >250 m, neighborhood averages often included effects from multiple gullies, thus potentially overestimating treeline advance, especially on the west side of ridges. Windows <120 m restricted classification neighborhoods, and a greater number of cells were unclassified due to the dispersed nature of trees at treeline. By running through the study area as a moving window, pixels in the 2012 layer were identified as (a) infilling if 1972 neighborhood averages exceeded the 2012 cell average, (b) advance if 1972 neighborhood averages were less than the 2012 cell value, and (c) downward shifts if trees were present in 1972 and absent in 2012.

We determined the distances of treeline advance by computing minimum vertical distances between points classified as advance in 2012 and nearest 1972 raster cells using feature-based proximity analysis in ArcGIS. For this vector analysis, the following steps were conducted: (1) raster cells were converted into polygons, (2) angles and overland distance for each point to the 1972 polygon were extracted using the "Near" tool, and (3) elevation differences were calculated from the DEM25 by taking component elevations of the 2012 point and the 1972 polygon. Distances of advance were then analyzed for distribution of normality using a Shapiro–Wilk test [43]. In cases of significant deviations from normality, data were tested using a nonparametric Mann–Whitney U Test (Wilcoxon rank sum test) for aspect comparison [44]. Differences were considered significant if the p value was smaller than 0.05. All calculations were conducted with the R software, version 3.0.1 [45].

2.3.2. Age Determination of Treeline Trees

We selected 4 sites for 60 m wide transects extending downslope from the highest recorded tree in 2012 (>0.5 m height) to below the highest tree recorded in 1972. Along the transects, trees were sampled around sampling points marked every 30 m. Cores from 124 trees, taken with a 5 mm increment borer, were extracted from between 2 and 25 cm above ground depending on the gradient and local growing conditions. Basal sections at the root collar from 32 additional trees were sampled due to their small diameters. In total, 85 larches, 46 pines, and 25 spruce were sampled. Highest priority was given to coring as close to the root collar as possible, but in cases where cores needed to be collected from positions higher on the stem, establishment dates were derived from ring counts plus estimates of age below core height based on age height correction curves for each species. For trees with multiple branches at the base, the largest diameter stem was taken.

Samples were dried and finely sanded for age determination according to standard methods [46,47]. The estimated age reported for all trees is the age taken as close to the root collar. Six samples with rotten cores were excluded from the analysis. For incomplete cores, where the pith was not sampled, we estimated the length of the missing radius by matching the curvature of the innermost rings to concentric circles drawn on paper [48]. The number of missing rings was estimated by calculating the mean number of rings for the radii of corresponding lengths from the basal sections of small trees (<5 cm diameter). The resulting age correction factors were added to the number of visible rings in the incomplete cores to estimate the age at coring height. Skeleton plots instead of cross-dating software were used to correct the age of 16 samples because the latter is unreliable for datasets of young trees [46].

2.3.3. Nonparametric Regression Analysis

To assess the underlying factors of treeline advance, we considered all raster cells with advancing trees between 1972 and 2012 and complemented them with an equal number of randomly selected cells. Presence/absence of trees was used as a categorical response variable. We conducted a nonparametric regression analysis using decision trees [49], in which we compared an initial set of 13 site variables (Table 1). Climate, biotic, land use, and disturbance variables were obtained from the UNESCO MAB Project 6 (1973–1987) [42]. To generate this dataset, aerial photographs and ground sampling techniques were combined, and the results were digitized. Most variables were derived by percent cover algorithms, although the methods varied [50]. Land use was mapped based on the historical analysis of [40] for 1900 and 1982. Land-use categories included "heavily cut", "cut", "grazing", and "no use" for 1900 and "grazed", "abandoned", and "no use" for 1982. To supplement the MAB project data, more recent remote sensing data were obtained to improve the accuracy of relief and snow cover variables. Accurate elevation data from 2010 in the form of a Digital Surface Model (DSM) was available for the Dischma Valley at 2 m resolution. We used this DSM to calculate topographic measures (elevation, slope, curvature, and exposure) and compared the DSM with a winter surface model to derive snow depths [51]. The R package "party" was used to calculate decision trees [52]. All variables with a p value smaller than 0.05 were included in the final decision tree.

Table 1. Explanatory variables used to analyze treeline advance in a decision tree analysis.

Variable (Unit)	Type
Climate-related variables	
Direct solar radiation (W/m^2/3000)	Continuous modeled variable derived from MAB [(1)]
Snow free days (days)	Continuous modeled variable derived from MAB
Snow depth (m)	Continuous modeled variable derived from DSM [(2)]
Topographic variables	
Elevation (m a.s.l.)	Continuous modeled variable derived from DSM
Slope (°)	Continuous modeled variable derived from DSM
Curvature	Continuous modeled variable derived from DSM [(3)]
Aspect (°)	Continuous modeled variable derived from DSM [(4)]
Disturbance variables	
1900 Land use	Categorical variable derived from MAB [(5)]
1982 Land use	Categorical variable derived from MAB [(6)]
Land-use change	Categorical variable derived from MAB [(7)]
Avalanche risk	Categorical variable derived from MAB [(8)]
Biotic variables	
Vegetation	Categorical variable derived from MAB [(9)]

[(1)] MAB = UNESCO Man and the Biosphere Programme [42]; [(2)] DSM = digital surface model of Swisstopo with 2 m resolution (Swisstopo 2014); [(3)] values: <0 for concave depressions and >0 for convex ridges and hilltops; [(4)] values: azimuth; [(5)] values: heavily cut, cut, grazed, and no use; [(6)] values: grazed, abandoned, and no use; [(7)] values: grazing, abandoned grazing, grazing with previous cutting, and no use; [(8)] values: no risk, potential risk, and high risk; [(9)] values: rubble and no vegetation, alpine grasslands on acidic siliceous bedrock, and dwarf shrubs.

3. Results

3.1. Infilling and Treeline Advance

Tree density in the treeline ecotone has strongly increased in the study area on north- and south-facing slopes of the Dischma valley over the 40-year study period. A total of 740 tree groups and 321 single trees with heights >0.5 m were recorded in the treeline ecotone in 2012. In the spatial analysis with a moving window algorithm, 21% (164 raster cells) of the 765 raster cells with trees or tree groups newly established since 1972 were classified as treeline advance, while the remaining 79% (601 raster cells) were classified as infilling between already existing trees and tree groups (Figure 1). Trees classified as advance in the 2012 survey were found on average at 25 m higher elevation on the north-facing slope and at 40 m higher elevation on the south-facing slope of the valley compared to the closest trees, which were already recorded in 1972. A total of 18 cells were classified as downward shift, with most of them clustered in avalanche paths. Above 2250 m a.s.l., 34% of the raster cells (119 cells) with newly established trees were classified as advance, while 64% (232 raster cells) represented infilling. The uppermost trees recorded in this study were larch trees at 2443 m a.s.l. on the south-facing slope in 2012.

The patterns of treeline advance and infilling strongly varied among different exposures and among different tree species (Figures 1 and 3). Overall, there was no statistically significant difference in the amount of advance between the two valley slopes. However, considering the westernmost 4 km of the valley (near the valley mouth) only, advance was significantly greater on the south aspect (46 m) than on the north aspect (24 m; $p = 0.014$). Larch was the dominant advancing tree species on the south-facing slopes with 42% of all recorded trees. The average elevation gain of this species was 47 m on such slopes vs. 24 m on the north-facing slopes. On the north-facing slopes, pine was the most frequently advancing species. On average, pine gained 36 m on these slopes and 31 m on the south-facing slopes. The overall greatest detected distance of advance was 167 m for a larch on the south-facing aspect compared to 122 m on the north aspect. By contrast, newly established spruce represented mostly an infilling below the 1972 treeline. They established more frequently on the south-facing slopes than on the north-facing slopes. Nevertheless, larch and pine also contributed strongly to the infilling below the treeline. In absolute numbers, their contribution was greater than the one of spruce.

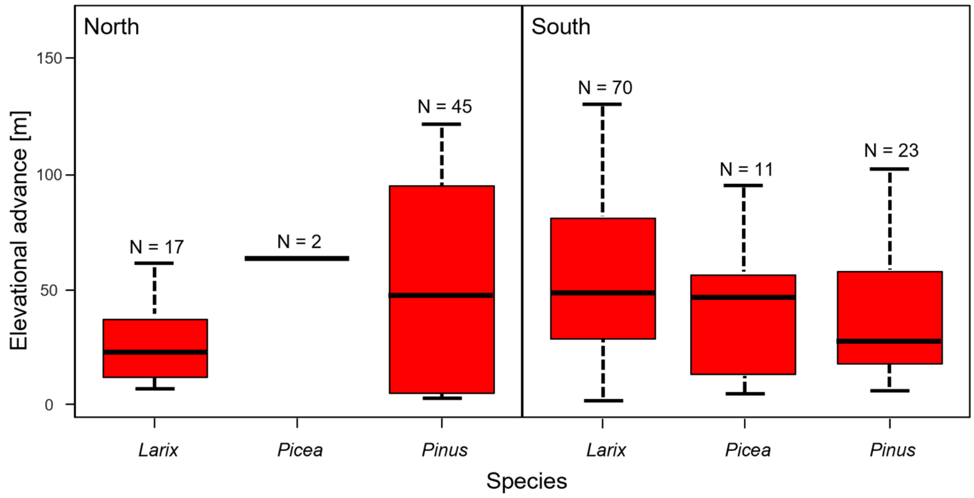

Figure 3. Distance of treeline advance (1972–2012) for north- and south-facing aspects (left and right panels, respectively) separated by the three study species. Distances were computed as the elevational difference between trees classified as tree advance (2012) and the nearest raster cell (1972) of trees recorded in the first field survey. No confidence intervals have been plotted for *Picea* advance on the north-facing slope due to the extremely small sample size.

To confirm these results, we conducted dendrochronological analyses of a subset of treeline trees. The age of these trees varied between trees classified as advance and those classified as infilling and according to species (Figure 4). Trees classified as advance showed a narrow range of ages with a median age of 21 years (5th percentile = 2 years; 95th percentile = 42 years). Among all advanced trees, the oldest individual was a 47-year-old larch. Trees classified as infilling exhibited a greater variability of ages: the median age was 34 years (5th percentile = 10 years; 95th percentile = 68 years), and the oldest tree was an 86-year-old larch. For both advanced and infilling trees, larch (median = 26 years) and spruce (median = 30 years) were on average older than pine (median = 18 years).

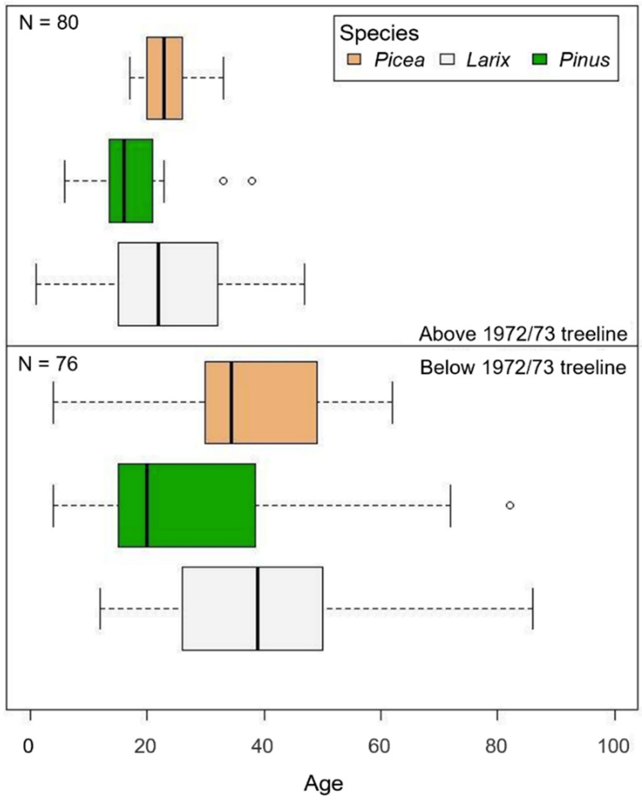

Figure 4. Tree age above (**upper panel**) and below (**lower panel**) the 1972 treeline based on dendrochronological analysis of a subsample of trees on both south- and north-facing valley slopes. Number of sampled trees above treeline: *Picea* (N = 9), *Larix* (N = 56), *Pinus* (N = 15) and below treeline: *Picea* (N = 29), *Larix* (N = 16), *Pinus* (N = 31).

3.2. Ecological Factors Influencing Tree Occurrence and Treeline Advance

Variable importance analysis for the occurrence of trees in the treeline ecotone indicated that elevation, as a proxy for several environmental factors, such as temperature and soil conditions, was the most important predictor for tree occurrence both in 1972 as well as in 2012. The importance of other relevant drivers partly changed between the two observations (Figure 5). For 1972, topography and current land use were the second and third most important variables, with trees more frequently occurring on convex sites (ridges) and where there was no current land use. Other variables, such as slope aspect, the occurrence of avalanches, snow disappearance, and slope angle, were less important. In 2012, slope aspect (with more trees occurring on the south-facing slopes), slope angle, and snow disappearance (more trees where snow disappeared early) increased in relative importance compared to current land use and vegetation.

Only five of the 13 variables considered as potential drivers for the advance of trees in a multivariate decision tree analysis were found to be significant ($p < 0.05$). Advance occurred at elevations above 2330 m a.s.l. mainly on microsites without dwarf shrub vegetation (i.e., alpine meadows or microsites without vegetation cover) or where dwarf shrubs occurred on microsites with high radiation (Figure 5). Below 2330 m, historical land use was the most important driver of tree establishment with higher rates of establishment where land use was present in 1900. Current land use had no significant effect on treeline advance.

On both valley slopes, larch was the species most affected by ungulate browsing in 2012, with 26% and 22% affected individuals on the north- and south-facing slopes, respectively. Pine with 7% and 4% on the north- and south-facing slopes, respectively, and spruce with 5% and 4% on the north- and south-facing slopes, respectively, were clearly less affected by browsing. *Phacidium infestans* infected 62% of the pines on the south-facing slope and 32% of the individuals of this species on the north-facing slope. Among them, 10% were severely infected by this snow fungus.

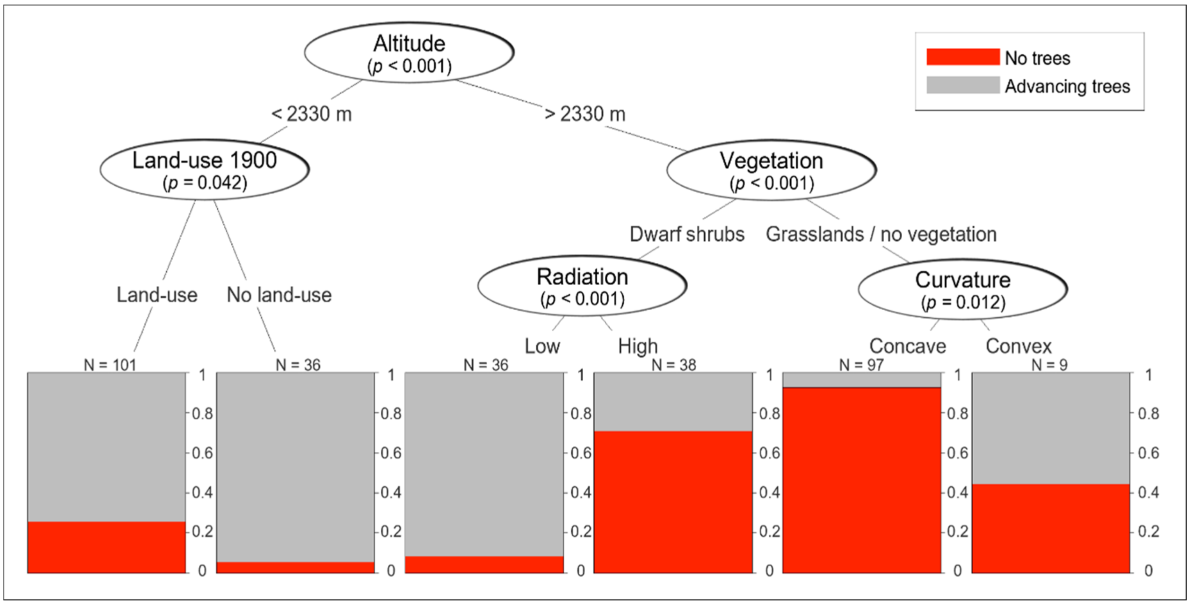

Figure 5. Decision tree showing the ecological factors that significantly influenced treeline advance between 1972 and 2012. The analysis was based on 164 raster cells classified as advance and 164 randomly chosen raster cells without advancing trees.

4. Discussion

This resurvey study repeated the ground-based mapping of all trees and tree groups in the treeline ecotone in the (sub)alpine Dischma valley near Davos. We found that treeline position in this inner-alpine valley has advanced by an average of 40 m over the past 40 years, i.e., 10 m per decade. In addition, substantial infilling of forest gaps below the former treeline was observed. While spruce was mostly restricted to infilling below the treeline, larch and pine contributed to both infilling and advance, with pine preferring ridges and north-exposed slopes and larch preferring open sites free of competition for light, mainly on the south-facing slope.

4.1. Densification of the Treeline Ecotone Due to Advance and Infilling

While advance of the uppermost tree positions and infilling were generalized phenomena in the study area, downward shifts of the treeline were only observed in very few localized instances associated with areas affected by natural disturbances, such as avalanche tracks [27]. As most of the advancing trees are still fairly small, they have not been strongly affected by avalanches and other disturbances. However, a negative impact on treeline advance may become more important once these trees growing along the treeline become taller [53]. Our detailed ground-based mapping in a small catchment confirmed and complemented the findings of treeline advance and infilling below treeline, which had been described in a larger-scale study based on remote sensing data covering the complete Swiss Alps [22]. While the study of Gehrig-Fasel, Guisan, and Zimmermann [22] was limited to a fairly short observation period of 12 years, our study covered an extended period of 40 years. Both studies found similar rates of treeline advance. Generally, treeline advance is a widespread phenomenon. It has been reported over large parts of Switzerland [22,54–56] but also for locations around the world [6,57,58]. However, treeline advance is not a ubiquitous phenomenon as literature reviews have revealed that only about half of the investigated treelines around the world are currently advancing [8,11].

Establishing a suitable metric for quantifying and comparing the magnitude of treeline advance is challenging because treelines vary in their structure (abrupt vs. diffuse boundaries), composition (mono- vs. multi-specific), prevailing tree form (krummholz vs. upright trees [59]), and tree spatial patterns [20]. Therefore, the change in the highest elevation at which trees grow has often been used to describe treeline shifts over time [60]. Determining the distances individuals have advanced with respect to historic treelines acknowledges the spatial heterogeneity of treeline elevation across an ecotone and quantifies variability of treeline advance. Gehrig-Fasel, Guisan, and Zimmermann [22] compared their results to historical treeline fluctuations and noted that the recent magnitude of advance, which is confirmed by the results of our study, is comparatively high when considering that temperature oscillations during the Holocene caused treeline fluctuations of around 100 m (e.g., [61]), as confirmed by pollen records and treeline models [62,63].

Our dendrochronological analyses revealed that trees growing above the 1972 treeline elevation were consistently younger than 40 years, which demonstrates that these trees had established only after the first survey. By contrast, trees growing below that line exhibited a wider age distribution comprising older and younger trees. These observations correspond to the expected pattern of age distribution [64]. Previous studies have indicated potential errors in identifying the patterns of tree establishment using remote sensing methods [22]. Due to the slow growth and suppressed stature of treeline trees, it is difficult to distinguish between trees that have established between two surveys and existing trees as the latter may increase in height beyond a certain detection threshold and mistakenly be classified as newly established trees. By combining ground-based surveys and a dendrochronological approach, this study was able to investigate tree establishment with higher accuracy.

Dendrochronology further revealed differential responses among tree species. As an early colonizer, larch advanced relatively constantly and occurred in a broad range of habitats following the environmental and land-use changes. By contrast, pine advanced mainly on favorable microsites and mostly in a short time window during the last decade. Although one might expect that the zoochorous dispersal of pine by the European nutcracker would generally allow for greater advance compared to other species, an earlier study found that sapling mortality was much higher in pine than in larch due to its susceptibility to snow fungi [65], thus overcompensating the dispersal advantage. Seedling and sapling mortality was found to be particularly high in some periods, which likely prevented a steady advance of pine [17]. Finally, spruce showed mainly infilling on sites with declining land-use pressure. The effect of slope aspect is less clear and may vary more strongly with tree species and over time.

4.2. Impact of Land Use and Other Environmental Drivers on Treeline Advance

Our results show that topographic variability in the study area produced favorable sites that facilitated opportunistic establishment of trees at high elevation, enabling them to encroach on the alpine tundra. The classification tree analysis reveals that factors influencing tree advances at higher elevation, i.e., above 2330 m a.s.l., vary significantly depending on vegetation cover. For sites where dwarf shrub cover is dominant, significantly more trees established under high solar radiation compared to low radiation. This was somewhat surprising as solar radiation is higher on the south-facing slopes, where shrub growth is usually denser. We would therefore have expected that tree regeneration and consequently treeline advance would be strongly limited on such sites [66]. Dense herbaceous or shrub cover can negatively affect establishment by reducing seedbed suitability and increasing competition for resources [67–70]. Vegetation competition may be an important limiting factor for larch due to its high light requirements for germination and the difficulty of light larch seeds to reach the seed bed. Dwarf shrubs are generally found on the north exposures, where radiation is considerably lower and temperature is generally limiting for growth. Thus, this result suggests a limitation of trees on the north exposed slopes, although facilitative effects of vegetation can be especially important at the emergent and seedling stage and may additionally have an effect [71]. As trees have established favorably on sites with high radiation, this result further suggests that exposure to sunlight does not inhibit establishment through water stress in this environment.

Conversely, where alpine grasslands or no vegetation are the dominant cover, terrain curvature was a significant factor, with concave depressions exhibiting a greater number of trees compared to convex ridges. This suggests that where shrub cover is not limiting, trees establish preferentially in concave depressions. On the south-facing slopes, where advance was more frequent, the favorable thermal conditions in such depressions may frequently outweigh the adverse effects of snow and cryophilic fungi on tree establishment, which are more common in these locations [17]. This study, conducted in the same valley but limited to a specific afforestation area, revealed that snowmelt date was always the most important environmental factor influencing sapling mortality, while elevation was the most important factor for growth. Microhabitat differences over short horizontal distances can have significant impacts on tree establishment and growth as microtopography can mimic temperature amplitudes that would correspond to large elevational gradients across very short horizontal distances [72]. The finding of favorable establishment in concave depressions may be particularly representative for larch due to the high proportion of larch among the newly established trees in this study. Generally, larch is known to establish preferentially in wide, concave landforms where colluvial soils provide optimal growing conditions [73,74]. Conversely, pine mainly grows on ridges with early snowmelt [75], which reduces the detrimental effects of snow fungi infection [17]. Based on the finding that treeline advances at the highest positions (i.e., above 2330 m a.s.l.) were not influenced by land-use change, we conclude that rising temperature due to climate change was likely the more important driver than land-use change for the advance of the uppermost tree positions.

At lower elevation (<2330 m a.s.l.), trees were more likely to establish in areas where land use was practiced in 1900 than in formerly unused areas. This variable was a good indicator of historical land use, showing areas that were, in many cases, agriculturally used at least for some decades after 1900. Furthermore, historically unused areas likely consisted mainly of very steep or rocky terrain less suitable for tree establishment. These results suggest that terrain, that is potentially suitable for agricultural use, is also more suitable for tree establishment and treeline advance. In the first 20 years after land abandonment, a window of opportunity for tree establishment is often observed [76,77]. Although land-use change has been identified as a major driver for treeline advance in several studies [23,29,78], land abandonment was not a statistically significant driver for treeline advance in our study area. However, it was likely an important factor favoring infilling below the 1972 treeline.

Unexpectedly, and in contrast to former land use, current land use, which in the study area consists mainly of cattle grazing, did not have a significant effect on treeline advance. A possible explanation may be that the interactions between tree establishment and grazing described in the literature are often complex and can exhibit considerably contrasting tendencies. Some authors have reported adverse effects on tree establishment and growth from trampling and consumption of seedlings, reduced growth due to browsing, suppressed reproductive age, and increased mortality [79,80]. Such effects are likely observed in areas with intense grazing pressure. Conversely, other authors have found that livestock creates favorable habitats for tree establishment and reduces competition for resources by suppressing the herbaceous and shrub layers [81,82].

5. Conclusions

In this study, we found substantial densification of the treeline ecotone over a 40-year observation period. Observed changes comprised both treeline advance and infilling of gaps below the former treeline. The varying responses among slope aspect, vegetation, tree species, and land use suggest that treeline processes are a complex interplay of multiple factors that cannot be reduced to a simplistic picture of tracking shifting isotherms due to climate warming [83]. It is expected that treeline changes will continue and may even accelerate due to ongoing climate change. However, the findings of this study show that future treeline changes will depend not only on the climate trajectory of the coming decades but also on future changes in land use as well as microecological conditions in the treeline ecotone.

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