



*40 Years of Alpine Treeline Shift in the Dischma Valley, Switzerland
By Lisa Erdle*

*A Thesis Submitted in Partial Fulfillment of the Requirements for the
Degree of*

*MASTER OF SCIENCE
in European Forestry (University of Eastern Finland and AgroParisTech)*



© Lisa Erdle, 2013 University of Eastern Finland All rights reserved.

Supervisory Committee

FRANCE

Dr. Ignacio Barbeito, Supervisor
Institut national de la recherche agronomique (INRA)

SWITZERLAND

Dr. Peter Bebi, Co-Supervisor
WSL Institut für Schnee und Lawinenforschung - WSL Institute for Snow and Avalanche
Research, SLF

Host Institutions

The work of this Master's thesis was realized in the Laboratory of forest and wood resources (LERFoB), in Nancy, France, a research facility of the Institut national de la recherche agronomique (INRA) in cooperation with the Mountain Ecosystems group of the WSL Institute for Snow and Avalanche Research, SLF in Davos, Switzerland. Both groups focus on research activities examining functioning of forest ecosystems, where long-term studies on forest stand development and plant distribution are common research themes.

LERFoB

LERFoB's active research activities involve work on forest stand dynamics, wood quality and structure of wood. Recent projects have taken a multi-scale approach using dendro-ecology, wood physics and chemistry to investigate the impacts of changing environments on tree growth processes with extensive field studies and a variety of modelling techniques. Additionally, LERFoB works with the French National Forest Inventory and has close partnerships with French and international organizations.

WSL

The WSL's Mountain Ecosystems group focuses on mountain forests and alpine ecosystems, and links ecosystem research with snow and avalanche topics of the SLF in Davos. Current research topics of the Mountain Ecology group include alpine flora distribution changes under climate change, interactions between mountain forests and protection functions, and evolution genetics of alpine plants. Long-term experimental research at the Stillberg afforestation plantation in the Dischma Valley provides long-term data on tree performance above the treeline.

Abstract

Growing evidence suggests that alpine communities are responding to recent climatic changes. Vegetation shifts are particularly rapid in regions where land-use change is coupled with increased temperature. Tree colonization to higher altitudes is modifying mountain regions, and an understanding of the processes behind treeline advance is therefore essential to understand future changes in structure and function of this alpine ecotone. This study examines the patterns of treeline change in the Dischma Valley, Switzerland over the last forty years. Larch advance was substantial; advancing up to 167 m. Distances of advance were greatest the south-facing slope. Pine exhibited considerable advances on north-facing slopes (up to 122m). Spruce mostly experienced an infilling below treeline. Our results suggest that species responses vary between north and south aspects, and that treeline advance is closely linked to fine scale topographic variables. Strong land-use influences were not detected, although areas with land use may have facilitated larch establishment 25-35 years ago. Dendroecological results thus far suggest that larch establishment is currently restricted, although more work is needed to establish whether this is related to climatic conditions or availability of suitable seedbed sites due to competing vegetation.

Table of Contents

ABSTRACT	1
TABLE OF CONTENTS.....	2
1. INTRODUCTION	3
1.1 <i>General Introduction</i>	3
1.2 <i>Study aims</i>	4
1.3 <i>Research Questions and Hypotheses</i>	4
2. STUDY AREA	5
2.1 <i>Climate</i>	5
2.2 <i>Geology and Topography</i>	6
2.3 <i>Wind and snow</i>	7
2.4 <i>Land-use history</i>	7
3. METHODS	8
3.1 <i>Summary</i>	8
3.2 <i>Preparation and analysis of existing data</i>	8
3.3 <i>Spatial and Statistical Analysis</i>	9
3.4 <i>Dendroecology</i>	14
3.4.1 <i>Tree age determination</i>	15
3.4.2 <i>Reconstruction of treeline advance</i>	15
4. RESULTS	15
4.1 <i>Spatial Results</i>	16
4.2 <i>Temporal Results</i>	20
5. DISCUSSION.....	20
5.1 <i>Spatial patterns of treeline change</i>	20
5.2 <i>Temporal patterns of establishment</i>	24
6. CONCLUSION	26
.....	33

1. Introduction

1.1 General Introduction

This thesis seeks to understand changes in the alpine treeline that have occurred in the Dischma Valley of the Swiss Alps over the last forty years. The alpine treeline can best be characterized as an ecotone, across which subalpine forest transitions to treeless alpine tundra (Körner 2012). As this boundary encompasses two distinct ecosystems and species range limits, treelines are ideal locations to investigate impacts of climate change on vegetation (Rochefort et al. 1994; Lenoir 2008). There exists some agreement that alpine flora (Walther et al. 2002, 2005; Lenoir 2008) and treelines (Parmesan 2006; Holtmeier & Broil 2007; Weiser 2007) are advancing to higher altitudes. There are, however, many anomalies to this trend that appear dependent upon local and regional conditions (Holtmeier & Broll 2005). Although temperature is considered to govern treeline at large-scales (Körner 2012), variability in geomorphological and ecological factors lead to complex climate change responses, and may be further complicated by thresholds, such as time-lags and ecological inertia (Malanson 2001; Klasner & Fagre 2002; Burkett et al. 2005; Lloyd 2005). Additionally, in the Alps, land-use history appears to be an important factor behind the rate of treeline advance (e.g. Gehrig-Fasel et al. 2007). Thus, documentation of treeline change and identifying underlying factors that promote or restrict treeline advance is critical to our understanding of future climate change impacts within this zone.

Many ecosystems are affected by climate warming but also by land-use changes that interact with the potential effects of climate change (Foley et al. 2005; Gehrig-Fasel et al. 2007). Alpine treelines in the Central Alps have likely been modified by farming practices for more than 5000 years (Vorren et al. 1993), however, socioeconomic shifts, largely triggered by the industrial revolution in the late 19th century, have led to intensification of agriculture on fertile and more accessible land at low elevations, and widespread declines in agricultural intensity at high elevations (Debussche et al. 1999; Niedrist et al. 2009). Through observational and experimental studies, abandonment of traditional pastures has shown to impact alpine species richness (Rusch & Oesterheld 1997), community composition (Collins et al. 1998), and functional groups (Mayer et al. 2009), and grazing has recently become an important strategy for biodiversity conservation in Europe (Zervas 1998; Austrheim et al. 1999; Barbaro et al. 2001). Since alpine areas are expected to experience above average warming under current climate change scenarios, (Theurillat & Guisan 2001), work on interactions between disturbance and ecosystem shifts is a priority.

1.2 Study aims

Surveys of individual trees and tree groups in the Dischma Valley were conducted in 1972/73 and repeated in 2012 serve as the starting point for this thesis. The 2012 survey was done as part of an extensive study recording individual trees between 2000 - 2450m above sea level (asl.), which provides the unique opportunity to investigate how the position of trees has changed in the last forty years (Leibold 2012). Treeline is often difficult to study with long-term repeated surveys since the Swiss National Forest Inventory (NFI) has comparatively few sample plots at the treeline (see Appendix 1 for NFI results). Further, while remote sensing techniques (high resolution satellite imagery, orthophotos, Lidar) are powerful tools to analyze treeline changes at large scales (Gehrig-Fasel et al. 2007) and in remote areas (e.g. Rees et al. 2002, Callaghan et al. 2002), these instruments often do not capture the small stature of individual high elevation trees. In the Dischma Valley, 928 out of 1035 treeline trees were less than 3m (Leibold 2012).

This study addresses the need to better understand the relationship between disturbance, climate, and local site conditions to put treeline advance into context of climate warming. Specifically, this study aims to (1) identify distances of treeline advance in the last 40 years of the Dischma Valley, (2) assess the underlying factors of treeline advance, and (3) evaluate whether tree establishment follow specific temporal patterns through a dendrochronological approach.

1.3 Research Questions and Hypotheses

The main hypothesis of this thesis is that alpine treeline change in the Dischma Valley is strongly affected by climatic variability as well as local site conditions. Moreover, it is expected that while land-use has played an important role in artificially suppressing the treeline, the effect of biophysical factors exert a stronger influence in driving treeline advance. More specifically, the following questions and hypotheses were formed related to spatial (Q1-2) and temporal (Q3) patterns of treeline advance in the Dischma Valley:

Q1: Has the Dischma Valley treeline advanced during the last 40 years?

H1: Trees have advanced in the last 40 years, and trees have established on favourable sites, specific to species physiology; pine and larch have advanced above the old treeline (pine on concave ridges with rocky outcrops, larch on open sites without light competition), whereas spruce is mostly characterized by an infilling below the treeline due to a competitive advantage in warm conditions.

H2.1: Factors restricting tree advance differ between aspect; on the north-facing slope, tree establishment is primarily limited by abiotic factors (snow cover and avalanche disturbance), whereas biotic factors (dense shrub cover) limit establishment on south facing slopes.

Q3: How have rates of tree establishment varied in the last 40-100 years?

H3.1: Temporal trends can largely be explained by climatic variation, with trees establishing less favourably on south-facing aspects due to increased drought sensitivity during warm periods.

H3.2: Light seeds dispersed by wind allow larch to advance large distances. It's predicted that trees exhibit "waves" of establishment, and trees that have advanced long distances have established in the same periods (responding to the same environmental variables) as trees that have advanced only short distances. Pine is dispersal-limited by the nutcracker, and will show less pronounced responses to climate variability.

In addition to addressing these questions, with a dendroecological approach, this study also aims to build on the master's thesis work of Leibold (2012) by providing ground truthing of trees established in the last 40 years by dating treeline trees. This will help evaluate the question of the usability of old maps to accurately investigate treeline shift.

2. Study Area

2.1 Climate

The study area is located in the Dischma Valley near Davos, Switzerland (46° 47' N, 09° 52' E) (Figure 1). Situated in the eastern Swiss Alps, the climate is influenced by the humid North Alps, and the continental Central Alps. Mean annual precipitation is relatively low compared to other areas in the Alps (1050mm; Stillberg monitoring station, 2090 m asl, 1975–2005) with high precipitation in July and August. Average annual temperature for the same period was 2.1°C. During recent decades, variation in climate shows temperature increases around the world, with rapid change at high altitudes (Solomon et al. 2007). Precipitation regimes are also expected to vary; timing of precipitation influences relative proportions of snow and rain, leading to annual differences in snowpack and moisture regimes. However, evidence from the last 80 years shows that at high elevations, no trends have been observed in altered snow depth or changes in the timing of spring snow disappearance above 1500m asl (Marty and Meister 2012).

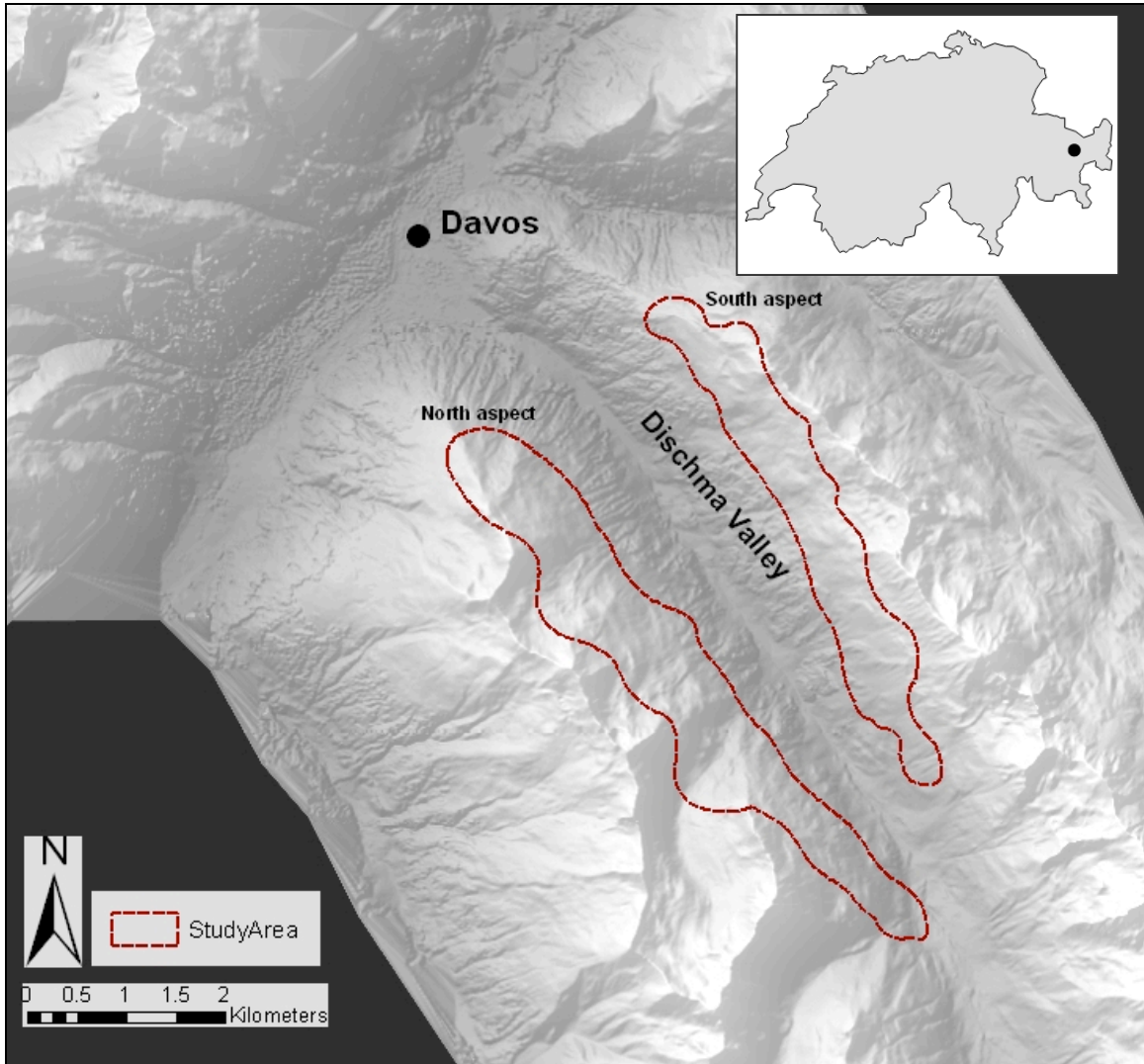


Figure 1: Dischma Valley, Switzerland ($46^{\circ} 47' N$, $09^{\circ} 52' E$).

2.2 Geology and Topography

The valley runs NNW – SSE, and the two slopes vary in geology and soils. Both aspects exhibit podzol soils from gneiss parent material (Blaser 1980), although relief is a key factor for differences in soil depth, texture, and biological activity. On cooler and wetter north-facing slopes, soils are characterized by well developed podzols with acidic humus layers (Walder 1983). South-facing slopes are weakly podzolized, but are characterized by rich humus layers (Walder 1983). On both sides of the valley, ridges and gullies differ in soil characteristics (Blaser 1980); ridges are highly exposed to wind, and exhibit shallow, dry soils whereas gullies are generally dominated by deeper soils. Due to steep slopes (30° to 50°), landslides and avalanches are common (Walder 1983).

2.3 Wind and snow

Patterns of wind and snow are also topography dependent (Wildi et al. 1986). Snow deposition from wind and avalanche regimes and are known factors in the distribution and growth form of trees. Deep snow packs lead to late snow melt and shorter growing seasons, but provide higher water availability during dry summer months (Hättenschwiler and Smith 1999) and may serve an important function against wind abrasion, especially for small trees and low stature vegetation (Wipf et al. 2009). Areas with deep snow have increased risk for mechanical breakage of living tissue, and are more vulnerable to snow fungi attacks (Barbeito et al. 2012).

2.4 Land-use history

In Switzerland, visual interpretations of aerial photography have been used since 1979 to classify land-use in Swiss inventories (Hotz & Weibel 2005). Standardized methodology -- interpreting land-use on a permanent grid of 100 x 100 m points, superimposed on photographs taken from 1979-1985 and 1992-1997 -- enables reliable comparisons over time (Brassel and Braendli, 1999). Land-use statistics, however, often can be traced back much further. In Switzerland, land-use statistics exist from 1912 (Hotz & Weibel 2005), and in some areas mapping and inventories date back much further. These old datasets and maps provide valuable information on land-use history despite being excluded from inventory assessments due to irregular survey intervals and a lack of standardized methodology and definitions (Hotz & Weibel 2005). Multi-temporal analysis of historical maps when combined with aerial photographs, satellite images, and GIS tools can be a strong method to reconstruct forest distribution (Corona et al. 2007; Tattoni et al. 2010; Garbarino et al. 2013) and land-use changes.

A great deal is known about land-use history in the study area. In the Dischma Valley, detailed land-use maps exist from 1900, and indicate the location and intensity of agricultural practices over time. In the past century, livestock grazing and fodder production has declined, and afforestation has occurred on farming land. Similar land-use changes have been recorded elsewhere in the Alps (Didier 2001; Walther et al. 2005; Garbarino et al. 2013), however, the relationship between anthropogenic disturbance and vegetation structure is complex and still poorly understood (Tasser et al. 2007). Due to limited accessibility, some of the Dischma valley remained forested and relatively free from anthropogenic pressure (Laely, 1952). Here there likely exists an aspect difference since in Switzerland many north facing slopes remained densely forested, while on south facing slopes, conversion of forest to pasture around Alps occurred (Ott 1978; Paulsen & Körner 2001). In the Dischma Valley there exists a long history grazing and forest clearing, including the use of fire. In the 13th century, fire was extensively

grazing was only brought to a stop in 1876 with the implementation of forestry regulations in Davos (Pfister, 1978), which also introduced substantial reforestation efforts (Hefti, 1986).

3. Methods

3.1 Summary

This study aims to examine change of the Dischma Valley treeline ecotone, and determine whether abiotic site conditions, land-use or climate are the main drivers of treeline advance. This question of how trees have colonized above the 1972/73 treeline is largely a question of scale, since climate exerts an influence on treeline position at a landscape level, and site variables enable (or restrict) establishment and persistence of trees at a local scale. The following methods first examine the patterns of treeline advance using field surveys conducted in 1972/73 and 2012. An analysis of the repeated surveys is designed to determine if treeline advance has occurred throughout the entire Dischma valley, or whether site-specific variables play a role in determining location of advance. This then provides the basis for selecting sites for a dendroecological analysis, which will examine climate influence on the temporal pattern of treeline advance. By investigating the underlying processes driving treeline shift at multiple scales (local variables and climatic variation) interactions between drivers of treeline advance can also be better understood.

3.2 Preparation and analysis of existing data

3.2.1 1972/73 and 2012 Surveys

Field surveys in 1972/73 and 2012 followed exhaustive recording of the three conifer species in the Dischma Valley present at treeline: European larch (*Larix decidua* L.), Norway spruce (*Picea abies*), and Cembran pine (*Pinus cembra* L.). In both surveys, trees >0.5m height were recorded for species and group size. A thorough description of field methods and admission criteria have been described by Leibold (2012) and therefore will not be discussed in detail here, however, it is important to note that in 1972/73 geographic positions were originally recorded by mapping (digitized in 2012), whereas the 2012 survey positioned all points with a GPS device. For subsequent raster analysis determining where new trees established between 1972/73 and 2012 (see section 3.3.1), a 50m-grid environment was applied; this accounts for the spatial uncertainty of the trees surveyed in 1972/73, and allows for consistent spatial analysis between the existing MAB dataset (see below) and field surveys.

3.2.2 Man and Biosphere (MAB) Data

For analysis in this study, site variables were obtained from the UNESCO Man and the Biosphere Programme (MAB) Project 6 (1973–1987). In Davos, an extensive set of variables were sampled to investigate the relationship between the primary human uses (tourism, agriculture and forestry) and the environment (Wildi & Ewald 1986). To generate this dataset, aerial photographs and ground sampling techniques were combined, and results were digitized on 50m-point grid. Most variables were derived by percent cover algorithms, although methods varied (Binz et al. 1986). A complete list of selected variables, MAB methods, and reclassifications performed in this study are listed in Table 1.

3.2.3 Remote Sensing Data

To supplement the 1980s data from the MAB project, more recent remote sensing data were obtained to improve the accuracy of relief and snow cover variables. A digital elevation model (DEM) with a spatial resolution of 25×25 m from the Swiss Federal Office of Topography (SwissTopo) was used for calculating elevation, slope, and exposure. Since exposure is variable on both sides of the valley, this calculation of site exposure was used to investigate whether larger scale aspect differences (north vs. south sides of the valley) or finer scale differences in exposure (impacting local temperature and moisture conditions), exerted a greater control on tree establishment.

Additionally, high resolution Light Detection and Ranging (LIDAR) was used for detailed topography measures. LIDAR is an airborne mapping technique, which uses a laser to measure the distance between the aircraft and the ground. Up to 100,000 measurements per second are made of the ground, allowing highly detailed terrain models to be generated at high spatial resolution. Accurate elevation data is available for the Dischma Valley at a 2m resolution, and is supplied as a 2010 Digital Surface Model (DSM) produced from the signal returned to the LIDAR (which includes heights of objects, as well as the terrain surface). This DSM was used to calculate curvature for the study area. In addition to providing detailed ground topography measures, summer and winter surface models have been compared to calculate snow depths (Bühler 2013). Since precipitation and topography can only weakly predict snow depths (Tappeiner et al., 2001), especially where wind redistributes snow (Wildi et al. 1986), this LIDAR-generated dataset can be used to investigate the effect of snow cover on tree establishment.

3.3 Spatial and Statistical Analysis

3.3.1 Derivation of Trees Established 1972/73 - 2012

To calculate the position of the treeline at the two time periods (1972/73 and 2012) and

By intersecting these two raster layers with a raster calculator, a new layer was created, identifying where trees had established between 1972/73 - 2012. Points from the 2012 survey intersecting this layer were further analysed to examine the processes driving tree infilling (densification below the treeline) and true advance.

3.3.2 Determining Treeline Advance and Infilling

Analysis of factors behind tree presence and absence give insight into the topographical and vegetation factors determining position of trees at treeline (Leibold 2012). These factors, however, do not give any information on the dynamics of the change; specifically, where densification of trees has occurred below the existing treeline, or where individual trees and tree groups have experienced greatest elevational advances. To identify the different dynamics between treeline infilling and advance and to quantify changes in treeline altitude in the last 40 years, a moving window algorithm was developed to classify whether trees established between 1972/73 and 2012 represented an upward advance of trees or an infilling below existing trees.

3.3.3 Zonal functions and moving windows

Moving windows and neighbourhood analysis are common boundary detection methods in ecological applications (Fortin & Dale 2005; Wallentin et al. 2008), and have been applied to treelines at the landscape scale to distinguish between advance and infilling (Gehrig-Fasel et al. 2007). To characterize whether trees established between 1972/73 and 2012 represented a treeline advance or an infilling, comparisons were made between the elevation of trees at the two survey periods using neighbourhood analysis in a GIS. Neighbourhood analysis computes cell statistics based on a predefined group of grid cells, which is moved throughout the study area as a “moving window” (Figure 2).

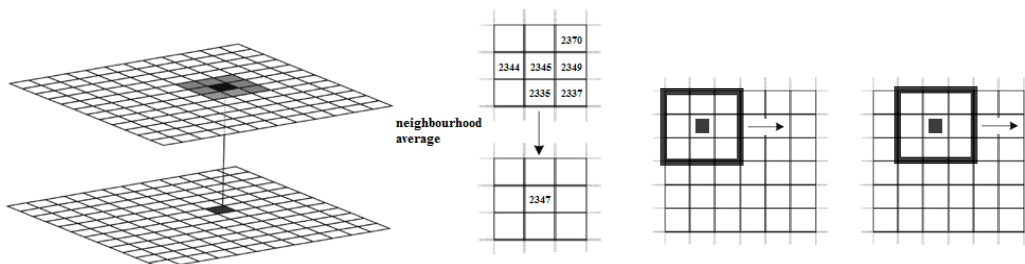


Figure 2: Model for neighbourhood statistics on focal cells based on a moving window algorithm.

The average elevation of neighbourhood cells was calculated for all cells with a neighbourhood of 3 x 3 cells, thus returning neighbourhood statistics for 150m x 150m groups. The neighbourhood average was computed on average elevation for each pixel. Cells where no trees

neighbourhood analysis. A new raster layer was created with values of neighbourhood averages, and these values were then compared with the 2012 layer. Pixels in the 2012 layer were identified as (a) infilling where 1972/73 neighbourhood averages were greater than the 2012 cell average and (b) advance if neighbourhood averages were lower than the 2012 cell (Figure 3).

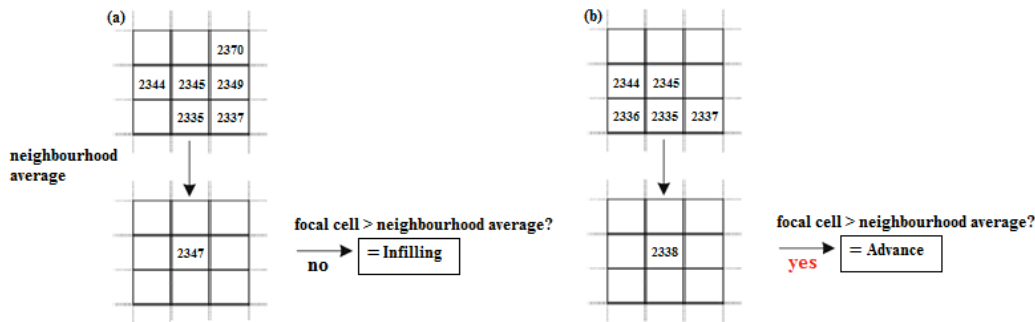


Figure 3: Decision criteria model of infilling and advance. Cells where new trees were recorded in the 2012 survey were classified as tree infilling or advance by comparing the average elevation of the 50m x 50m cell with the average elevation of a 150m x 150m window.

A 150m x 150m window was chosen, as the aim was to capture local establishment patterns at upper elevations. The analysis was run with windows at varying sizes (30, 90, 120, 150, 250, 350m; windows <150m were computed with a 10m raster), and a 150m window resolution 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 >250m, neighbourhood averages often included effects from multiple gullies, thus potentially over estimating treeline advance, especially on the west-side of ridges. (Treeline elevation is ca. 100m lower at the east end of the study area due to the effect of cold air funnelling from the Dischma Glacier). Windows <120m restricted classification cells were unclassified due to the dispersed nature of trees at treeline, and neighbourhoods, enough trees were captured in each window averages. In cases where all neighbourhood cells were classified as “NO DATA” (no trees were recorded in 1972/73 within the moving window), a second classification criterion was used. Unclassified cells were classified as advances where elevation exceeded the elevation of nearby cells classified as advance under the moving window. These cases represent cells with trees experiencing the furthest advances from trees in 1972/73. All other unclassified cells were classified as infilling.

3.3.4 Identifying Downward shifts

To assess where treeline had experienced downward shifts (where 1972/73 position altitude

was applied to the 1972/73 layer. Cells were classified as a downward shift if neighbourhood averages of pixels where trees were identified in 2012 were less than the 1972/73 cell average.

3.3.5 Distances of advance

Minimum distances between points classified as advance and nearest 1972/73 raster cells were computed using the feature-based proximity analysis in ArcGIS to examine distance of advance. 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 1972/73 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 point at the 1972/73 polygon.

Distances of advance were then analyzed for distribution of normality using a Shapiro and Wilk test. In cases of significant derivations from normality, data was tested using a non-parametric Mann-Whitney ranked sum test (U-test) for aspect comparison. All differences were considered significant when the p value was below 0.05. All calculations were conducted with the R software, version 3.0.1. Distances of advance were additionally used for the pre-selection of sites for the dendroecological analysis (see section 3.4).

3.3.6 Factors behind tree advance

While identifying the underlying drivers of this shift is challenging, several environmental conditions are likely driving the spatial and temporal patterns of treeline advance. Examining distances of advance helps explain why some trees have advanced long distances from the 1972/73 treeline, however, cannot investigate the constraining factors of where trees have experienced no advances. Thus, to assess the underlying factors of treeline advance, a comparison of tree presence and absence is necessary. To assess the underlying factors of treeline advance, a comparison of tree presence and absence was conducted using classification trees.

Presence and absence was used as a categorical response variable in a classification tree to evaluate the determinants of tree establishment above the 1972/73 upper limit. A set of biotic and abiotic factors were used in this analysis. Variables included are listed in Table 1. These variables were analyzed in a nonparametric regression approach using decision trees (Breiman et al. 1984). All variables with a p value was below 0.05 were included in the decision tree. This approach differs in some key ways from other modelling techniques. Linear regression models, for example, combine information from all predictor variables together. Regression trees, on the other hand, allow for variables to have interactions at different levels and are non-parametric. Since the association rules do not need to be determined in advance, associations between

in stepwise linear regression the relationship between the predictor variables and the dependent variable is still linear, and higher interactions are limited (generally restricted to two-fold interactions).

Table 1: Independent variables used to analyze advance distances of trees established (1972/73 - 2012)

Variable	Unit	Source	Calculations and conversions
Climate-related variables			
Direct solar radiation	W/m ² /3000	MAB	STRAHL_4
Snowfree days	days	MAB	AP82DAYA - AP82DAYS
Snowdepth	m	DSM (2m)	-
Topographic variables			
Elevation	m asl	DSM (2m)	Calculated from DSM
Slope	degrees	DSM (2m)	Calculated from DSM
Curvature	< 0 for concave depressions, > 0 for convex ridges and hilltops	DSM (2m)	Calculated from DSM
Aspect	azimuth	DEM (25m)	Calculated from DEM
Disturbance variables			
1900 Land-use	Numeric factor with levels: "Heavy cut", "Cut", "Grazed", "No use"	MAB	NUTZUNG_5, converted to factor
1982 Land-use	Numeric factor with levels: "Grazed", "Abandoned", "No use"	MAB	NUTZNEU_1, converted to factor
Land-use change	Numeric factor with levels: "Grazing", "Abandoned grazing", "Grazing (with previous cutting)", "No use"	MAB	Calculated factor from NUTZNEU_1 and NUTZUNG_5
Avalanche risk	Factor: "No risk", "Potential risk", "High risk"	MAB	GEFAR_5, converted to factor
Biotic variables			
Vegetation	Factor with levels: "Rubble and no vegetation", "Alpine grasslands on acid silicate", "Dwarf shrubs"	MAB	VEGET50_3, converted to factor

In this analysis, presence was defined as where trees have established (and survived) between 1972/73 - 2012, and absence was determined by randomly selecting the same number of points as points classified as advance with the moving window. Points were selected from a GIS polygon where the lower and upper limits were defined by the 1972/73 treeline and the tree with the highest recorded altitude in 2012, respectively. This was done separately for the two valley aspects to control for the greater advance exhibited on the south-facing slope.

3.4 Dendroecology

3.4.1 Field sampling

Using information from the moving window analysis, sites were selected where treeline advance has occurred in the last 40 years. The study area was stratified by tree colonization distance, and aspect, and then 2 sites were selected randomly on the south-facing slope. This stratified random sampling is a common sampling design in dendrochronology research in ecotones to investigate tree responses to site factors such as aspect (Danby & Hik 2007), and soil type (Vittoz et al. 2008), and improves the statistical power of results. In selecting sites, slopes with frequent avalanche disturbance were excluded since these communities are largely controlled by the disturbance regime, and maintain a narrow range of species (light tolerant), structures (early successional stages), and processes (frequent mortality and reestablishment) (Bebi et al. 2001; Kulakowski et al. 2006).

At each site, we randomly located a 60 m wide × 330 m long (1.98 ha) transect extending downslope from the highest tree (>50cm height). Sampling points were situated along each of the 2 transects at 30m intervals. The transects were established to include the upper tree species line and trees that were mapped in 1972/73 (Walder 1983). The sampling points along each transect were marked by running a measuring tape down slope from the pre-selected upper point. Points were flagged, and marked with a GPS to record position and elevation. Thus, at each point (a maximum of) 6 trees were sampled from each sampling point: 3 tree cores and 3 basal sections. To avoid double counting of trees, all samples were collected at the same slope or upslope from the sampling points, and within a 30m radius. The distance and compass direction of each tree to the sampling point was recorded.



Figure 4: Increment borer for age estimation of pine

Trees with a diameter > 5cm were cored to pith, taken from a down slope position, parallel to the slope (Figure 4). 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, coring heights were recorded.¹ Since mineral soil level is not a strong indicator of root collar level (Gutsell & Johnson 2002), especially at treeline (Batllori and Gutiérrez 2008), cores were obtained by excavating a 'coring hole' at the tree base and/or angling the increment borer to approach the root collar as much as possible (Villalba & Veblen 1997a). For trees less than ca. 5cm, a 10cm long basal section was cut at the root collar. Diameter at root collar was recorded for all samples. Where samples were collected from higher positions on the stem, diameter at coring height was also taken.

3.4.1 Tree age determination

Samples dried and finely sanded for age determination, according to standard methods (Stokes & Smiley 1968; Cook et al. 1990). Annual rings were counted with a resolution up to 0.01mm. The estimated age reported for all trees is the age taken as close to the root collar. Since we did not cross date the cores due to the young age of most trees, potential errors in estimating missing rings, age structure is best interpreted in age classes. This technique has been performed in other dendroecological studies to reconstruct tree colonization patterns (Payette et al. 1990; Hattenschwiler & Smith 1999). Samples with rotten cores were excluded from the analysis.

3.4.2 Reconstruction of treeline advance

Upon determining tree ages, individuals were superimposed with GPS coordinates into ArcGIS to verify whether sampled trees were in areas classified as advance under the moving window or were below the 1972/73 treeline. The maximum treeline advance was calculated for these predetermined time periods.

4. Results

The following results present characteristics of change in the alpine treeline from a GIS analysis, field work, and a dendrochronological study. First, the spatial results of treeline advance are presented; results from the moving window analysis present the patterns of tree infilling and advance and the factors influencing the magnitude of treeline advance are examined. The second

¹ This will be used in future analysis for age correction by building three reference chronologies (one for each species) and performing age-height regression analysis (Stokes & Smiley 1968). Further age correction will be performed for incomplete samples where samples were not cored to the pith: age-diameter regression combined with the fitting of a circle template to the ring curvature can estimate the distance of the core to the centre. For each chronology, standard descriptive statistics -- percentage of missing rings, mean sensitivity, and the common variance among trees in each chronology -- will be calculated (Fritts 1976, Briffa

section focuses on the timing of treeline advance within the alpine treeline; results from field collection data present the temporal variability of individual tree establishment.

4.1 Spatial Results

4.1.1 Derivation of Trees Established 1972/73 - 2012

Of all tree individuals and groups recorded in 2012, 765 out of 970 points were classified as trees established between the two field survey periods (1972/73 - 2012). The remaining 205 points -- points intersecting raster cells where trees were present in 1972/73 -- were excluded from the analysis since these trees represented neither an infilling nor advance. To verify that that this exclusion did not systematically bias the results, a distribution of the points was performed (Appendix 2). Similar patterns for species and aspect were observed between the excluded points and as trees classified as infilling under the moving window (Figure 3). The 765 points representing trees established between 1972/73 - 2012 were further analysed as infilling or advance.

4.1.2 Downward shifts

Downward shifts were identified for 18 points. 14 of these points showed a strong clustering effect, and were located in avalanche hazard areas.

4.1.3 Treeline Advance and Infilling

The valley-wide moving window analysis of trees from the two field surveys showed that both aspects of the Dischma Valley have experienced infilling and advance between 1972/73 and 2012 (Figure 5). When analysing all new tree individuals and groups, 21% (164 points) were found to have advanced above the 1972/73 treeline and 79% (601 points) were classified as an infilling. When restricting analysis to points above 2250m (see Gehrig-Fasel et al. 2007), 34% (119 points) advanced compared to 64% (232 points) that were an infilling. A distribution of trees classified as infilling and advance by elevation classes can be found in Appendix 3. Results showed that for both aspects, larch and pine exhibited advance and spruce mostly represented an infilling below the 1972/73 treeline (Figure 5). Species differences were observed between aspects; on the north aspect, most trees classified as advance were pine (27% of all points), whereas on the south aspect, larch was the dominant advancing species (42% of all points). 65% of trees classified as advance were between 2250 - 2400 m, corresponding to 150 - 300 m above the potential regional treeline, defined for the region at 2100m (Paulsen & Korner 2001) (Figure 6). Only 6% of characterized as advance were below this level.

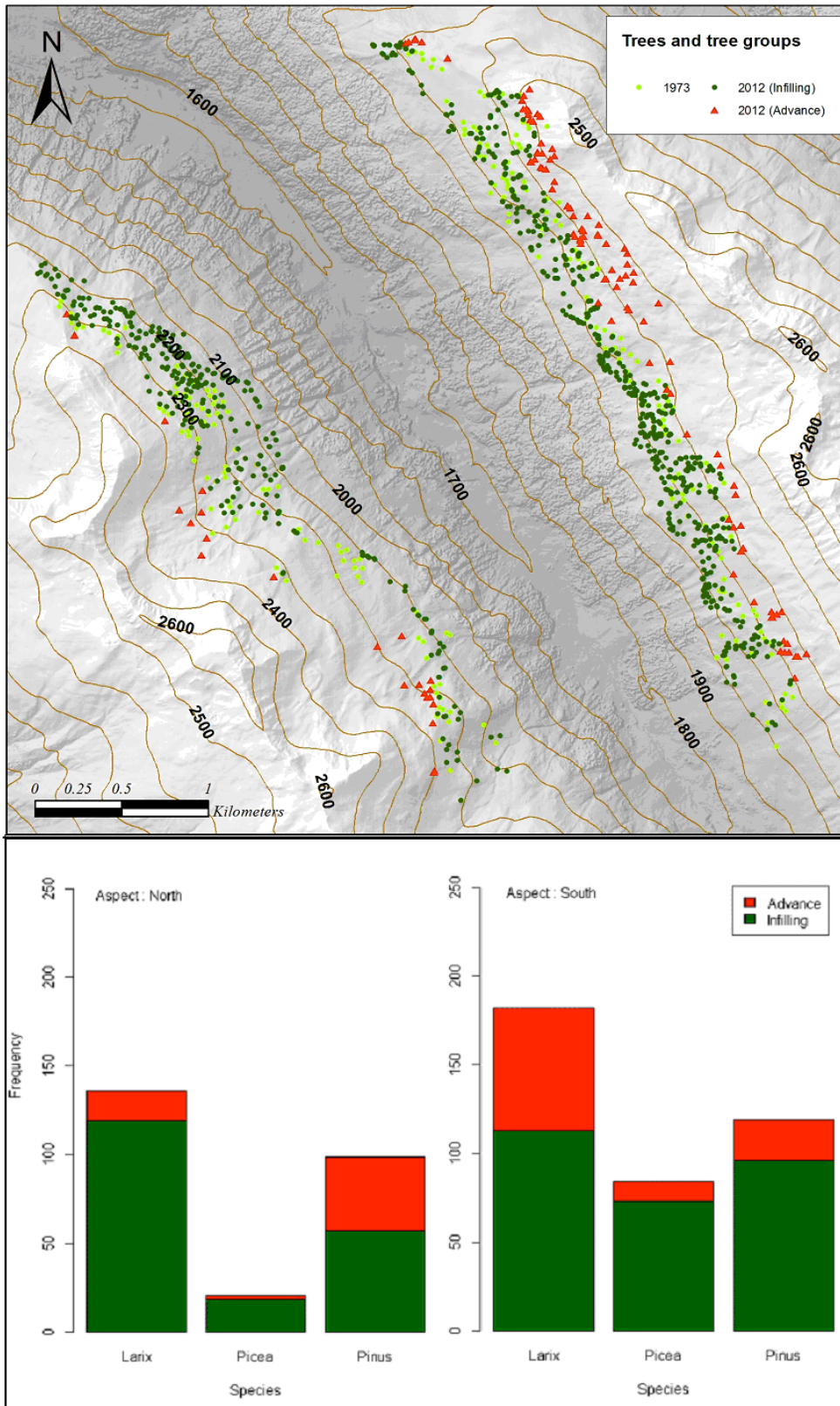


Figure 5: Results of the moving window analysis. Red triangles represent individual trees classified as advance, and dark green circles are trees classified as infilling. Classification was determined at a 50m pixel resolution using a neighbourhood elevation analysis comparing position of trees and tree groups in 2012 to 1973 (73 (light green circles) to 2012 (dark green circles) for infilling and red triangles for advance).

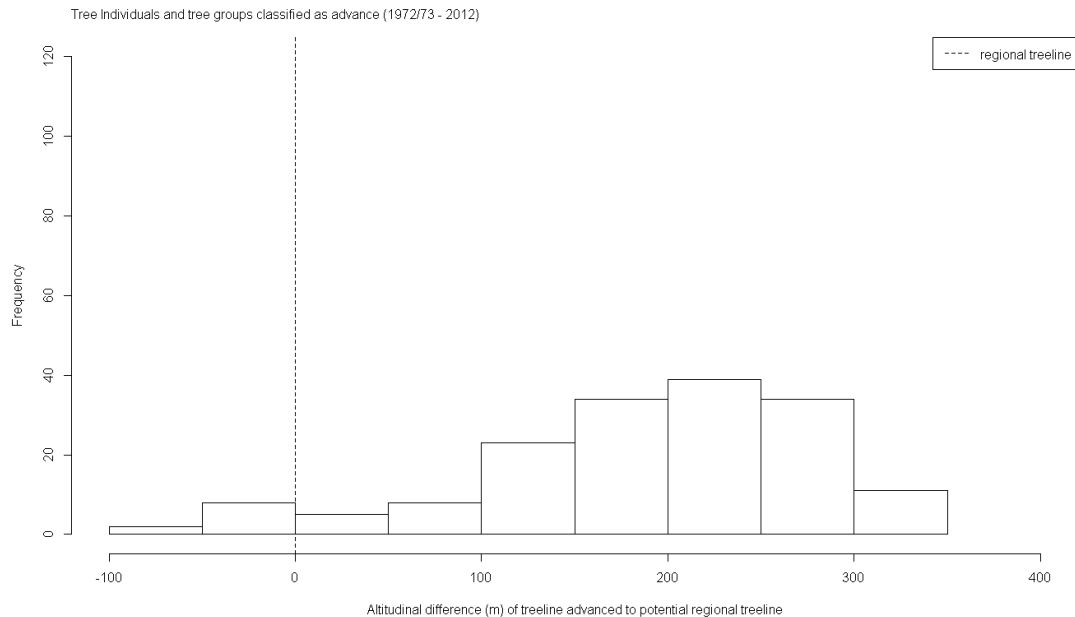


Figure 6: Frequency of tree individuals and tree groups classified as a treeline advance per altitude band. The 0 line is in reference to the potential regional treeline (2100m asl) defined by Paulsen and Körner (2001).

4.1.4 Distances of advance

The GIS analysis quantified the altitude increase for points classified as advance. Most trees advanced between 1 and 75 m between 1972/73 and 2012 (Figure 7). Larch was found to have advanced more on the south facing aspect, and pine more in the north. Distance of spruce advance appears greater on the north facing slope, although a small sample size limits a reliable aspect comparison. The maximum distance of advance was on the south aspect (167 m, compared to 122m on the north aspect). Although no statistically significant differences were found between north and south aspects, differences in the mean advance by aspect could be detected when the valley was sub sampled into segments: examining the western-most 4km of the valley, it was found that trees advanced an average of 24m (north aspect) and 46 m (south aspect), see Appendix 4. This was found to be significantly different ($p = 0.014$).

Small moving windows may lead to an over-localization of results (Gehrig-Fasel et al. 2007), and in this analysis an over-localization could have the potential to (erroneously) identify advances below treeline since tree density is low above 2250m. A low proportion of trees recorded as advance at low elevations (Figure 6) and normal distribution of trees classified as infilling (Appendix 3) helps confirm the functioning of the moving window algorithm.

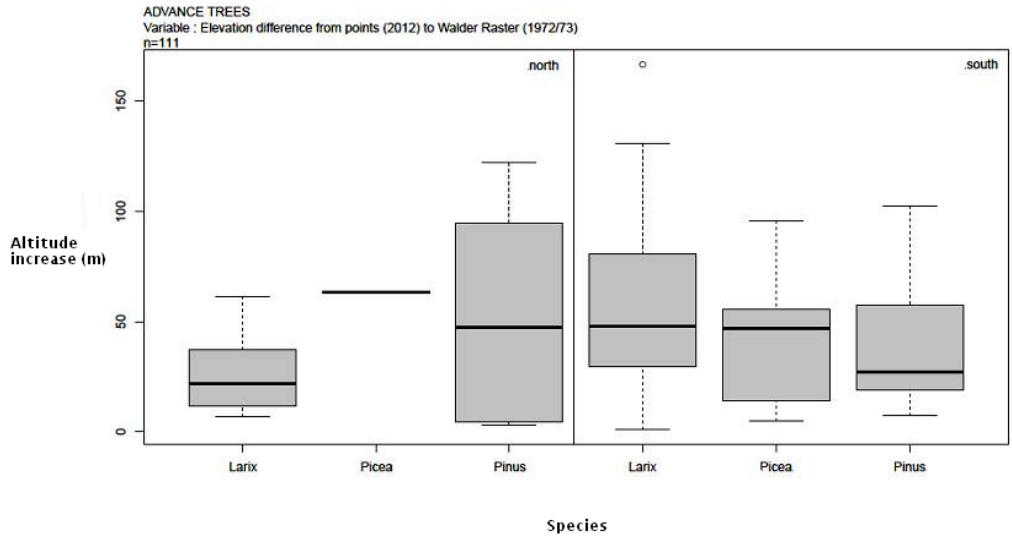


Figure 7: Distance of treeline advance (1972/73 - 2012) between north and south-facing aspects (left and right panels, respectively) separated by the three study species. Distances were computed with elevation difference between trees classified as tree advance (2012) and nearest raster cell (1972/73) of trees recorded in the first field survey. n = 164; 61 north, 103 south. No confidence intervals have been plotted for Picea advance on the north facing slope due to the extremely small sample size (n=1).

4.1.4 Factors of tree presence / absence above 1972/73 treeline

Of the 13 variables considered in the decision tree, only five site variables were found to be significant. At altitudes < 2330m asl, land-use in 1900 was a significant factor. At high altitudes (>2330m asl), vegetation cover was significantly linked with radiation (for dwarf shrubs) and curvature (for alpine grasslands or no vegetation cover).

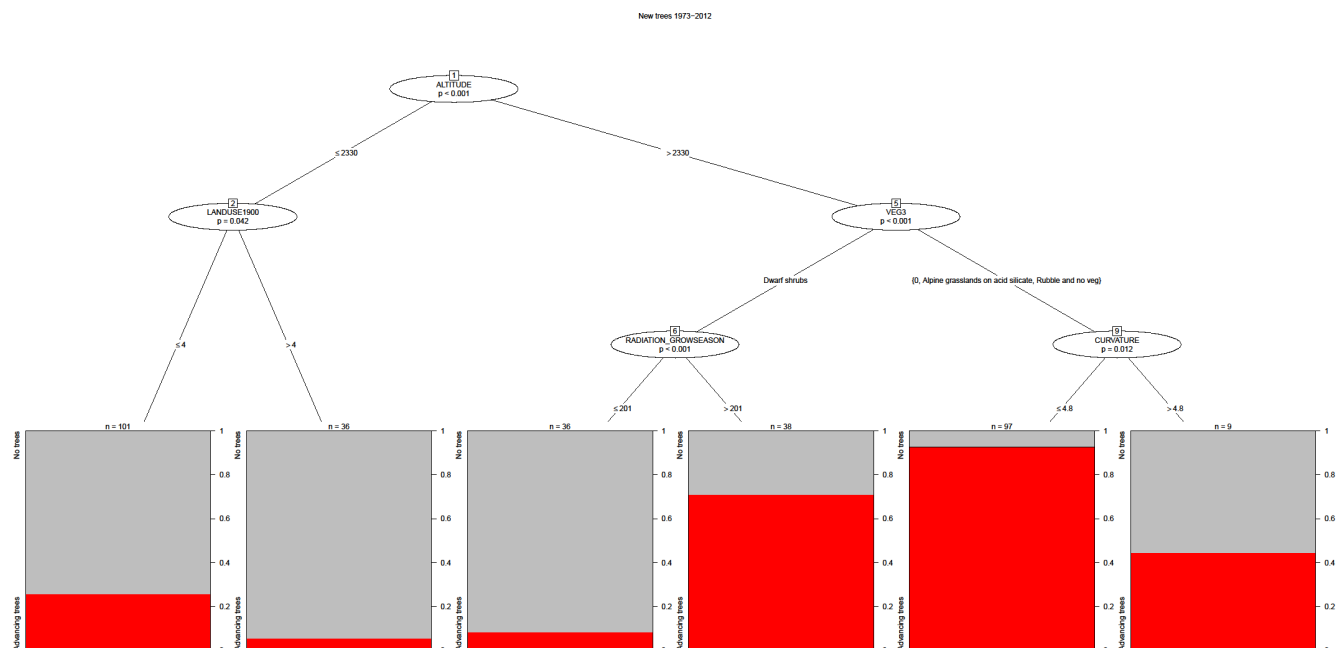


Figure 8: Results from analysis of 164 points classified as advance (1972/73 - 2012), and 164 random points.

4.2 Temporal Results

Ages were estimated for 96% of trees sampled. In 33% of cores the pith was absent. The age structure varied between trees above (advance) and below the 1972/73 treeline (left graph, Figure 9). For plot sections classified as advance under the moving window algorithm, all trees were < 45 years (median = 30, 5th percentile = 7; 95th percentile = 40). The plot sections below the 1972/73 treeline, trees exhibited a higher range in ages: the most frequent age classes were from 20 to 45 years (median = 31, 5th percentile = 12; 95th percentile = 65), and oldest tree was a 77 year old pine. Temporal patterns of establishment (e.g. episodic patterns of establishment) could not yet be accurately assessed due to a small sample size (n = 70; ongoing field measurements) and coarse age estimation.

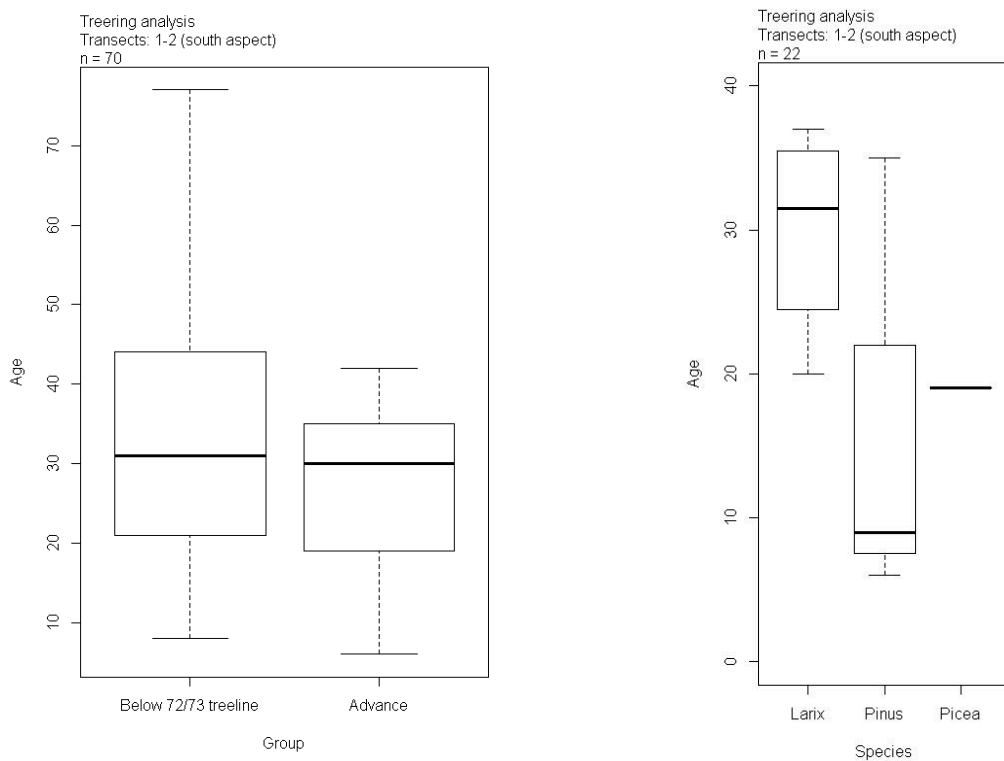


Figure 9: The left graph shows a greater age range of trees sampled below the 1972/73 treeline than above (Advance). Species differences of trees above the 1972/73 treeline are presented in the right graph. Note the different y-axis scale.

Species trends were observed for trees that had advanced above the 1972/73 treeline (right graph, Figure 9). Larch exhibited a much narrower age range compared to pine. The mean age of larch ($\bar{x} = 31$) was also found to be considerably higher than pine ($\bar{x} = 9$).

5. Discussion

This analysis indicates that over forty years, treeline position has advanced in the Dischma Valley. Changes are spatially heterogeneous throughout the study area, although trees were recorded at higher altitudes on both north and south aspects, and the treeline showed no evidence of a substantial downward shift. Only in localized instances was treeline found to be higher in 1972/73 compared to 2012, which is consistent with mortality in areas with natural disturbance. Conversely, if treeline had not advanced (remained stable or retreated), one would expect a greater number of instances where treeline was higher in 1972/73 from the moving-window analysis. Thus, these results confirm the observed trend of recent treeline advance in Switzerland (Hotz & Weibel 2005; Gehrig-Fasel et al. 2007; Vittoz et al. 2008) as well as the Scandes (Kullman 2007), South America (Daniels and Veblen 2004) and North America (Danby & Hick 2007).

5.1.1 Infilling below the 1972/73 treeline

A large proportion of trees established between 1972/73 and 2012 were found to have resulted from infilling below the treeline. While many recent studies have focused on upward advance above tree limits, considerable changes have also been observed below treeline (Jakubos et al. 1993; Klasner & Farge 2002; Batllori et al. 2010). High-elevation trees below treeline are responding to rising temperatures by increased growth rates (Paulsen et al. 2000; Kessler et al. 2007), and shifts in optimal range (Lenoir 2008).

Our results support the hypothesis that spruce dynamics can mainly be characterized by an infilling. Few spruce individuals in this study were identified as an advance beyond the 1972/73 tree limit, and the relatively high degree of infilling suggests that spruce establishes favourably in the lower treeline. Spruce exhibits a high sensitivity to frost compared to pine and larch, (Schönberger 1975; Larcher 2003), which could explain why spruce establishment was largely limited to infilling, where temperatures are warmer. Spruce establishment is also dependant on moisture. Evidence from white spruce (*Picea glauca*) in North America suggests that spruce establishment may have a significant aspect effect, and this may differ according to limiting factors. Danby & Hik (2007) found that spruce experienced greater changes on south facing slopes where temperature was the major limiting factor in the Yukon, Canada. Conversely, where moisture is limiting, evidence from southcentral Alaska, USA found more spruce establishment on cooler and relatively more humid north-facing aspects (Dial et al. 2007). Walder (1983) and Leibold (2012) observed higher proportions of spruce on south-facing slopes in the Dischma Valley, and a lack of spruce on low radiation exposures. These results suggest that spruce advance is constrained by temperature (not moisture) due to low elevation establishment and greater establishment on the south facing aspect.

Aspect differences could also be observed for larch and pine. Larch advanced more on the south facing aspect, whereas pine has responded more on north faces compared to the south. The magnitude of advance also differed between slopes. Distance of advance is especially striking for larch, where advance on south-facing aspect reached 167 m, whereas this was only 63m on the north facing slope. The dominant advancement larch on the south facing slope could be explained by the requirement of larch for high light levels and warm temperatures. Larch is unable regenerate in shaded conditions that are ideal for the emergence and survival of pine seedlings and saplings (Motta & Lingua, 2005). Landform has also found to be significant in the spatial recolonization patterns of pine and larch (Didier 2001). The topographic variability on the north facing slope with numerous ridges favourable for pine establishment could help explain why pine has advanced more on the north facing slope.

While evidence shows that roughly half of the world's treelines are advancing (Harsch et al. 2009), establishing a suitable metric for quantifying and comparing the magnitude of treeline advance is challenging. Since treelines vary in structure (abrupt and diffuse boundaries, monospecific and multi-species, krummholtz and upright tree form, etc.), to describe shifts over time, the highest altitude of trees has been used, although this cannot account for variability in altitude over a landscape or even an individual valley. Determining distances individuals have advanced from historic treelines acknowledges the spatial heterogeneity of treeline altitude across an ecotone, and quantifies variability of treeline advance. The results from this study show that treeline has mostly advanced up to 75m over the last forty years (Figure 7). This rate is lower than recent treeline advances reported in the Swedish Scandes (up to 150 m over fifty years) (Kullman 2002), although is higher than other reported rates of advance (Daniels and Veblen 2004; Danby & Hick 2007).

The magnitude that treelines have shifted up to 75 m in the last forty years is a surprising result, especially when maximum advances are considered (167 m and 122m on south and the north aspects, respectively). Gehrig-Fasel et al. (2007) compared moving window results to historical fluctuations and noted that recent magnitude of treeline advance is considerably high when considering temperature oscillations in the Holocene were responsible for treeline fluctuations around 100 m (e.g. Burga & Perret 1998; Haas et al. 1998), which has been confirmed by pollen records (Tinner & Theurillat 2003) and treeline models (Heiri et al. 2006). Gehrig-Fasel et al. (2007) attributes high rates of advance estimated in moving window algorithms to be from identifying shifts in neighbourhoods of trees, which does not represent the mean treeline advance, but movement of the 'treeline front.'

5.1.3.1 Microtopography and favourable sites

Our results show that at high elevation, topographic variability produced favourable sites that facilitated opportunistic establishment at high elevations, enabling trees to invade the alpine tundra. The classification tree suggests that processes at high elevation (>2330m asl) differ significantly with vegetation cover: where shrub cover predominates, the effect of radiation is significant, whereas for alpine grasslands and areas with no vegetation cover, the effect of curvature is the decisive factor. While aspect was not a significant factor as originally predicted, results suggest that site variables restricting tree establishment vary topographically at finer spatial scales.

Where shrubs were the dominant vegetation, trees were more likely to be found on areas with high radiation. This is surprising since high solar radiation is found on south facing exposures, where shrub growth is denser, and predicted to have a stronger limiting effect on tree regeneration (Körner 1998). Dense herbaceous or shrub cover can negatively effect establishment by reducing seedbed suitability, and increasing competition for resources (Moir et al. 1999; Batllori et al. 2009, Dufour-Tremblay et al. 2012). Vegetation competition may be a major limiting factor for larch due to high light requirements for germination and difficulty of light seeds to reach the seed bed. Dwarf shrubs, however, 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 north exposed slopes, although facilitative effects of vegetation can be especially important at the emergent and seedling stage, and may additionally have an effect (Germino et al. 2002). This result, since trees have established favourably in sites with high radiation, further suggests that exposure to sunlight does not inhibit establishment through water stress. Trees on north-facing slopes were found to respond more to radiation than trees on south-facing slopes (see Appendix 5).

Where alpine grasslands and no vegetation are the dominant cover, curvature is a significant factor: low curvature values (concave depressions) exhibit a greater number of trees compared to high values (convex ridges). This result suggests that where shrub cover is not limiting, trees establish favourably in concave depressions. Although snow accumulation and cryophilic fungi are assumed to be underlying factors restricting tree establishment in concave depressions (Barbeito et al. 2012), favourable thermal conditions in these depressions may be more influential in tree establishment than the adverse effects of snow and fungi. Microhabitats over short horizontal distances can have significant impacts on tree establishment and growth. Scherrer & Körner (2010) recently showed that microtopography can mimic temperature amplitudes of large elevational gradients over very short horizontal distances. Due to the high

depressions may be more representative of larch microhabitats. Pine mainly grows on ridges with early snowmelt (Ellenberg 1988) where the impact of snow fungi is lower (Barbeito et al. 2012), whereas larch have been shown to establish on wide, convex landforms where colluvial soils are optimal for larch establishment (Holtmeier 1995; Didier 2001).

5.1.3.2 Indirect site effects of land-use

Land-use change has been identified as a major driver for treeline advance (Surber et al. 1973; Gellrich et al. 2007), and this study shows that cultural legacies of alpine grazing may have an effect on treeline advance in the Dischma Valley. At lower altitudes (<2330 m asl), trees were more likely to have established in areas where land-use was practiced in 1900. This suggests that site conditions on areas with previous and current land-use are linked with higher levels of tree establishment. Although land abandonment is not one of the most influential drivers -- moderate grazing pressure in the Dischma Valley, has experienced less grazing declines compared to other areas in the Alps (Surber et al. 1973; Mather & Fairbairn 2000) -- interactions between grazing and reduction of the shrub layer could help explain this result.

Cattle grazing, the only current land-use practice in the Dischma Valley alpine also does not appear to have a significant effect on the spatial pattern of treeline advance. Interactions between tree establishment and grazing are complex; they exhibit considerable contrasting tendencies. Some authors report adverse effects on tree establishment and growth from trampling and consumption of seedlings, reduced growth due to browsing, suppressed reproductive age, and increase mortality (Scott et al. 2000; Zamora et al. 2001; Chauchard et al. 2006; Speed et al. 2010). This is likely true for areas with intense grazing pressure. Conversely, others have found that livestock create favourable habitats for tree establishment and reduce competition for resources by reducing the herbaceous and shrub layers (Scott et al. 1993; Castro et al. 2004). The higher levels of establishment in areas with landuse suggests that trees are responding to favourable site conditions for establishment and growth in areas of previous and current land-use, such as reduced vegetation competition from the shrub layer, suitable seedbeds, and moderate steepness of slopes.

5.2 Temporal patterns of establishment

Treeline advance was observed through the expected pattern of older tree ages at lower elevations, and younger trees at higher elevations (Lloyd & Fastie, 2003). This provides sound validation for the field surveys and results of the moving window algorithm. Previous studies have indicated potential errors in identifying the patterns of tree establishment using remote sensing methods (Gehrig-Fasel et al. 2007): due to slow growth and suppressed stature of

periods and existing trees, since existing trees may increase height class beyond a certain detection threshold and be classified as new trees. By developing a dendrochronological approach in this study, establishment can be investigated with finer precision. It should be noted, however, that age can only roughly estimate age, since ages have not been corrected for absent pith, and coring heights above the root collar. Thus, tree ages may be older than the results presented. While age in this study may be underestimated, results thus far agree with treeline advancement.

Temporal patterns of treeline advance are different between larch and pine; larch exhibited a narrow age range with a higher mean age, whereas pine established more gradually and was younger than the larch. At Stillberg, an afforestation experiment of 92 000 trees in the Dischma Valley showed that high mortality in late snowmelt areas was linked to snow fungi (Senn 1999; Barbeito et al. 2012), which could explain the young age structure of pine. While the relationship with climate is still to be explored, the episodic pattern of larch establishment suggests that larch may have established favourable conditions 25-35 years ago. Alternatively, this result may suggest a favourable expansion in years following land-use decline, prior to shrub encroachment. Pine establishment is more gradual, which may be explained by variable recruitment strategies, which is in line with the original hypotheses.

Seed dispersal and seedling establishment are essential mechanisms for plants to tackle spatial and temporal habitat changes (Cain et al. 2000), and plays an important role in treeline advance (Carrer et al. 2013). Both larch and pine exhibit seed characteristics enabling long-distance seed dispersal (Larcher 2003), which is confirmed in this study with distances of pine and larch advancing up to 122m and 167 m from the 1972/73 treeline. Strategies vary between anemochory (wind dispersal) of larch and zoochory (animal dispersal) of pine: larch seeds are light weight and wind-dispersed, and pine is typically dispersed by the European nutcracker (*Nucifraga caryocatactes*) and small mammals (Contini & Lavarello 1982; Zong et al. 2010). Results of distances larch and pine have advanced show that both species have considerable potential for long-distance dispersal, which are in line with the findings of Vitasse et al. (2012) that seed dispersal distances do not limit the magnitude of recruitment of trees above their current range. Pine is typically found in small patches (Tomback et al. 1993), and is likely limited by seed caches of the nutcracker, but the elevation limits of seed caches exceeds the upper range of pine (Holtmeier & Broll 2005). Temporal patterns, conversely, suggest greater species differences; larch establishment is more episodic, and pine establishment is more gradual. This shows different regeneration strategies of these two species (Motta & Lingua, 2005), and may suggest that establishment of larch has more climate-specific regeneration requirements

6. Conclusion

While natural treelines are difficult to study over long time scales, this study combines field survey results from repeated surveys (1972/73, 2012), GIS spatial analysis and dendrochronological analysis to investigate treeline change in the Dischma Valley.

Results from this study produced three main conclusions:

- i. The Dischma Valley treeline has advanced in the last forty years, and exhibits a high rate of change. Pine and larch have advanced beyond the 1972/73 treeline, although species responses varied between aspects. Larch advance was more numerous, and distances of advance were greater on the south facing slope, advancing up to 167 m. Pine did not advance as far as larch, (up to 122m) and exhibited the greatest differences on the north aspect.
- ii. Treeline advance is best described by local site variables, suggesting microsite effects from local topography are important for the spatial pattern of treeline advance. Land-use was found to have a significant effect on treeline advance, although only at elevations below 2330m asl. Since areas with previous and current land-use exhibit greater treeline advance, evidence suggests that the observed land-use effect is not driven by land abandonment but is instead related to indirect effect of reduced vegetation competition which has favoured past establishment.
- iii. Temporal patterns of tree establishment suggest that larch established a favourable wave of establishment 25 – 35 years ago, although more work is needed to investigate if this relationship is linked with climate

While temporal responses to climate variation are unclear due to coarse age estimation and a small sample size, future work aims to investigate whether climate or topographic site factors and vegetation competition exert a greater control on treeline advance in the Dischma Valley. The results presented here are results of ongoing work. A more thorough dendrochronological sampling, which will include the north-facing aspect and additional transects on the south-facing slope, will search for relationships with climate and give more insight into the influence of climate variability on tree establishment at treeline.

Works Cited

- Austrheim, G., Gunilla, E., Olsson, A., & Grontvedt, E. (1998). Land-use impact on plant communities in semi-natural subalpine grasslands of Budalen, central Norway. *Biological Conservation*, *87*, 369–379.
- Barbeito, I., Dawes, M. a, Rixen, C., Senn, J., & Bebi, P. (2012). Factors driving mortality and growth at treeline: a 30-year experiment of 92 000 conifers. *Ecology*, *93*, 389–401.
- Batllori, E., Camarero, J. J., & Gutie, E. (2010). Current regeneration patterns at the tree line in the Pyrenees indicate similar recruitment processes irrespective of the past disturbance regime, *Journal of Biogeography*, *37*, 1938–1950.
- Binz, H. ., Seidl, K., & Wildi, O. (1986). *Methoden und Organisation des Projektes*. (O. Wildi & K. Ewald, Eds.) *Der Naturraum und dessen Nutzung im alpinen Tourismusort von Davos* (Berichtt 2., pp. 31–43). Birmensdorf: Anstalt für das forstliche Versuchswesen.
- Breiman, L. (2001). Random forests. *Machine Learning*, (45), 5–32.
- Breiman, L., Friedman, J. ., & Olshen, R. . (1984). *Classification and Regression Trees*. New York: Chapman & Hall.
- Briffa, K., & Jones, D. (1990). Basic chronology statistics and assessment. Pages in E. , editors. In R. Cook & L. Kairuikstis (Eds.), *Methods of dendrochronology* (pp. 137–153). Amsterdam: Kluwer Academic Publishers.
- Burga, C. ., & Perret, R. (1998). *Vegetation und Klima der Schweiz seit dem jüngerem Eiszeitalter*. Thun: Ott Verlag.
- Burkett, V. ., Wilcox, D. ., Stottlemeyer, R., Barrow, W., Fagre, D., & Baron, J. (2005). Nonlinear dynamics in eco- system response to climatic change: case studies and policy implications. *Ecological Complexity*, *2*, 357–394.
- Callaghan, T. V, Werkman, B. R., & Crawford, R. M. M. (2002). The tundra–taiga interface and its dynamics: Concepts and applications. *Ambio Special Report*, *12*, 6–14.
- Carrer, M., Soraruf, L., & Lingua, E. (2013). Convergent space–time tree regeneration patterns along an elevation gradient at high altitude in the Alps. *Forest Ecology and Management*, *304*, 1–9.
- Castro, J., Zamora, R., Hódar, J., & Gómez, J. (2004). Seedling establishment of a boreal tree species (*Pinus sylvestris*) at its southernmost distribution limit: consequences of being in a marginal Mediterranean habitat. *Journal of Ecology*, *92*, 266– 277.
- Contini, L., & Lavarelo, Y. (1982). *Le Pin Cembro (Pinus cembra L.)*. *Végétation, Écologie, Sylviculture et Production*. Paris.
- Corona, P., Fattorini, L., Chirici, G., Valentini, R., & Marchetti, M. (2007). Estimating forest area at the year 1990 by two-phase sampling on historical remotely sensed imagery in Italy. *Journal of Forest Research*, *12*, 8–13.

- Danby, R. K., & Hik, D. S. (2007). Variability, contingency and rapid change in recent subarctic alpine tree line dynamics. *Journal of Ecology*, 95, 352–363.
- Daniels, L. D., & Veblen, T. T. (2004). Spatiotemporal influences of climate on altitudinal treeline in northern Patagonia. *Ecology*, 85, 1284–1296.
- Debussche, M., Lepart, J., & Dervieux, A. (1999). Mediterranean landscape changes: evidence from old postcards. *Global Ecology and Biogeography*, 8, 3–15.
- Dial, R. ., Berg, E. ., Timm, K., McMahon, A., & Gecke, J. (2007). Changes in the alpine forest-tundra ecotone commensurate with recent warming in southcentral Alaska: Evidence from orthophotos and field plots. *Geophysical Research Letters*, 112.
- Didier, L. (2001). Invasion patterns of European larch and Swiss stone pine in subalpine pastures in the French Alps, *Forest Ecology and Management* 145, 67-77.
- Dufour-Tremblay, G., Lévesque, E., & Boudreau, S. (2012). Dynamics at the treeline: differential responses of *Picea mariana* and *Larix laricina* to climate change in eastern subarctic Québec. *Environmental Research Letters*, 7(4), 044038.
- Ellenberg, H. (1988). *Vegetation Ecology of Central Europe* (4th ed., pp. 731). Cambridge: Cambridge University Press.
- Foley, J. ., Kutzbach, J. ., Coe, M. ., & Levis, S. (1994). Feedbacks between climate and boreal forests during the Holocene. *Nature*, 371, 52–54.
- Fortin, M.-J., & Dale, M. (2005). *Spatial Analysis: A Guide for Ecologists*. Cambridge: Cambridge University Press.
- Fritts, H. . (1976). *Tree rings and climate* (p. 576). New York: Academic Press.
- Garbarino, M., Lingua, E., Weisberg, P. J., Bottero, A., Meloni, F., & Motta, R. (2013). Land-use history and topographic gradients as driving factors of subalpine *Larix decidua* forests. *Landscape Ecology*, 28, 805–817.
- Gehrig-Fasel, J., Guisan, A., & Zimmermann, N. E. (2007). Tree line shifts in the Swiss Alps: Climate change or land abandonment? *Journal of Vegetation Science*, 18, 571–582.
- Germino, M. J., Smith, W. K., & Resor, A. C. (2002). Conifer seedling distribution and survival in an alpine-treeline ecotone. *Plant Ecology*, 162, 157–168.
- Harsch, M. a, Hulme, P. E., McGlone, M. S., & Duncan, R. P. (2009). Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology letters*, 12, 1040–1049
- Heiri, C., Bugmann, H., Tinner, W., Heiri, O., & Lischke, H. (2006). A model-based reconstruction of Holocene treeline dynamics in the Central Swiss Alps. *Journal of Ecology*, 94, 206–216.
- Holtmeier, F., & Broll, G. (2005). Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. *Global Ecology and Biogeography*, 14, 395–410.

- Holtmeier, F., Broll, G. (2007). Treeline advance – driving processes and adverse factors. *Landscape Online*, 1, 1–33.
- Hotz, M. C., & Weibel, F. (2005). *Arealstatistik Schweiz: Zahlen - Fakten – Analysen*. Neuchâtel.
- Jakubos, B., & Romme, W. . (1993). Invasion of sub-alpine meadows by lodgepole pine in Yellowstone National Park, Wyoming, USA. *Arctic and Alpine Research*, 25, 382–390.
- Kessler, M., Bohner, J., & Kluge, J. (2007). Modelling tree height to assess climatic conditions at tree lines in the Bolivian Andes. *Ecological Modelling*, 207, 223–233.
- Klasner, F., & Fagre, D. (2002). A half century of change in alpine treeline patterns at Glacier National Park, Montana, USA. *Arctic, Antarctic and Alpine Research*, 34, 49–56.
- Körner, C. (1998). A re-assessment of high elevation treeline positions and their explanation. *Oecologia*, 115, 445–459.
- Körner, Christian. (2012). *Alpine Treelines - Functional Ecology of the Global High Elevation Tree Limits* (p. 217). Basel: Springer.
- Kulakowski, D., Rixen, C., & Bebi, P. (2006). Changes in forest structure and in the relative importance of climatic stress as a result of suppression of avalanche disturbances, 223, 66–74.
- Laely. (1952). *Davoser Heimatkunde, Band 1, Buchdruckerei Davos* (pp. 275).
- Larcher, W. (2003). *Physiological plant ecology: ecophysiology and stress physiology of functional groups* (4th ed.). Germany: Springer.
- Leibold, E. (2012). Räumlich-zeitliche Analyse der alpinen Waldgrenze während der letzten 40 Jahre im Dischmatal (Davos) Masterarbeit von Elisabeth Leibold Zur Erlangung des akademischen Grades Diplomingenieurin der Forstwirtschaft.
- Lenoir, J., Gégout, J.-C., Marquet, P. A., De Ruffray, P., & Brisse, H. (2008). A significant upward shift in plant species optimum elevation during the 20th century. *Science*, 320, 1768–1771.
- Lloyd, A., & Fastie, C. (2003). Recent changes in treeline forest distribution and structure in interior Alaska. *Écoscience*, 10, 176–185.
- Malanson, G. (2001). Complex responses to global change at alpine tree line. *Physical Geography*, 22, 333–342.
- Marty, C., & Meister, M. (2012). Long-term snow and weather observations at Weissfluhjoch and its relation to other high-altitude observatories in the Alps. *Theoretical and Applied Climatology*, 5, 84–93.
- Mather, A., & Fairbairn, J. (2000). From floods to reforestation: The Forest Transition in Switzerland. *Environmental History*, 6, 399–421.
- Mayer, R., Kaufmann, R., Vorhauser, K., & Erschbamer, B. (2009). Effects of grazing exclusion on species composition in high-altitude grasslands of the Central Alps. *Basic and Applied Ecology*,

- Moir, W., Rochelle, S., & Schoettle, A. (1999). Microscale patterns of tree establishment near upper treeline, Snowy Range, Wyoming, USA. *Arctic, Antarctic and Alpine Research*, 31, 379–388.
- Motta, R., & Lingua, E. (2005). Human impact on size, age, and spatial structure in a mixed European larch and Swiss stone pine forest in the Western Italian Alps. *Can. J. For. Res.*, 35, 1809–1820.
- Ott, E. (1978). Über die Abhängigkeit des Radialzuwachses und der Oberhohen bei Fichte und Larche von der Meereshöhe und Exposition im Lotschental. *Schweizerische Zeitschrift für Forstwesen*, 3, 169–193.
- Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.*, 37, 637–669.
- Paulsen, J., & Körner, C. (2001). GIS-Analysis of Tree-Line Elevation in the Swiss Alps Suggests no Exposure Effect. *Journal of Vegetation Science*, 12, 817–824.
- Pfister, M. (1978). *Die Landschaft Davos, Haupt, Bern*. (pp. 112).
- Rees, G., Brown, I., Mikkola, K., Virtanen, T., & Werkman, B. (2002). How can the dynamics of the tundra-taiga boundary be remotely monitored? *Ambio Special Report*, 12, 56–62.
- Rochefort, R. M., Little, R. L., Woodward, A., & Peterson, D. L. (1994). Changes in sub-alpine tree distribution in western North America: a review of climatic and other causal factors. *The Holocene*, 4, 89–100. doi:10.1177/095968369400400112
- Rusch, G., & Oesterheld, M. (1997). Relationship between productivity, and species and functional group diversity in grazed and non-grazed Pampas grassland. *Oikos*, 78, 519– 526.
- Scherrer, D., & Körner, C. (2010). Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *Journal of Biogeography*, 16, 2602–2613.
- Schönenberger, W. (1975). Standortseinflüsse auf Versuchsaufforstungen an der alpinen Waldgrenze (Stillberg, Davos). *Mitteilungen der Eidgenössischen Anstalt für Forstliches Versuchswesen*, 51, 357–428.
- Scott, P. ., Hansell, R. I. ., & Erickson, W. . (1993). Influences of wind and snow on northern tree-line environments at Churchill, Manitoba, Canada. *Arctic, Antarctic and Alpine Research*, 46, 316–323.
- Senn, J. (1999). Tree mortality caused by *Gremmeniella abietina* in a subalpine afforestation in the Central Alps and its relationship with duration of snow cover. *European Journal of Forest Pathology*, 29, 65–74.
- Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K. ., Tignor, M., et al. (Eds.). (2007). *Climate change 2007: The physical science basis*. Cambridge: Cambridge University Press.
- Strobl, C., Malley, J., & Tutz, G. (2009). *An Introduction to Recursive Partitioning An Introduction to Recursive Partitioning: Rationale, Application and Characteristics Bagging and Random Forests* (pp. 87). Munich.

- Tappeiner, U., Tappeiner, G., Aschenwald, J., Tasser, E., & Ostendorf, B. (2001). GIS-based modelling of spatial pattern of snow cover duration in an alpine area. *Ecological Modelling*, *138*, 265–275.
- Tasser, E., Walde, J., Tappeiner, U., Teutsch, A., & Noggler, W. (2007). Land-use changes and natural reforestation in the Eastern Central Alps. *Agr Ecosyst Environ*, *118*, 115–129.
- Tattoni, C., Ciolli, M., Ferretti, F., & Cantiani, M. G. (2010). Monitoring spatial and temporal pattern of Paneveggio forest (northern Italy) from 1859 to 2006. *Forest -Biogeosciences and Forestry*, *3*, 72–80.
- Theurillat, J., & Guisan, A. (2001). Potential Impact of Climate Change on Vegetation in the European Alps: A Review, *Climatic Change*, *50*, 77–109.
- Tinner, W., & Theurillat, J. (2003). Uppermost limit, extent, and fluctuations of the timberline and treeline ecocline in the Swiss Central Alps during the past 11,500 years. *Arctic, Antarctic and Alpine Research*, *35*, 158–169.
- Tomback, D., Holtmeier, F., Mattes, H., Carsey, K., & Powell, M. (1993). Tree clusters and growth form distribution in *Pinus cembra*, a bird-dispersed pine. *Arctic, Antarctic and Alpine Research*, *25*, 374–381.
- Vitasse, Y., Hoch, G., Randin, C. F., Lenz, A., Kollas, C., & Körner, C. (2012). Tree recruitment of European tree species at their current upper elevational limits in the Swiss Alps. *Journal of Biogeography*, *39*(8), 1439–1449.
- Vittoz, P., Rulence, B., Largey, T., & Freléchoux, F. (2008). Effects of Climate and Land-Use Change on the Establishment and Growth of Cembra Pine (*Pinus cembra* L.) over the Altitudinal Treeline Ecotone in the Central Swiss Alps. *Arctic, Antarctic, and Alpine Research*, *40*(1), 225–232.
- Vorren, K.-D., Mørkved, B., & Bortenschlager, S. (1993). Human impact of the holocene forest line in the Central Alps. *Vegetation History and Archaeobotany*, *2*, 145–156.
- Walder, U. (1983). Ausaperung und Vegetationsverteilung im Dischmatal (German). *Mitteilungen*, *212*.
- Wallentin, G., Tappeiner, U., Strobl, J., & Tasser, E. (2008). Understanding alpine tree line dynamics: An individual-based model. *Ecological Modelling*, *218*(3-4), 235–246.
- Walther, G., Beißner, S., & Burga, C. A. (2005). Trends in the upward shift of alpine plants. *Journal of Vegetation Science*, *16*(5), 541–548.
- Walther, G. R., Post, E., Convey, P., Menze, I, A., Parmesan, C., Beebee, T. J. C., Fromentin, J. M., et al. (2002). Ecological responses to recent climate change. *Nature*, *416*, 389–395.
- Walther, G.-R., Beißner, S., & Burga, C. A. (2005). Trends in the upward shift of alpine plants. *Journal of Vegetation Science*, *16*(5).
- Weiser, C. (2007). Current concepts for treelife limitations at the upper treeline. In C. Wieser & M. Tuasz (Eds.), *Trees at their upper limit: Tree life limitations at the alpine tree line* (pp. 1–18). Dordrecht: Springer.

Wildi, O., & Ewald, K. (1986). *Der Naturraum und dessen Nutzung im alpinen Tourismusgebiet von Davos* (p. 313). Birmensdorf.

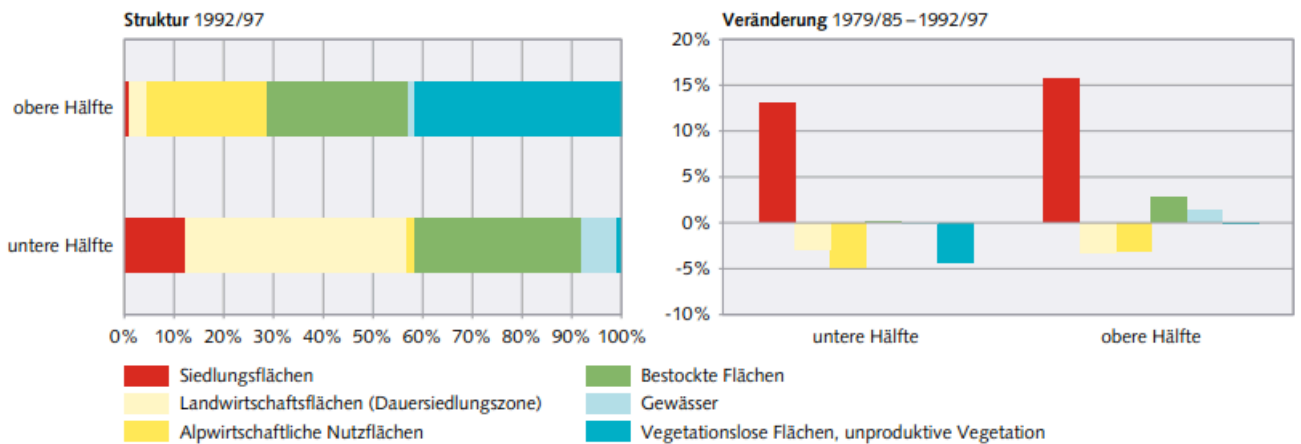
Wipf, S., Stoeckli, V., & Bebi, P. (2009). Winter climate change in alpine tundra : plant responses to changes in snow depth and snowmelt timing.

Zervas, G. (1998). Quantifying and optimizing grazing regimes in Greek mountain systems. *Journal of Applied Ecology*, *35*, 983–986.

Zong, C., Wauters, L. ., Van Dongen, S., Mari, V., Romeo, C., Martinoli, A., Preatoni, D., et al. (2010). Annual variation in predation and dispersal of Arolla pine (*Pinus cembra* L.) seeds by Eurasian red squirrels and other seed-eaters. *Forest Ecology and Management*, *260*, 587–594.

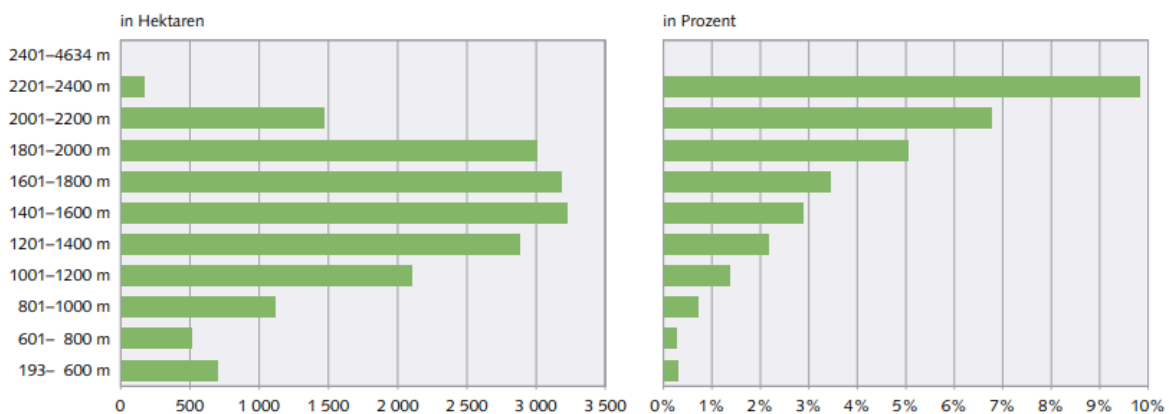
Appendix 1: Land-use and land-use change in Switzerland (above) and Increase the forest cover by elevation over 1979/85 - 1992/97 (below). Both figures from Hotz & Weibel (2005)

Over a 12-year period (1979/85 - 1992/97), agricultural area in Switzerland declined by a total of 3% (Hotz & Weibel 2005). Hotz & Weibel (2005) attribute this change to two main factors; i) urban encroachment in the densely populated Central Plain and ii) rural exodus from remote mountain regions, leading to successional shrub and forest cover in the alpine (see “alpwirtschaftliche” in the upper figure). Increases in forest cover (“bestockten Flächen”) has been higher in upper elevations (obere Hälfte) compared to lower elevations (untere Hälfte). Forest cover increases were greatest between 1400 - 2000 m, although when analyzed on a percent cover basis, forest increase was directly related to elevation: > 2200m forest cover increase was nearly 10% whereas this decreased with lower altitude classes (Hotz & Weibel 2005).



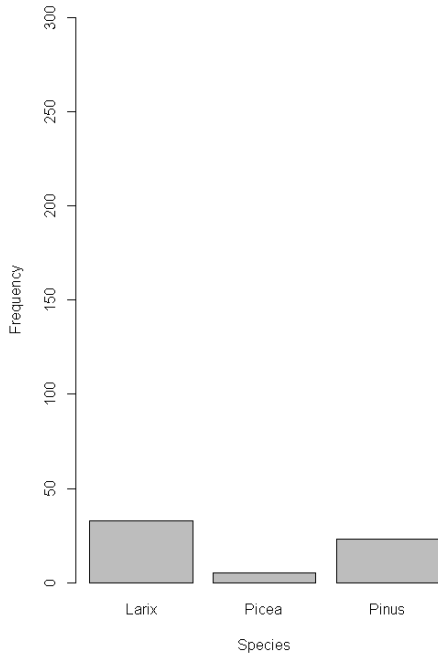
Zunahme der Waldflächen nach Höhenstufen
Veränderung 1979/85 - 1992/97

G 4.9

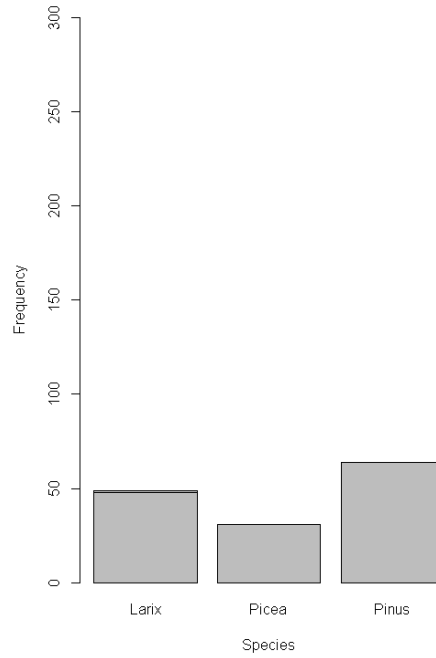


Appendix 2: Excluded points in analysis of infilling and advance

Old Trees (No infilling, no advance)
Aspect : North

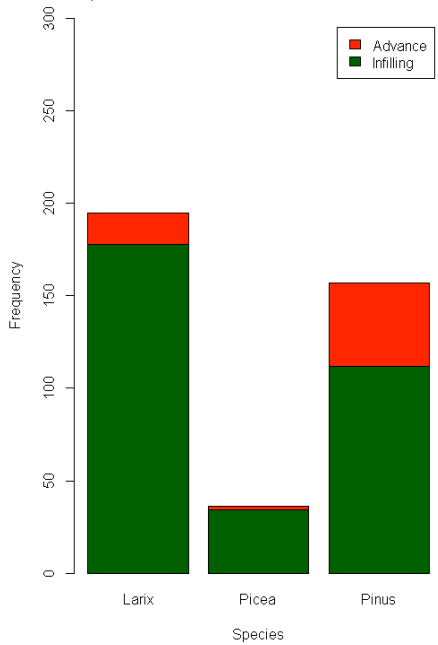


Old Trees (No infilling, no advance)
Aspect : South

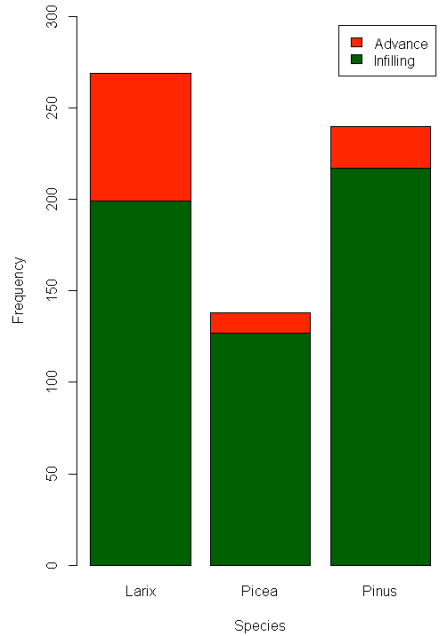


ALL TREES:

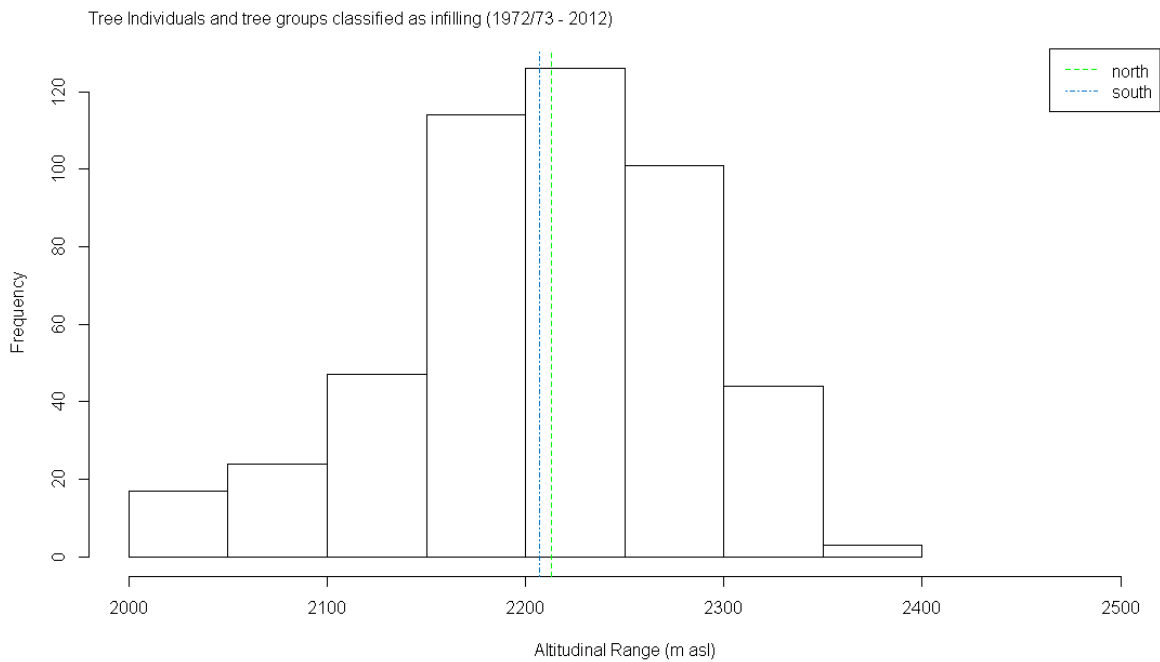
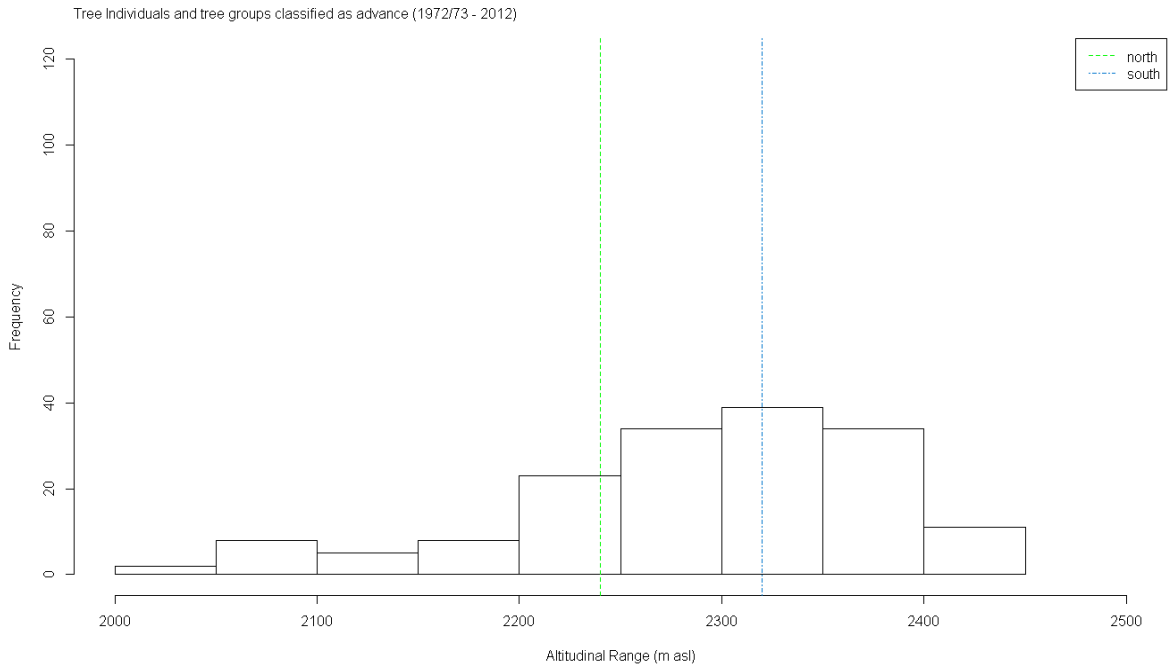
New trees established 1972/73 - 2012
Aspect : North



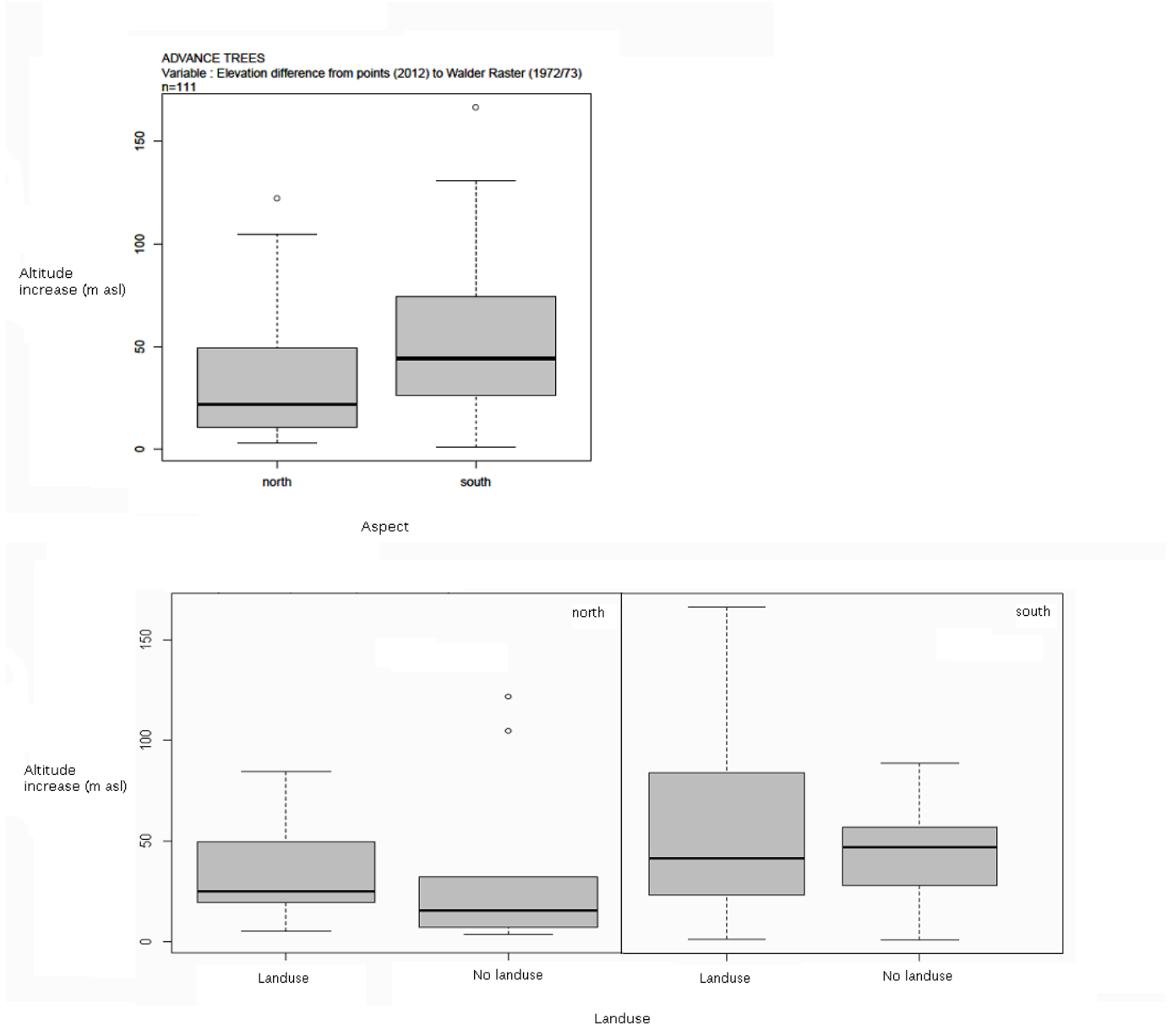
New trees established 1972/73 - 2012
Aspect : South



Appendix 3: Frequency of tree individuals and tree groups classified as a treeline advance (above) and infilling (below) per altitude band with means for north (green dotted line) and south (blue dotted-dash line) aspects.



Appendix 4: Top: distance of treeline advance (1972/73 - 2012) for a subset of the Dischma Valley. An analysis of 111 points in the western 4km of the valley showed aspect difference for distances of advance. Distances computed with elevation difference between trees classified as tree advance (2012) and nearest raster cell (1972/73) trees. Below: distance of treeline advance separated by aspect and land-use.



Appendix 5: Radiation and a positive effect on distance of advance. The positive relationship between radiation and advance is stronger on the north-facing slope. Direct radiation (May 16 - September 30). Radiation measured in total modelled radiation / 3000).

