Master's Thesis:

TREE MORTALITY IN PEATBOGS IN CENTRAL SWITZERLAND

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S̲ummary

Increasing mortality of mountain pine (*Pinus montana*) and Norway spruce (*Picea abies*) have been detected in the recent years in the peatbogs of the Entlebuch biosphere reserve. Using dendrochronological methods, 150 mountain pines and Norway spruces were sampled in five plots where abundant tree mortality was observed. Prior to this study, it was unclear, first, how the temperature and precipitation affected tree growth in that region, second, when these trees died, third, what influenced the lifespan of the dead trees, and fourth, why some trees are dead while others are alive.

First, the analyses have shown that mountain pines grew better if snow accumulation in the current January were high and precipitation in the current September low. For the future growth of the mountain pine, it is therefore necessary to maintain cold winters with high snow accumulation and warm end-of-summer months with little precipitation. For the growth of Norway spruces in plot 4 to 5, no common pattern was identified. Second, it was found that the majority of the mountain pines and Norway spruces died between 2001 and 2006. However, as a result of the summer drought in 2003, most of the mountain pines died in the years 2003 and 2004 and most of the Norway spruces in the year 2003. Third, these analyses showed that over 80% of both dead tree species had a lifespan between 100 and 200 years. For the mountain pines, an increasing DBH (diameter at breast height, i.e., 130 cm above the ground) also increased the lifespan, whereas an increasing early growth decreased the lifespan. For the Norway spruces, an increasing DBH, higher number of neighbouring trees and a medium sphagnum cover increased the lifespan, whereas an increasing early growth and low and high sphagnum cover decreased the lifespan. The slow-growing dead trees of both tree species reached a higher lifespan than the fast-growing dead trees. Forth, the analyses revealed that the mortality probability of the mountain pines decreased with increasing height and increasing neighbouring trees. The mortality probability of the Norway spruces decreased with increasing recent growth as well as increasing sphagnum cover and increased with decreasing neighbouring trees.

Overall, the tree mortality appeared to be a result from a combination of the species specific morphology, growth, competition with neighbouring trees, and their environmental surrounding such as sphagnum cover. However, the summer drought of 2003 has led to the highest mortality of both tree species. As the climate-induced tree mortality is expected to increase in Switzerland in the future, summer droughts may further increase tree mortality in peat moss forests.

Keywords: tree mortality, mountain pine, Norway spruce, dendrochronology, peatbogs, Switzerland

1 INTRODUCTION

Peatbogs cover about 3% of the terrestrial surface of the earth (Artz et al. 2014; Bragazza et al. 2012). Peatbogs are defined as areas with or without vegetation with a naturally accumulated peat layer at the surface (Joosten & Clarke 2002). Peat (*Sphagnum*) results from the decomposition of plant material and is the composition of different dead organic material (Joosten & Clarke 2002; Küchler et al. 2018). Most of the peatbogs (97%) occur in the northern hemisphere in the boreal and subarctic wetland regions (Leng & Hammer 2009; Tarnocai 2006). In Europe, peatbogs cover about 5.4% of the entire continent (Jurasinski et al. 2020). In Switzerland, the largest surface of peatbogs is located in central Switzerland in the Entlebuch biosphere reserve (see Figure 1).
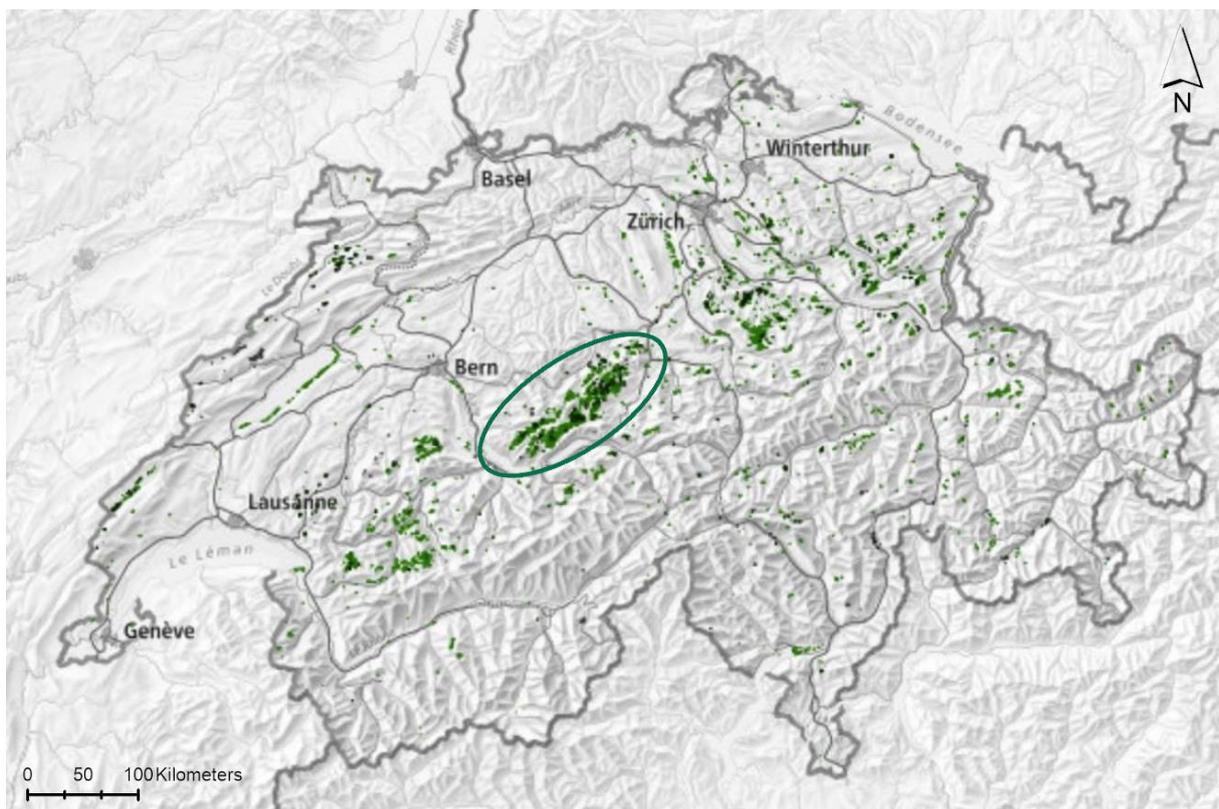
Figure 1: The remaining peatbogs of Switzerland in 2020 (green) and the location of the Entlebuch biosphere reserve (dark green circle). (Bundesamt für Umwelt 2020)

Peatbog ecosystems have a unique biodiversity with highly specialized species (Rydin et al. 2013; Verhoeven 2014). After the oceanic sediments, peatlands are the largest reservoir of long-term accumulation of CO_2 (Minayeva & Sirin 2012) and store approximately 30% of global soil carbon (Dise 2009; Heijmans et al. 2013). This is the reason why pristine peatbog ecosystems are nowadays regarded as valuable natural CO_2 sinks and play a significant role in maintaining the balance of the CO_2 cycles on earth (Breeuwer et al. 2009; Joosten 2019). However, since the 18th century, peatbogs are used by many stakeholders for fuel production, industry, pollution control, agriculture, and recreation (Joosten & Clarke 2002). As a consequence, peatbogs are fragmented worldwide and the ecosystems have not recovered since the 18th century as their development is very slow (Leng & Hammer 2009). Additionally, peatbog ecosystems are very sensitive to any climatic changes, because the upper peat layers depend primarily on precipitation, temperature, and evapotranspiration (Alekseychik et al. 2018;

Helbig et al. 2020; Linderholm & Leine 2004). In Switzerland, the loss and fragmentation of peatbogs largely stopped since 1987 thanks to the protection act of the Federal Constitution of Switzerland of 1987 (Fischer et al. 2014). The few remaining peatlands in Switzerland are, however, still spatially isolated and have continued to lose quality in recent years due to the historical human-induced and ongoing climatic disturbance (Bergamini et al. 2020; Küchler et al. 2018). Due to that, peatlands in Switzerland and all over the world turned into nutrient-rich habitats and are more overgrown with trees (Bergamini et al. 2020; Küchler et al. 2018).

The increasing tree growth on peatbogs have been reported by various scientists (see e.g. Barber et al. 2000, Edvardsson 2015; Heijmans et al. 2013; Linderholm et al. 2002; Smiljanic et al. 2014). Edvardsson (2015) and Linderholm et al. (2002) claim that tree growth on peatbogs depend mainly on the depth of the water table, which is regulated by seasonal and annual variations in temperature and precipitation and in disturbed peatbogs by human drainage systems. According to Heijmans et al. (2013), the water table sank through evapotranspiration in dry summers. This increases the availability of mineralising nutrients and dry out the soil, which enhanced tree growth (Barber et al. 2000; Heijmans et al. 2013).

The concern about the increasing tree growth in peatbogs is legitimate because peatbogs have been known as nutrient-poor habitats, which is why trees usually did not occur in such ecosystems (Küchler et al. 2018). In the Entlebuch biosphere reserve, however, mountain pines *(Pinus montana)* and Norway spruces *(Picea abies)* had been able to grow under the prevailing conditions (Küchler et al. 2018). Mountain pines resist frost and low temperatures, are shade-intolerant tree species, and grow at calcareous and dry but also acid and moist sites (Bigler 2016). Norway spruces occupy an intermediate tree species type, which occur not only in the lowlands but likewise in the alpine and boreal zones of Europe (Andreassen et al. 2006; Schütt et al. 2006). This also applies to shade tolerance, as Norway spruces belong to the semi-shade tree species, whereby the need for light increases with advancing age (Schütt et al. 2006). Thus, both species fit well into the moist and sparse tree covered peat moss forests of the Entlebuch biosphere reserve. Nevertheless, in recent years, a substantial amount of dead standing trees have been discovered in the Entlebuch biosphere reserve by the forest authorities and the biosphere reserve managers (see Figures 2 and 3).

Figure 2: Tree mortality in the Entlebuch biosphere reserve in winter 2019 (Catoja 2019).

Figure 3: Tree mortality in the Entlebuch biosphere reserve in summer 2020 (Catoja 2020).

In recent years, tree mortality exceeded the natural deaths within forest stand dynamics (Etzold et al. 2019) and were reported more frequently in Switzerland and all over the world (Allen et al. 2010; Greenwood et al. 2017; Schuldt et al. 2020). Many forests are used for industrial services such as timer, urbanization, agriculture, watershed protection but also recreation (Allen et al. 2010; Watson et al. 2018). In addition, forests provide a cooling climate effect as they store atmospheric CO_2 (Luyssaert et al. 2008). Intact forest ecosystems are indispensable for addressing the rapid climate change and maintaining the regional specialised forest biodiversity (Watson et al. 2018). As a result of climate change, warmer summers and milder winters occur in combination with more frequent and extreme precipitation and drought events (Gessler et al. 2017; Heijmans et al. 2013). Examples for these changes are the extreme droughts in Switzerland in 2003, 2015, and 2018 (Schuldt et al. 2020). Although, trees can suffer rather long periods of time of low growth prior to dying (Peltoniemi & Mäkipää 2011), many trees in Switzerland have died in recent years due to drought-induced stress (Barber et al. 2000; Etzold et al. 2019). Moreover, trees growing on sites with generally low nutrient availability, such as peatbogs, cannot compensate for the negative effects of droughts on nutrients supply after drought-induced stress (Gessler et al. 2017).

In addition to the drought-induced stress, tree mortality also depended on changes in surface topography such as the slope and soil cover (Pawlik et al. 2013). As peat is an unstable and windswept surface (Linderholm et al. 2002; Smiljanic et al. 2014), changes in the topography (e.g. changes of the slope and soil cover) in advancing age of a tree, increase the probability of tree trunks to bend downslope, resulting in even low wind exposure during storms leading to a greater risk of uprooting and tree falling (Dietze & Moorcroft 2011; Pawlik et al. 2013; Toledo et al. 2011). Another factor leading to tree mortality is the competition with neighbouring trees (Das et al. 2011; Schmid et al. 2006). The more similar the heights and DBH of the neighbouring trees the higher their competition for light (Schmid et al. 2006). More neighbouring trees have, additionally, the potential to weaken trees, making them an easy target for pathogens and insect infestations (Das et al. 2011; Manion 1981; Peltoniemi & Mäkipää 2011).

If trees are weakened with advancing age due to competition, their recent growth will decrease leading to death eventually (Bigler & Bugmann 2003). If trees are weakened early in their lives, their early growth is slowly. However, this does not necessarily lead to death as slow-growing mountain pines had longer lifespan than fast-growing mountain pines (Bigler 2016). Furthermore, it was observed that slow-growing Norway spruces accumulate more chemical defence, have higher wood density, and thus reach longer lifespan than fast-growing Norway spruces (Castagneri et al. 2012; Rötheli et al. 2011).

Tree mortality is affected by different biotic and abiotic impacts, which influence the trees to varying degrees depending on the species and site. In the Entlebuch biosphere reserve it is unknown what has most influenced the increasing tree mortality in recent years. The overall aim of this study is to find explanations for the dieback of mountain pines and Norway spruces in the Entlebuch biosphere reserve. For this purpose I complied the following four research questions:

1. How does temperature and precipitation affect tree growth in peatbogs?
   As tree growth immediately respond to changes (Schweingruber 1988), I hypothesize that the growth of both tree species respond positively to more precipitation and negatively to high temperatures of the previous and current months of the growing season (Andreassen et al. 2006; Barber et al. 2000; Edvardsson & Hansson 2015; Heijmans et al. 2013).
2. When did the trees die?
   After extreme droughts and heatwaves, I predict an increase in the mortality of mountain pines and Norway spruces (Allen et al. 2010; Etzold et al. 2019; Williams et al. 2012).
3. What influenced the lifespan of the dead trees?
   (a) For mountain pines and Norway spruces, I expect that the lifespan is decreasing with decreasing soil cover (e.g. in this study sphagnum cover as this is one of the main characteristic of peatbogs) and increasing slope due to the decrease in moisture, greater risk of uprooting, and tree falling (Dietze & Moorcroft 2011; Pawlik et al. 2013; Toledo et al. 2011). (b) As mountain pines and Norway spruces are both shade-intolerant in their adulthood, I predict that more neighbouring trees decrease the survival and thus the lifespan of the dead mountain pines and Norway spruces (Das et al. 2011; Schmid et al. 2006; Peltoniemi & Mäkipää 2011). (c) I hypothesize that slow-growing mountain pines and Norway spruces had longer lifespan than fast-growing mountain pines and Norway spruces (Bigler 2016; Rötheli et al. 2011). Although tree mortality is present in several places in the Entlebuch biosphere reserve I suspect species- and side-specific differences in the expression of the mentioned influences.
4. Why are some trees dead while others are alive?
   With the calculation of a mortality probability for mountain pines and Norway spruces in the Entlebuch biosphere reserve, prognoses can be made for future tree mortality in peatbogs. As little is known about mortality probabilities of mountain pines and Norway spruces in peatbogs in central Switzerland, the following hypothesis is an own assessment: I expect that the mortality probability increases with (a) decreasing height and DBH, (b) increasing neighbouring trees, (c) decreasing recent growth, (d) increasing slope, (e) decreasing sphagnum cover, and (f) decreasing lifespans. As in the third research question, I expect also for these analyses species- and side-specific differences in the expression of the mentioned influences on the mortality probability.

2 MATERIAL AND METHODS

Sampling sites and selection of study plots

The sampling sites are located in Switzerland at Sörenberg in the Entlebuch biosphere reserve where many peatbogs are still intact. The plots were chosen due to their similar topography on aerial photos of the Swiss Confederation (Bundesamt für Umwelt 2020). Each plot has approximately the same size ($\approx$ 10,000 m^2), shape (a circle with Ø $\approx$ 100 m), and elevation ($\approx$ 1,200 – 1,500 m). The plots have at least $100\,m$ distance between each other. Peatbogs are very heterogeneously shaped and have therefore – compared to their sizes – large ecotones (Küchler 2018). To avoid edge effects of these ecotones in this study, the plots were placed at least 50 m away from the edge of the peat moss forest.

To have a partly randomized sample, ten suitable plots were selected and divided into two subgroups (see Table A.1 and Figure A.2). Each of the two subgroups cover sites where tree mortality in the Entlebuch biosphere reserve was predominant on the aerial photos. From the first subgroup, which covers the western peatbog sites, three out of six plots were selected. From the second subgroup, which covers the eastern peatbog sites, two out of four plots were chosen. The selection of the plot of the two subgroups was randomly chosen using the R software version 3.6.1 of 2019. The visualisation of the plots was done with the ArcGIS software version 2.7 of 2019 (ESRI, Redlands, USA). The five plots cover different sites of the affected areas (see Figure 4).
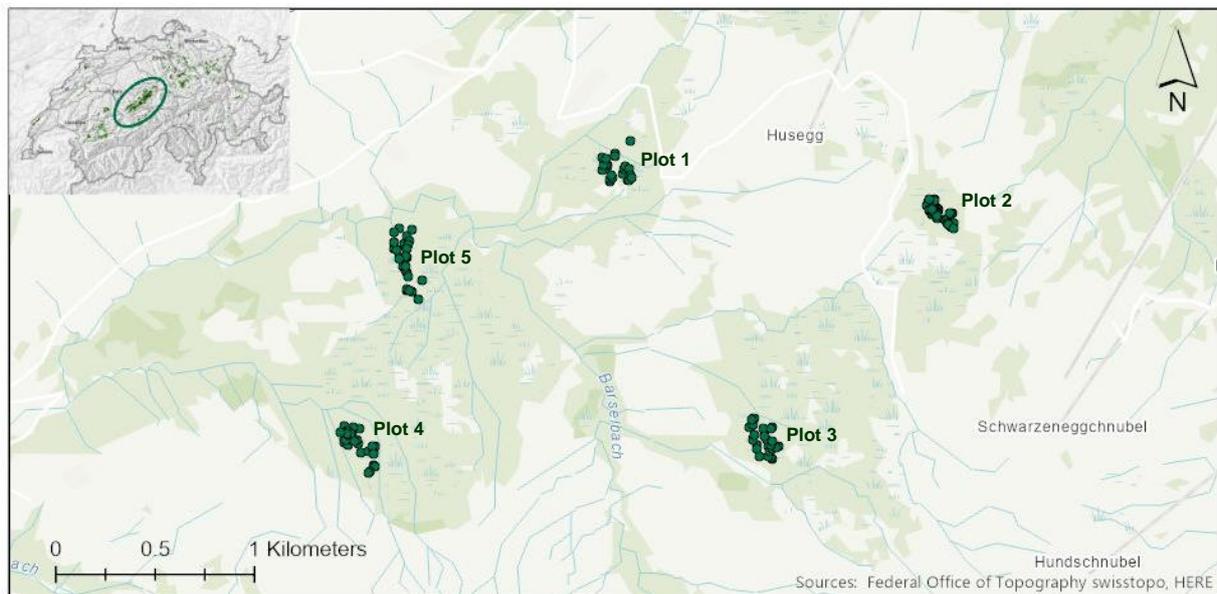
Figure 4: The five sampling sites in the peatbog at the Entlebuch biosphere reserve in Switzerland (Federal Office of Topography 2021). Each of the dark green points are one of the total 150 sampled trees of which each plot include 10 living and 20 dead trees.

Sampling design

In this observational study, dead and living trees were sampled using common dendrochronological sampling methods. Dendrochronology is one of the most important environmental recording techniques. It provides the possibility to reconstruct the growth dynamics of trees over several years, decades and centuries. The sum of immediate responses are expressed in annual tree-ring widths (Schweingruber 1988; Speer 2010). According to Schweingruber et al. (1990), 15-20 dominant trees per sampling site would ideally be collected to reach the longest possible time-series.

Within each of the five plots, 20 dead and ten living trees were randomly chosen starting from the coordinates in the middle of each plot. The 20 dead trees were chosen based on the following morphological requirements: (1) the trees had to be standing, (2) their trunks unbroken and not twisted or knotted, and (3) their DBH had to be 15 cm at least. The dead tree closest to the middle point coordinate, which fulfilled these morphological requirements, was chosen first and tree core samples were taken. If this process was successful, a second core was extracted. After every second sampled dead tree, a living tree, which had morphologically similar characteristics, was sampled in the nearest surrounding. The sampled living tree formed the new starting point. This procedure was repeated until 30 tree samples per plot were collected. However, if a tree fulfilled the morphological characteristics but no tree core sample could be taken due to branches or decayed wood (see Figures 5 and 6), the nearest dead tree in the surrounding was sampled next. In total, 150 tree samples were collected between July and September 2020. The samples were unbalanced on purpose (1) as the living trees served as a reference for the dead trees, and (2) as the main focus was on the dead trees.

Figure 5: Tree core sample with decayed bark and wood of plot 1.

Figure 6: Tree core sample with a branch and decayed wood of plot 4.

The following data was reported from the cored living and dead trees:

(1)   Tree species (determined first in the field, later verified in the laboratory)

(2)   DBH in cm (only trees with ≥ 15 cm DBH); using a tree clump

(3)   Height in m; using a Vertex IV hypsometer and a transponder (Haglöf Sweden AB, Langsle, Sweden)

(4)   Sphagnum cover; 1 m around the tree (ordinal scale using five categories: 0 = no sphagnum, 1 = 0.01-25%, 2 = 25.01-50%, 3 = 50.01-75%, 4 = 75.01.-100%)

(5)   Distance in m to all living and dead neighbouring trees; using a measuring tape (all neighbouring trees with ≥ 15 cm DBH and located within a 5 m radius were included)

(6)   Coordinates (CH1903); using a Global Position System GPSmap 64st (Garmin GmbH, Schaffhausen, Switzerland)

Laboratory methods

After the field work, all tree core samples were (1) glued onto a core mount (with the fibre direction aligned vertically), (2) sanded, (3) measured with 0.01 mm resolution using a Leica MZ6 microscope with the Leica CLS 150X extern light source (both from Leica, Wetzlar, Germany), the LINTAB 5 measuring bench, and TSAP-Win software (both from Rinntech, Heidelberg, Germany), and (4) cross-dated with the software COFECHA (Holmes 1983) according to standard dendrochronological procedures (Speer 2010).

After measuring the ring widths of all samples, the tree-rings were crossdated. Crossdating is the most crucial procedure in tree-ring analysis (Fritts 1976; Schweingruber 1988; Speer 2010) and allows to assign each tree-ring to the correct calendar year by comparing tree-ring patterns of different trees from different sampling sites. Crossdating is necessary to identify whether (1) tree-rings are missing or false, (2) tree-ring features were identified wrongly, or (3) errors in counting or measuring happened (Fritts 1976; Holmes 1983; Speer 2010). In the best case, the samples are compared with already existing chronologies of the same tree species in a similar region of the "International Tree Ring Data Bank" (ITRDB). In this study, however, no existing chronologies of the same tree species in a similar region was found in the ITRDB. Therefore, I developed chronologies with the living trees of the same species and at the same plot. With these chronologies of the living trees, the establishment of the dead and living trees, the year of death and the lifespan of the dead trees were determined. The COFECHA software searches for associations in all measured tree-ring series of each tree sample in segments of 50 years (see Tables B.1 and B.2). The correlations range from -1 to 1, with -1 indicating that there is no association at all and 1 indicating a 100% association. In dendrochronological analyses with a sample segment of 50 years, the aim is to reach a high positive significant correlations over 0.3281 ($p < 0.01$).

Data analyses

For the analysis of the four research questions, the following subgroups were formed: (1) all living mountain pines, (2) all dead mountain pines, (3) all living Norway spruces, and (4) all dead Norway spruces. The same subdivision was applied per plot.

The mortality of mountain pines *(Pinus montana)* and Norway spruces *(Picea abies)* in the Entlebuch biosphere reserve appeared to be equally frequent. The 150 randomly sampled trees accounted for 75 mountain pines and 75 Norway spruces. Out of 150 samples, there were 14 living mountain pines, 51 dead mountain pines, 16 living Norway spruces, and 49 dead Norway spruces. The distribution of the tree species in the plots was unbalanced. Plot 1 to 3 included mainly mountain pines whereas plot 4 to 5 only included Norway spruces. Plot 1 included four, plot 2 and plot 3 of one living Norway spruces each. Plot 1 contained one, plot 2 two, and plot 3 six dead Norway spruces (see Table 1).

Table 1: Overview of the 150 sampled trees in the Entlebuch biosphere reserve.

Plots	Elevation (m)	Mountain pines		Norway spruces	
		Living	Dead	Living	Dead
Plot 1	~ 1,354	6	19	4	1
Plot 2	~ 1'467	9	18	1	2
Plot 3	~ 1,444	9	14	1	6
Plot 4	~ 1,362	0	0	10	20
Plot 5	~ 1,277	0	0	10	20
Total	-	24	51	26	49

As Norway spruces were only weakly represented in plots 1 to 3, they were not taken into account in the analyses when comparing plots of the same tree species with each other. Further information of these samples can be found in the appendix (Figures F.1, H.1-H.3). Additionally, the tree species were not compared with each other in the analyses. The elevation of all plots ranged from 1,277 m to 1,467 m (see Table 1). Plot 5, followed by plot 1 and 4 is at the lowest elevation. Plots 2 and 3 were both about 100 m higher than the other three plots.

1. How does temperature and precipitation affect tree growth in peatbogs?

The first research question investigates the effect of temperature and precipitation on tree growth in peatbogs. For this approach only the tree-ring measurements of the sampled living trees were used. In this study, the detrended tree-ring chronologies were compared with meteorological data of the national monitoring centre MeteoSwiss from 1961 to 2018. These are daily interpolated meteorological data on a 1 km to 1 km grid. The coordinates on the 1 km to 1 km grid, which were the closest by the respective plot are used for the comparison. None of the five plots had exactly the same coordinates on the 1 km to 1 km grid. The daily average temperature and total precipitation were transformed into mean monthly temperatures and total monthly precipitations. Tree-rings are formed in the summer months (Speer 2010). Therefore, only the months April to September from 1961 to 2018 were selected for the climate -series.

The tree-ring data were (1) detrended (R-Package: dplR, detrend method: "Friedman") and (2) a residual chronology was developed (see Figures C.1-C.9). With this method, the trees' natural biological annual

growth trend is removed so that only the actual annual growth is visible (Friedman 1991). To get a robust tree-ring signal, at least five to ten (ideally 10 to 20) trees should cover the entire time span of the climate -series. The detrended tree-ring chronologies were derived in plot 1 from six mountain pines and four Norway spruces, in plot 2 from nine mountain pines, in plot 3 and plot 4 from nine mountain pines, and in plot 4 and plot 5 from ten Norway spruces each.

With the formed climate -series and detrended tree-ring chronologies of the living trees per plot, the response function can be calculated (R-package: treeclim). Response functions analyses the relationship between monthly climate variables and tree growth (Fritts et al. 1971; Fritts 1976). A correlation coefficients of the response function with a significance level of $p < 0.05$ was considered as reliable (Edvardsson & Hansson 2015). The results of the response function were visualised and compared within each species.

2. When did the trees die?

The second research question, which examines the time of death of the dead mountain pines and dead Norway spruces in each plot, was answered with descriptive statistics using the in the laboratory determined years of death.

3. What influenced the lifespan of the dead trees?

The third research question analysed the relationship between the lifespan, early growth, tree size, sphagnum cover, slope, and the competition of the neighbouring trees. To visualize the response variable lifespan of all sampled trees, time-series plots of the annual ring widths were created. However, for the model analysis only the dead trees were included.

The independent variable early growth was calculated with the mean of the first 50 years of trees' life using the measured tree-ring widths in mm and the R software. With the measured coordinates during the fieldwork and ArcGIS Pro software, the mean slope and standard deviation of the slope was calculated with a radius of 5 m around the sampled trees. To estimate the slope as accurate as possible, the standard deviated slope was subtracted from the mean slope. The independent variables tree size represented by DBH and height, as well as sphagnum cover and number of neighbouring trees were already determined during the fieldwork. To take the distance-dependent competition into account Hegyi's competition index (1974) was calculated for each sample:

$$Hegyi's\ CI_i = \sum_{j=1}^{N_i} \frac{d_j}{d_i} \frac{1}{D_{ij}} = \sum_j \frac{\frac{d_j}{d}}{D_{ij}} \tag{1}$$

The DBH of the target tree is d_i, the DBH of the competitor j is d_j, and the distance between the trees i and j is D_{ij}. In this index the competitors were defined as all trees that were within a given distance (D_{max} = 5 m) from the target tree (Hegyi 1974). As the index is a sum, the trees with more neighbouring trees generally have a larger value. In order to account for this, all CI values have to be log transformed. Because some of the sampled trees had zero neighbouring trees, the CI values could not have been log transformed without excluding samples from the whole analyses (number of neighbouring trees > 0). That is why the CI was excluded in all the analyses. Instead the number of neighbouring trees were

included as both variables correlated with the lifespan in a similar way (see Figures D.1-D.2). The height was as well excluded from the model, as the height of trees are known to be correlated with the DBH. The effect of the early growth, DBH, neighbouring trees, sphagnum cover, plots and the slop on the lifespan were modelled using the following linear regression model:

$$Lifespan = \beta_0 + \beta_{Early\ growth}X_{Early\ growth} + \beta_{DBH}X_{DBH} + \beta_{Neighbours}X_{Neighbours} \qquad (2)$$
$$+ \beta_{Sphagnum\ cover}X_{Sphagnum\ cover} + \beta_{Plots}X_{Plots} + \beta_{Slope}X_{Slope} + \varepsilon$$

$$\varepsilon \sim \mathcal{N}(0, \sigma_\varepsilon^2)$$

In the linear regression model β_0 is the intercept and ε the error term. The model selection was done by starting with the full model, which includes all independent variables. The best model was selected with the p-value, adjusted R squared (adjusted R^2) and the corrected Akaike information criterion (AICc).

The p-value is the probability of obtaining test results at least as extreme as the observed results assuming the null-hypothesis is true. If a model reaches a p-value under 0.05, it indicates that the null-hypothesis, which does not predict any effect of the independent variables on the response variable, can be rejected (Neyman and Pearson 1933).

The adjusted R^2 is a modification of R^2 and takes the number of independent variables into account:

$$adjusted\ R^2 = 1 - \frac{(1 - R^2)(n - 1)}{n - k - 1} \qquad (3)$$

The n denotes the sampling size and k the number of estimated parameters in the model. The adjusted R^2 is expressed as percentage, with 100% indicating a perfect correlation between the independent and response variable and zero indication no correlation at all (Harel 2009).

The AICc is an extension of the Akaike information criterion (AIC) and suitable for small sampling sizes. Under the assumption that the true model exists, AICc is used to find the model which is closest to the true one (Anderson et al. 1998). The AICc is calculated as follows (Hurvich & Tsai 1989):

$$AIC_c = 2k - 2\ln(\hat{L}) + \frac{2k^2 + 2k}{n - k - 1} \qquad (4)$$

The n denotes the sample size, k the number of independent variables in the model, and the ($\hat{L}$) the maximum value of the likelihood of the model (Fraser 2019). The model with the smallest AICc value is closest to the true model.

4. Why are some trees dead while others are alive?

To predict whether a tree is dead or living in the Entlebuch biosphere reserve, a mortality model is made using a logistic generalized linear model (logit-GLM). Logistic regressions are seen as presence/absence models (Fielding & Bell 1997) and are used to predict a binary outcome. To have species independent results the logit-GLM is calculated per tree species:

$$\ln(\frac{l}{1-l}) = \beta_0 + \beta_{Height}X_{Height} + \beta_{Neighbours}X_{Neighbours} + \beta_{Recent\ growth}X_{Recent\ growth}$$
$$+ \beta_{DBH}X_{DBH} + \beta_{Slope}X_{Slope} + \beta_{Lifespan}X_{Lifespan} + \beta_{Plots}X_{Plots}$$
$$+ \beta_{Sphagnum\ cover}\ X_{Sphagnum\ cover}$$

(5)

The variable condition (living or dead) of the trees is set as the response, the variables height, neighbouring trees, recent growth, DBH, slope, lifespan, plots, and sphagnum cover as independent variables. The recent growth is the mean growth in the last ten years of a trees' life. As the response variable condition has only two possible outcomes, it follows a Bernoulli distribution and therefore needs to be transformed into the factors 1 (= living trees) and 0 (= dead trees). The other variables either have the class factor or are numeric. For a better understanding of the output, it is important that the condition *living* is the reference level.

The best model is selected with the Area under the curve (AUC) method that is based on a two by two table confusion matrix that shows the true outcome against the predicted outcome (Zipkin et al. 2012). In such a logit-GLM, two possible model prediction errors can appear (see Table 2):

Table 2: A confusion matrix (with possible prediction errors in bolt).

	Reality: +	**Reality: –**
Predicted: +	True Positive (TP)	**False Positive (FP)**
Predicted: –	**False Negative (FN)**	True Negative (TN)

A false positive (FP) error means that the model predictions seem true but are wrong in reality. A false negative (FN) error means, on the other hand, that the model predictions seem wrong but are in reality true. These two errors are calculated with a receiver operating characteristic (ROC) curve, which provides a single measure of overall accuracy that is not dependent upon a particular threshold (Deleo 1993). This ROC curve is represented in a plot, in which the true positive (TP) on the y-axis are plotted against the true negative (TN) on the x-axis (Fielding & Bell 1997). In such a plot, the AUC is the whole area under the ROC curve.

AUC values ranges from 0 to 1, where 0 means that the model predictions are completely wrong and 1 means that the model predictions are completely true (Fielding & Bell 1997). A value of 0.5 indicates that the model performs at random and thus has no pattern (Hosmer & Lemeshow 2000; Zipkin et al. 2012). Values greater than 0.5 indicate increasingly better discrimination capabilities (Hosmer & Lemeshow 2000).

Due to the fact that the sampling sizes of 75 mountain pines of plot 1 to 3 and 60 Norway spruces of plot 4 to 5 is rather low and the number of dead and living trees is unbalanced, the AICc was as well calculated for the logit-GLMs. In cases where the highest AUC value and the lowest AICc value do not select the same model as best performing, the model with the lowest AICc was selected as best performing model. The calculations of the AUC were done with the R software (package: pROC).

3 RESULTS

1. How does temperature and precipitation affect tree growth in peatbogs?

a Mountain pine (*Pinus montana*)

The growth of the 24 sampled living mountain pines of plot 1 to 3 correlated mostly with the total monthly precipitation of the months April to September (see Figure 7). In the years where the total monthly precipitation was high the growth of the living mountain pines were as well high. After 2011, total monthly precipitation decreased in the months April, June, July and September, what seem to influence the growth of the living mountain pines positively.
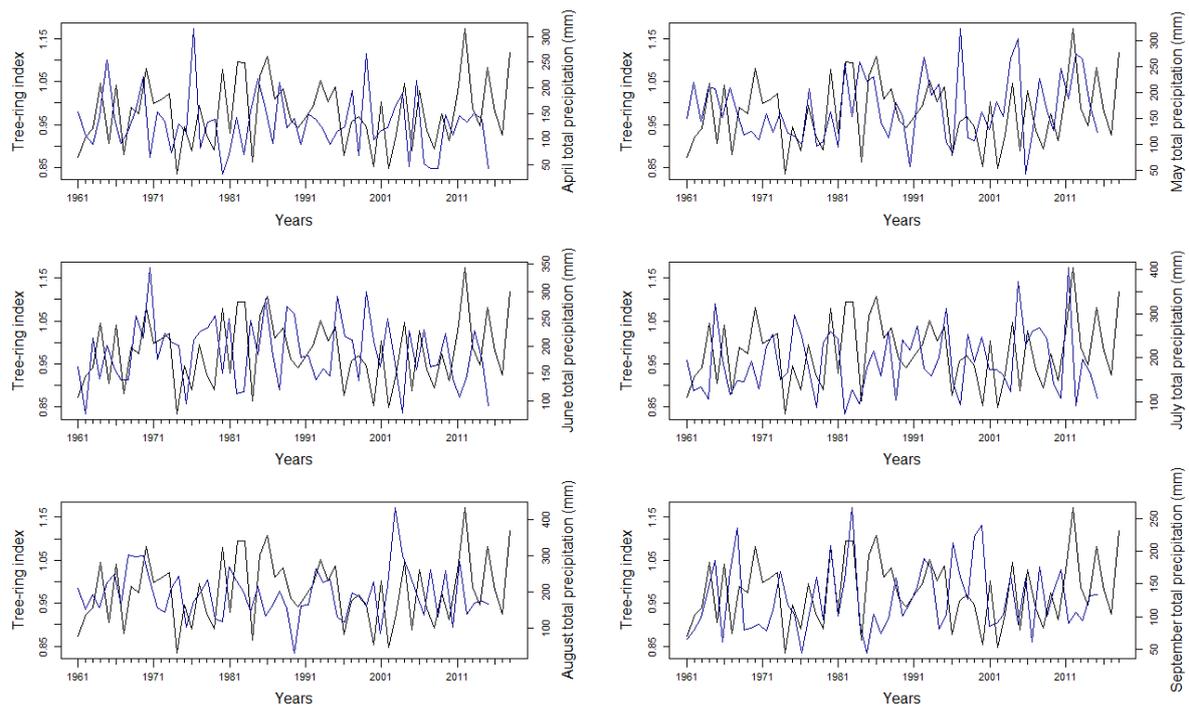
Figure 7: Relationship of the detrended chronologies of all 24 sampled living mountain pines (in black) and total monthly precipitation of the months April to September between 1961 and 2018 (in blue).

The growth of the sampled living mountain pines was at the beginning of the growth season in April and at the end of the growth season in August and September positively influenced by the rising temperatures (see Figure 8). In these month the growth of the mountain pines increased with the increasing mean monthly temperatures. In May the growth of the mountain pines decreased with increasing mean temperatures, especially between the years 1995 and 2011. In June and July, the growth of the mountain pines were decreasing after 2000 and was significantly low in 2003 even the mean temperatures increased.
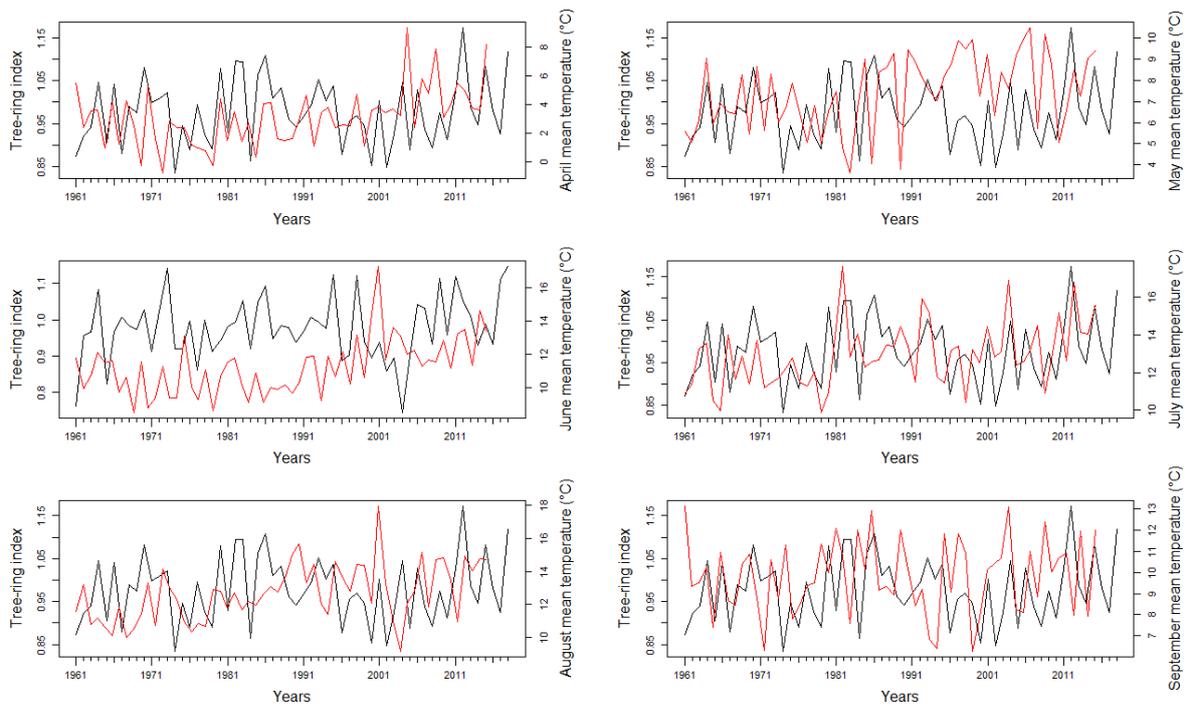
Figure 8: Relationship of the detrended chronologies of all 24 sampled living mountain pines (in black) and mean monthly temperature of the months April to September between 1961 and 2018 (in blue).

In plot 1, neither the precipitation of the previous year nor that of the current year influenced the growth of the sampled living mountain pines significantly (see Figure 9). But there is a significant correlation between the current May temperature and the growth of the living mountain pines. Consequently, the mountain pines in plot 1 grew better, when May temperatures were high.
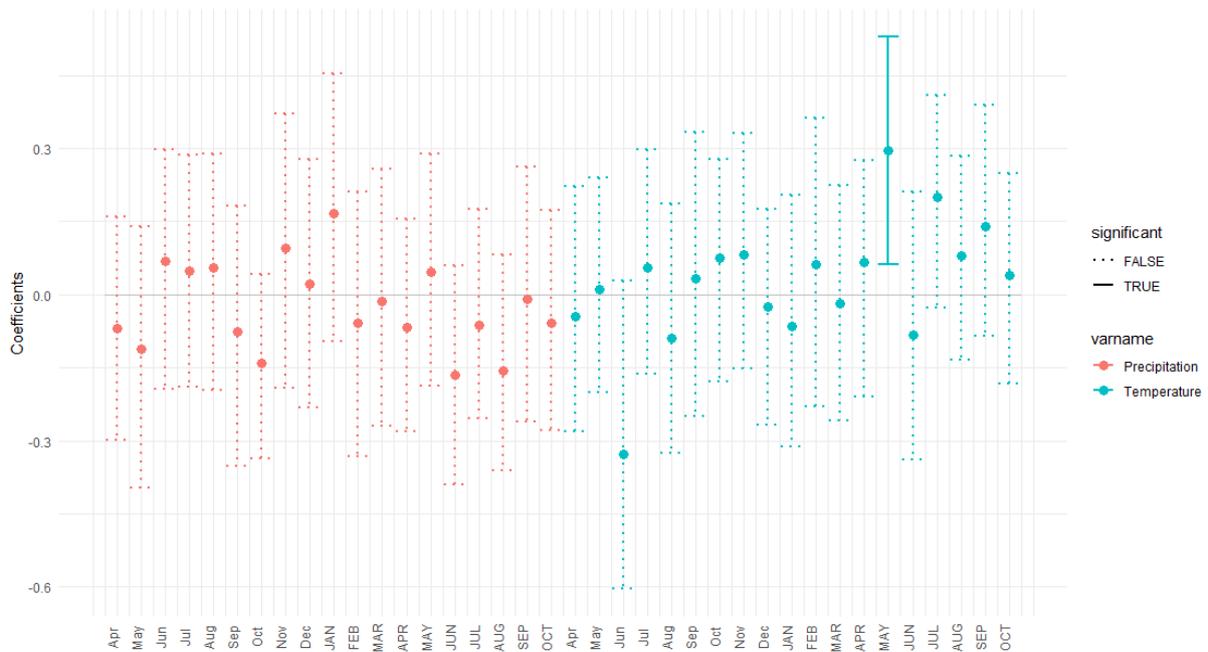
Figure 9: Response function of the 6 living mountain pines, total precipitation and mean temperature of plot 1 in the Entlebuch biosphere reserve. The output for precipitation (in red) in each of the plots is shown on the left part and the output for temperature on the right part (in light blue). On the x-axis,

lowercase letters (April to December) indicate months of the previous year and uppercase letters (January to November) from the current year. The dots are the values of the response coefficients. The vertical lines are the 95% confidence intervals of which dotted lines are non-significant coefficients (p > .05) and solid lines are significant coefficients (p < .05).

In plot 2, current January and April precipitation were significant positively correlated with the growth of the living mountain pines (see Figure 10). However, the correlation between the current September precipitation and growth of these living mountain pines were negative. This implies that the growth of the living mountain pines in plot 2 was influenced by precipitation of the current year and increased with decreasing precipitation and decreased with increasing precipitation. The sampled living mountain pines grew better, when the snow accumulation was high in the current January and precipitation low in the current September. For the sampled living mountain pines, high current September temperatures influenced their growth positively.
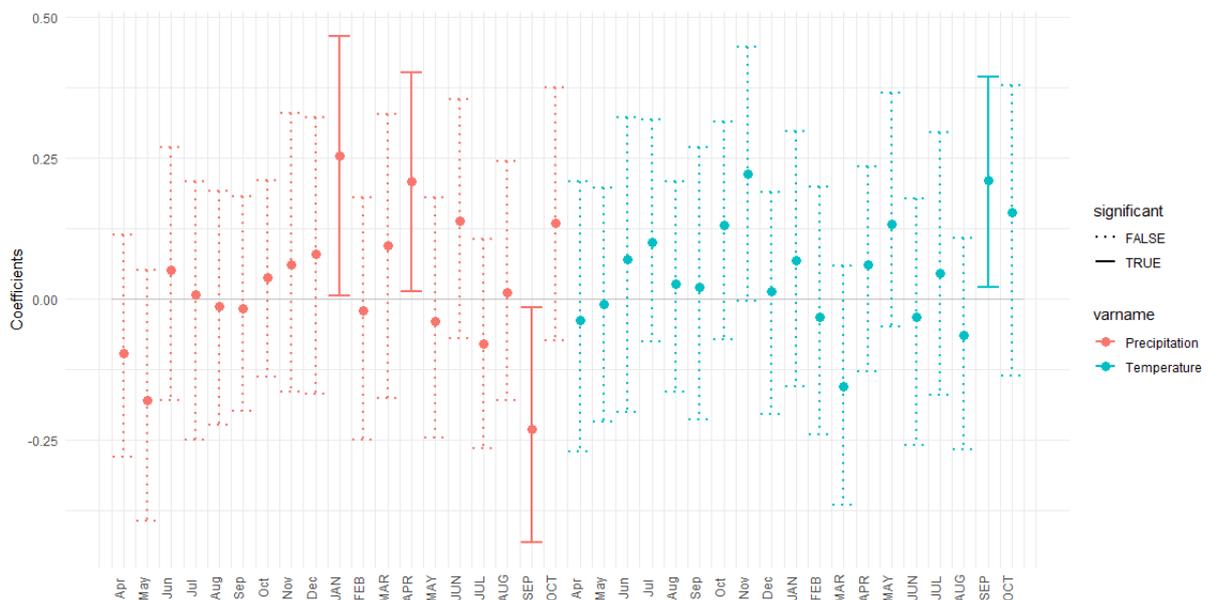
Figure 10: Response function of the 9 living mountain pines, total precipitation and mean temperature of plot 2 in the Entlebuch biosphere reserve See description of figure 7.

The growth of the mountain pines in plot 3 responded positively to the current January snow accumulation and April precipitation and negatively to the current September precipitation (see Figure 11). This indicates that the growth of the sampled living mountain pines in plot 3 increased when precipitation in the current January was high and when precipitation in the current September was low.
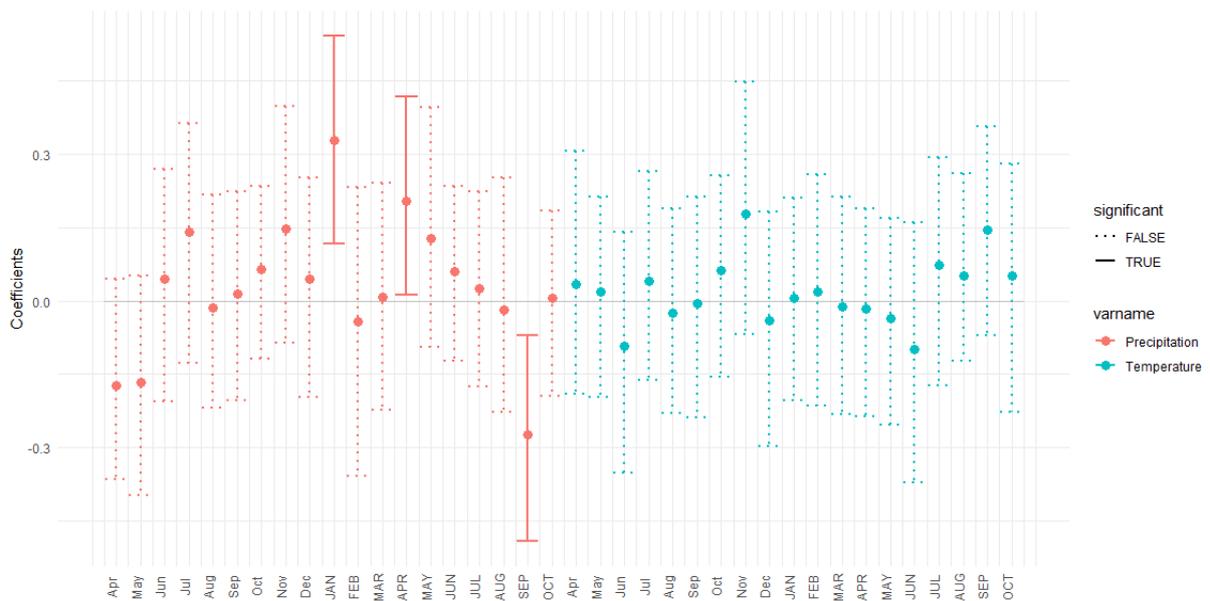
Figure 11: Response function of the 9 living mountain pines, total precipitation and mean temperature of plot 3 in the Entlebuch biosphere reserve See also legend description of Figure 7.

Overall, if the response function is calculated with all 24 sampled living mountain pines of plot 1 to 3 together, the current January snow accumulation is positively and current September precipitation is negatively correlated with the growth of the mountain pines (see Figure F.1). The current September temperature has like in in the response function of plot 2 a positive relationship with the growth of the mountain pines.

b   Norway spruce (*Picea abies*)

The mean growth of all 26 sampled living Norway spruces of plot 4 to 5 correlated mostly with the total monthly precipitation of the months April to September (see Figure 12). In the months of April and August, however, the growth of Norway spruces increased significantly between the years 1985 and 1990, although the total precipitation decreased in this years. The same pattern was see in the months May and August between the years 2001 and 2005 and in July between the years 2003 and 2005. In the months April to July the total monthly precipitation in total decreased after 2011 and the growth of the Norway spruces significantly increased after 2011.
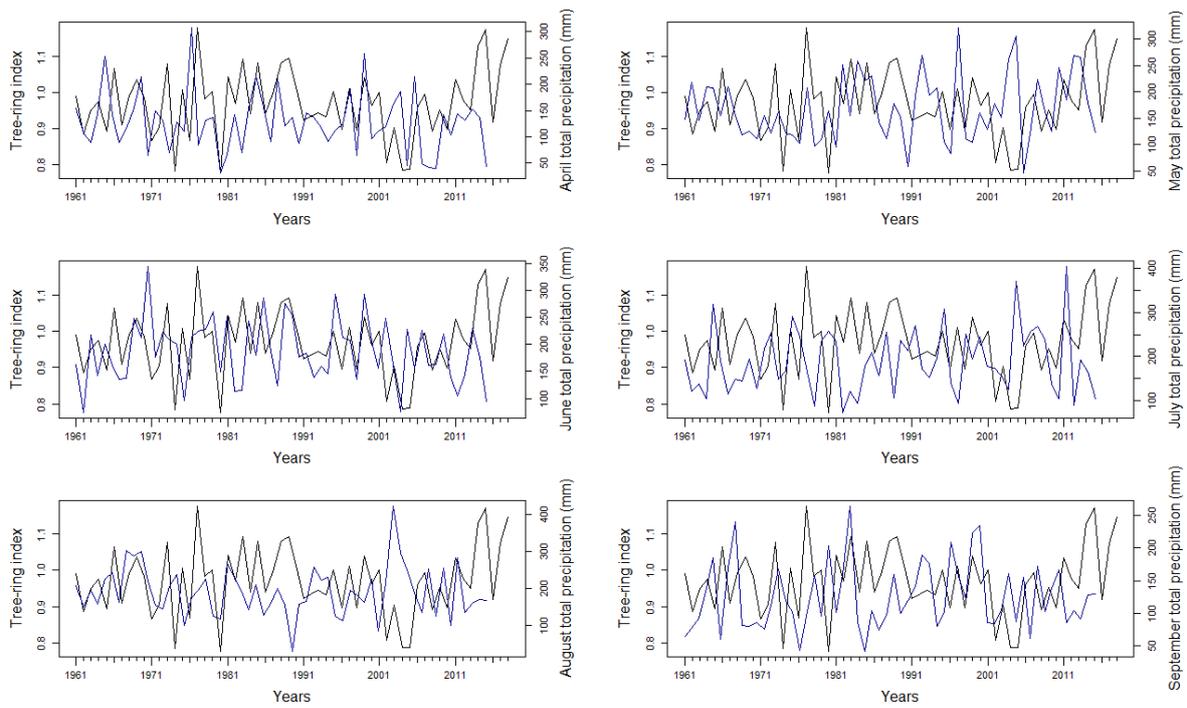
Figure 12: Relationship of the detrended chronologies of all 26 sampled living Norway spruces (in black) and total monthly precipitation of the months April to September between 1961 and 2018 (in blue).

The 26 sampled living Norway spruces of plot 4 to 5 reacted overall rather negatively to the rising temperature (see Figure 13). In the months April and June between 1980 and 1990 and in all months (except August) between the years 2000 and 2005 the growth of the Norway spruces significantly decreased while the mean monthly temperatures significantly increased in these years.
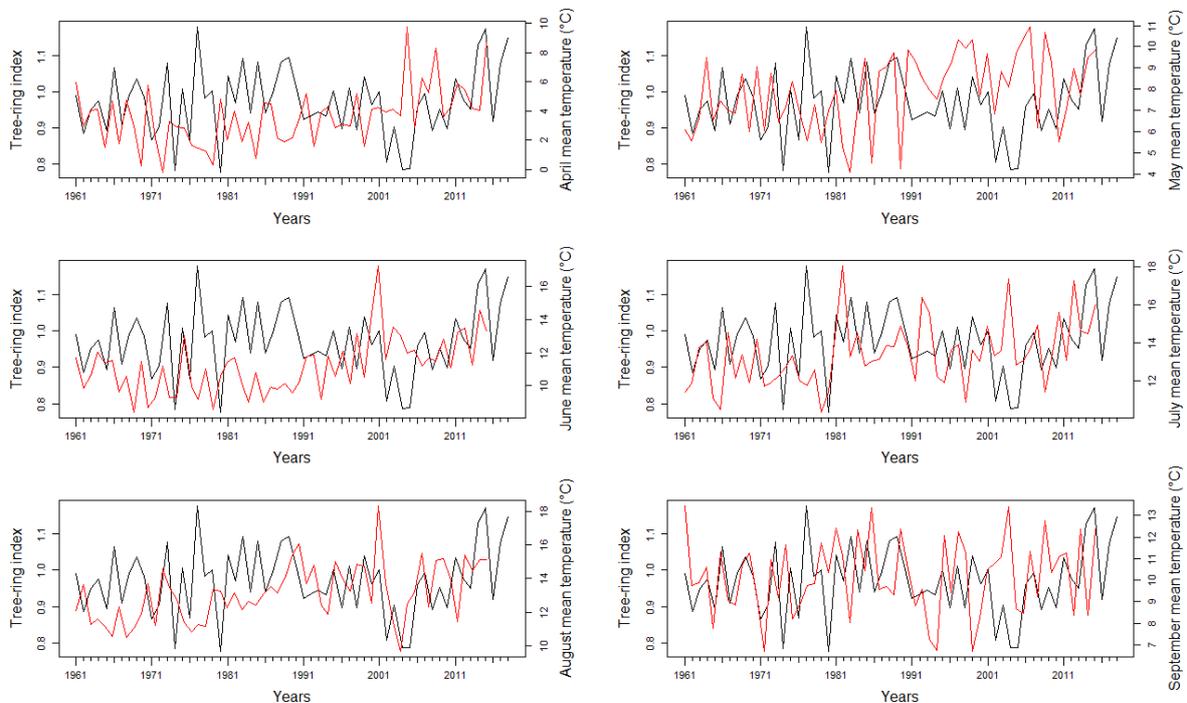
Figure 13: Relationship of the detrended chronologies of all 26 sampled living Norway spruces (in black) and mean monthly temperature of the months April to September between 1961 and 2018 (in blue).

The sampled living Norway spruces in plot 4 responded positively to current February precipitation and current October temperatures (see Figure 14). Accordingly, the high snow accumulation at the beginning of the current year and high temperatures at the end of the current year favoured the growth of the mountain pines in plot 4.
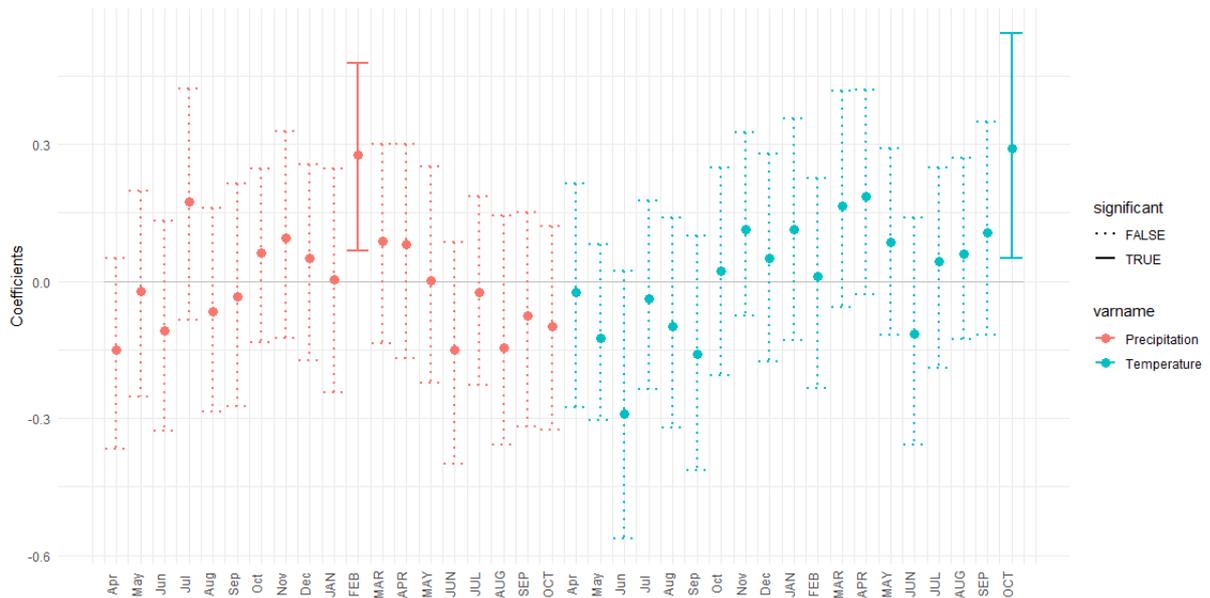
Figure 14: Response function of the 10 living Norway spruces, total precipitation and mean temperature of plot 4 in the Entlebuch biosphere reserve. See also legend description of Figure 7.

The precipitation of the current and previous years did both not significantly influenced the growth of the sampled living Norway spruces in plot 5 (see Figure 15). Previous May and August temperatures were, however, negatively related to the growth of the Norway spruces in plot 5. Consequently, these Norway spruces grew better, when the temperatures in May and August of the previous year were low.
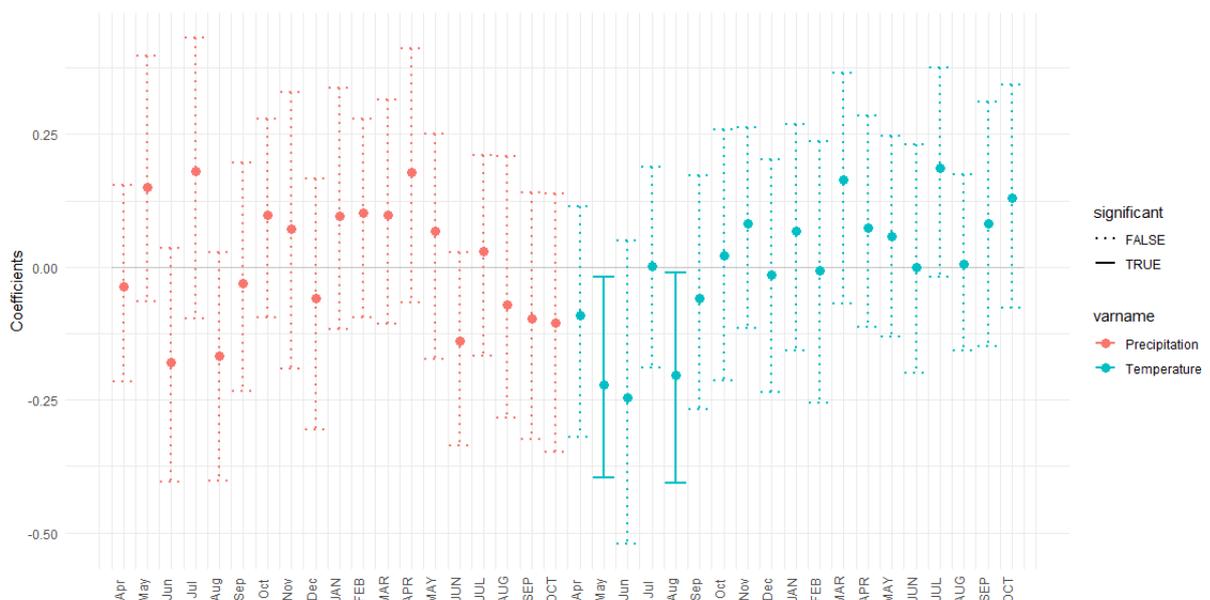
Figure 15: Response function of the 10 living Norway spruces, total precipitation and mean temperature of plot 5 in the Entlebuch biosphere reserve. See also legend description of Figure 7.

If the response function is calculated with all 20 sampled living Norway spruces of plot 4 and 5, only the current October temperature is positively correlated with the growth of the Norway spruces (see Figure F.2). As the calculated response function is identical as that of plot 4 and plot 5 has different results, no clear pattern can be identified between the climate and the growth of Norway spruces in the Entlebuch biosphere reserve. For the living Norway spruces in plot 1 to 3 (see Figure F.3), as well no significant relationship was found between the climate and growth.

2. When did the trees die?

a   Mountain pine (*Pinus montana*)

The second research question investigated when the sampled dead mountain pines and dead Norway spruces died. The mortality of mountain pines increased in 2001, reached its maximum in 2004, and declined thereafter. The majority of the Norway spruces died in the year 2003 and the following year 2004. The sampled mountain pines in plot 1 died between 1952 and 2018, in plot 2 between 1943 and 2017, and in plot 3 between 1996 and 2019. Each of the plots 1 to 3 had between three to five mountain pines which died before 2000 and after 2010 (see Figure 16).
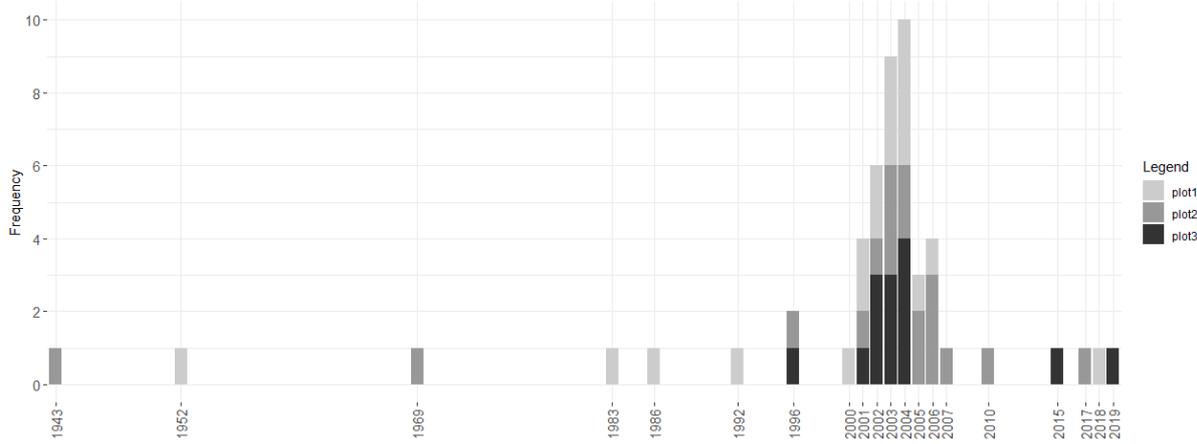
Figure 16: Bar chart of the approximate death year of the sampled dead mountain pines in plot 1-3

b   Norway spruce (*Picea abies*)

The approximate death years of the Norway spruces were more widely spread and start increasing in the year 2000. The sampled Norway spruces in plot 4 died between 1980 and 2019 and in plot 5 between 1984 and 2008. Only one of the sampled Norway spruces of plot 5 has already died in 1958. However, the majority of the Norway spruces died in 2003. After that, the mortality of Norway spruces declined (see Figure 17).
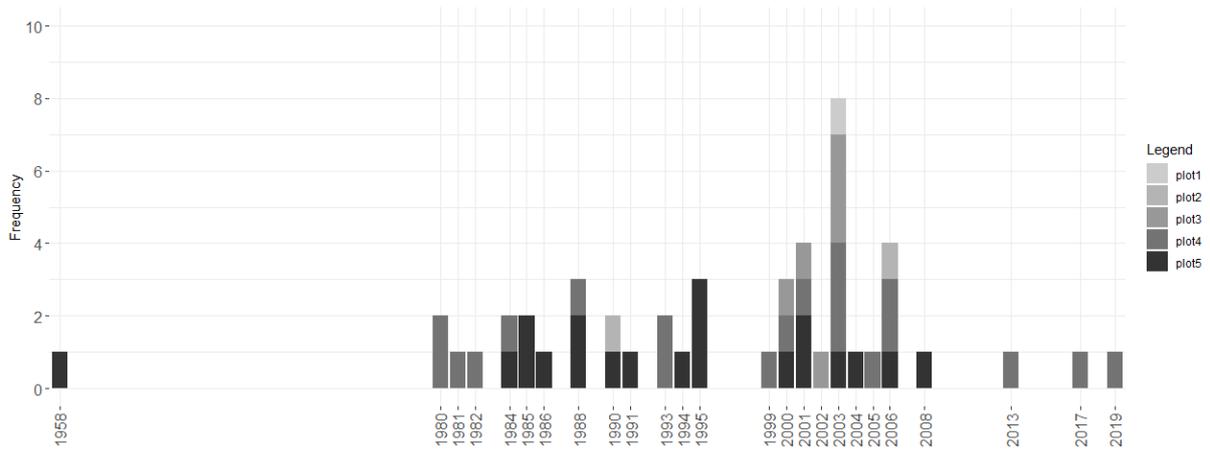
Figure 17: Bar chart of the approximate death year of the sampled dead Norway spruces of plot 1-5. For the sake of completeness, this bar chart also includes the death year of the nine dead Norway spruces of plot 1-3.

3. What influenced the lifespan of the dead trees?

Of all sampled dead mountain pines, only 6% had a lifespan under 100 years and only 8% over 200 years. The majority of the dead mountain pines (86%) reached a lifespan between 100 and 200 years. None of the sampled dead mountain pines reached a lifespan over 300 years (see Figure 18). Of all sampled living mountain pines, 8% had in summer 2020 so far a lifespan under 100 years, 79% a lifespan between 100 and 200 years, and 13% a lifespan over 200 years (see Figure G.1).
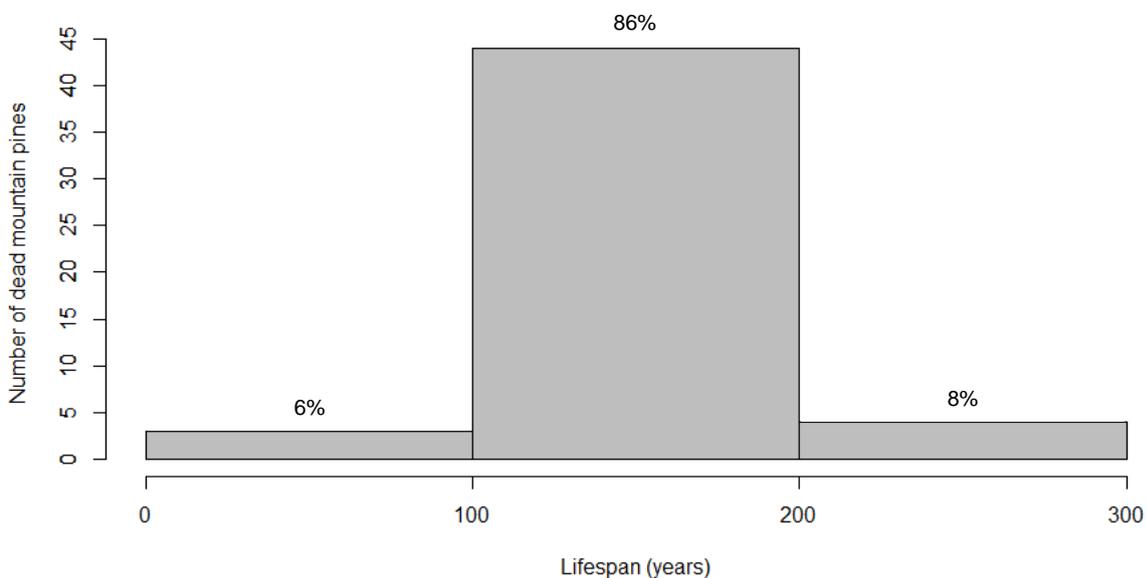
Figure 18: Histogram of the lifespan of all dead mountain pines of plot 1-3.

Of all sampled dead Norway spruces, only 4% had a lifespan under 100 years and 14% had a lifespan over 200 years. Only one Norway spruces reached a lifespan of over 300 years. The majority of all dead Norway spruces (82%) reached a lifespan between 100 and 200 years (see Figure 19). Of all sampled living Norway spruces, 15% had in summer 2020 so far a lifespan under 100 years and 85% a lifespan between 100 and 200 years (see Figure G.2).
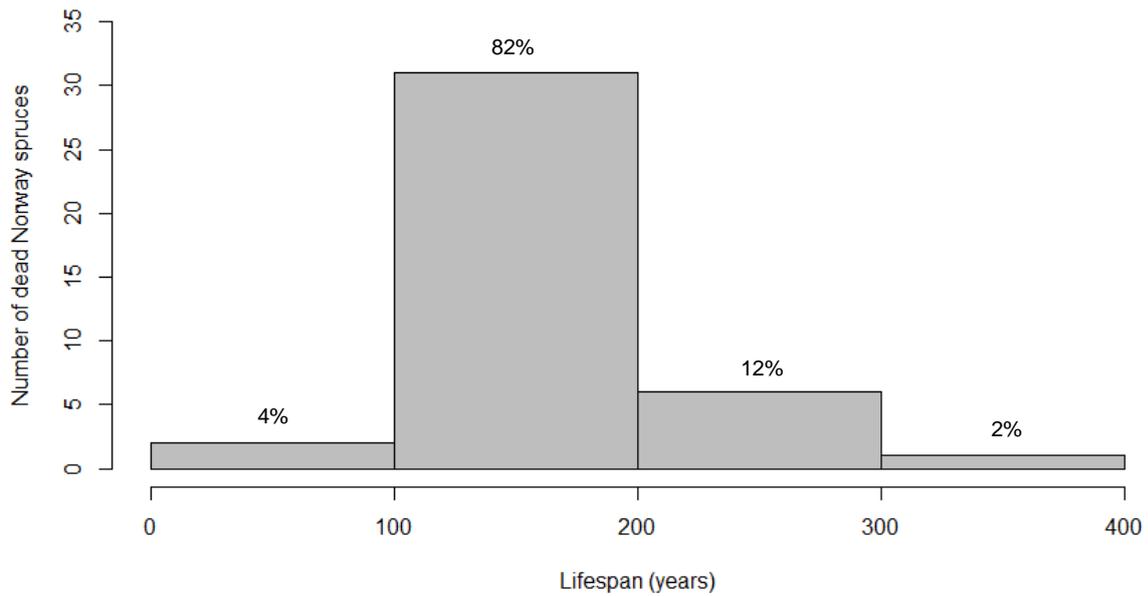
Figure 19: Histogram of the lifespan of all dead Norway spruces of plot 1-5.

The lifespan of the sampled dead mountain pines in plot 1 was between 82 and 190 years (see Figure E.2). The oldest dead mountain pine established in 1802, whereas the oldest living mountain pine established in 1838 (see Figure E.3). The growth of the sampled dead mountain pines was between the years 1900 and 1950 higher than around the year 2000. While the growth of the sampled dead mountain pines mostly decreased from 2000 onwards, the growth of some living mountain pines strongly increased from 2000 onwards (see Figure 20).
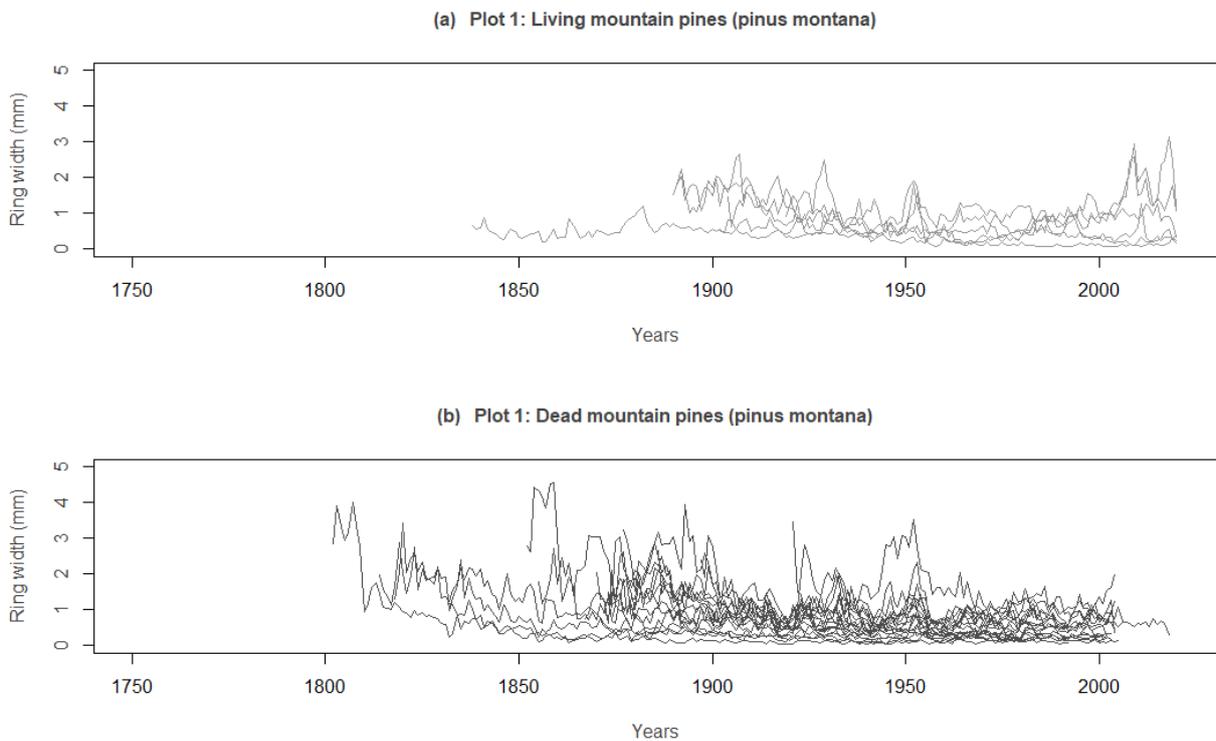
Figure 20: Time-series plots of the tree-ring widths of the (a) sampled living mountain pines and (b) dead mountain pines in plot 1.

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The lifespan of the sampled dead mountain pines in plot 2 was between 79 and 239 years (see Figure E.2). Thus, the oldest sampled dead mountain pine in plot 2 lived 49 years longer than the oldest sampled dead mountain pine in plot 1. This is the oldest mountain pine that has been found in this study. The growth of both the living and the dead mountain pines tended to decrease around the year 2000, with few exceptions (see Figure 21).
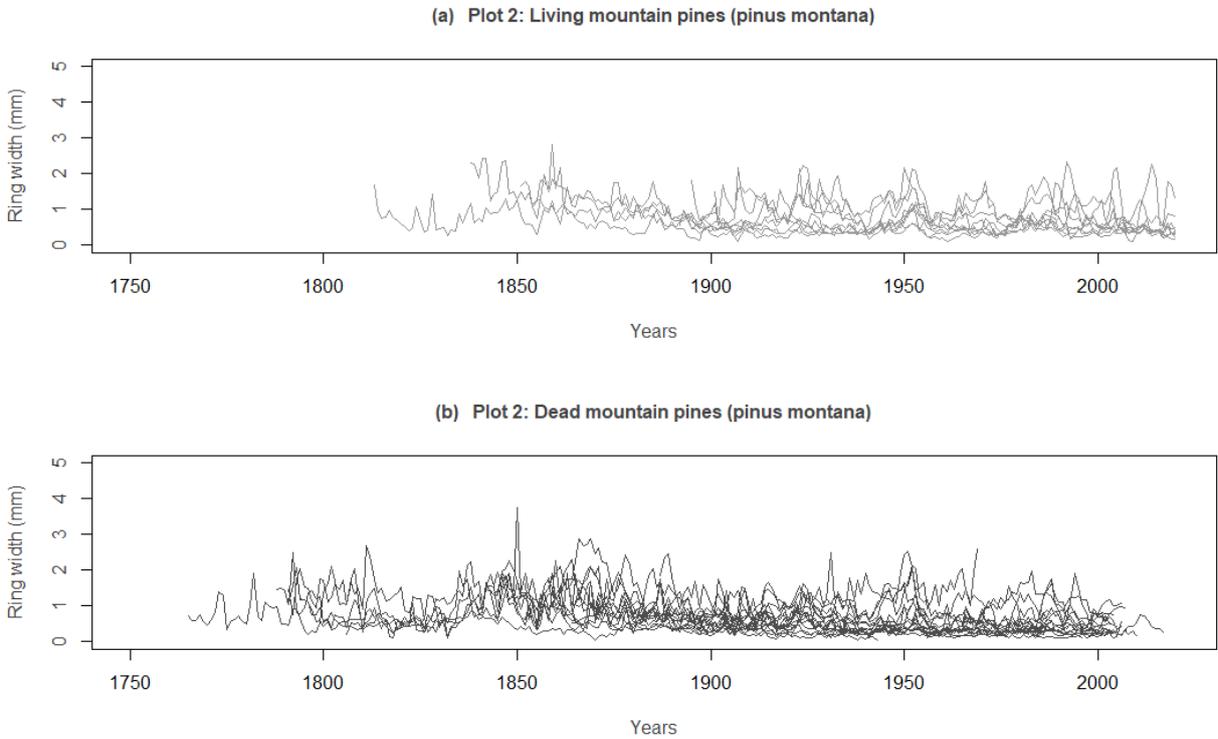
Figure 21: Time-series plots of the tree-ring widths of the (a) sampled living mountain pines and (b) dead mountain pines in plot 2.

The lifespan of the sampled dead mountain pines in plot 3 lied between 102 and 193 years (see Figure E.2). The mountain pine with the lowest lifespan, lived 20 years longer than the youngest mountain pine in plot 1 und 2. As in plot 1, none of the dead mountain pines lived over 200 years. In plot 3, there is only a minimal difference between the establishment of the sampled dead and the living mountain pines. In return, the growth of the sampled dead and living mountain pines differed after 1950: The growth of many living mountain pines increased and the growth of most dead mountain pines decreased (see Figure 22).

(a) Plot 3: Living mountain pines (pinus montana)

(b) Plot 3: Dead mountain pines (pinus montana)
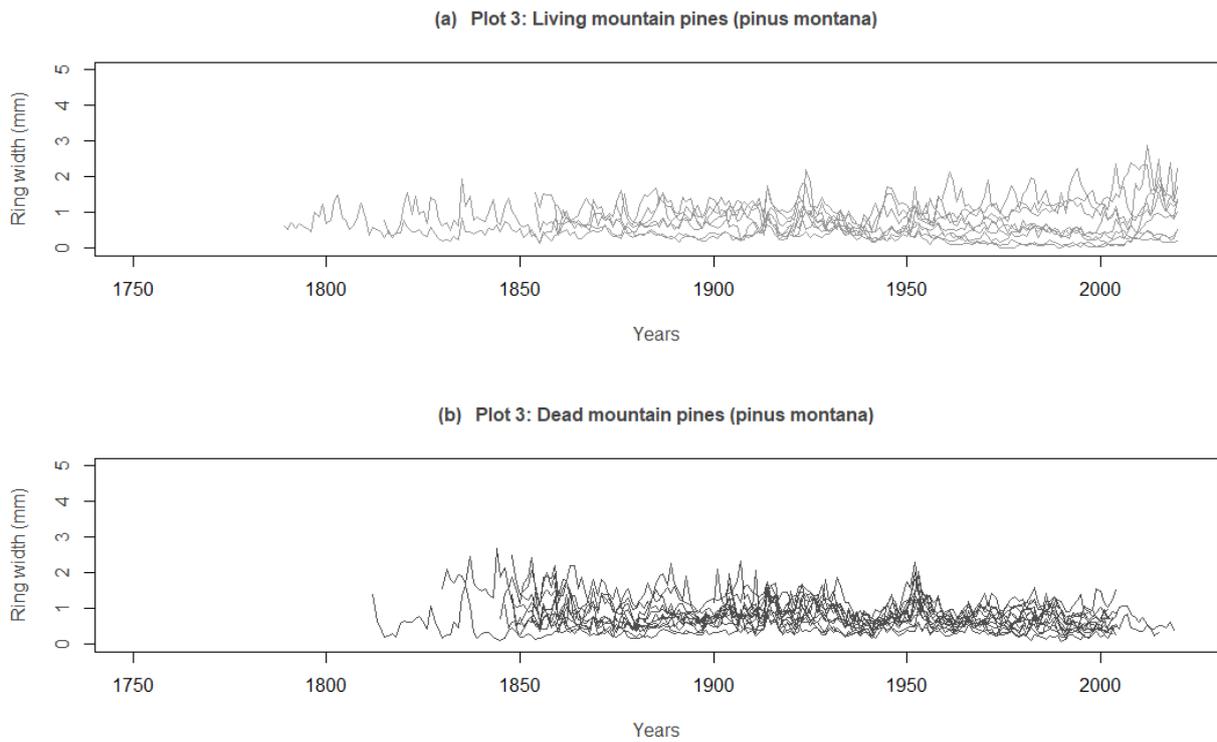
Figure 22: Time-series plots of the tree-ring widths of the (a) sampled living mountain pines and (b) dead mountain pines in plot 3.

The sampled dead Norway spruces in plot 4 lived between 92 and 267 years (see Figure E.2) and established between 1735 and 1926 (see Figure E.3). The sampled living Norway spruces established more recently compared to the dead Norway spruces, meaning between 1845 and 1956. The growth of most dead Norway spruces remained constantly low from 1950 onwards, with only one outlier (see Figure 23). The growth of the living Norway spruces increased remarkably after the year 2000.

(a) Plot 4: Living Norway spruces (picea abies)

(b) Plot 4: Dead Norway spruces (picea abies)
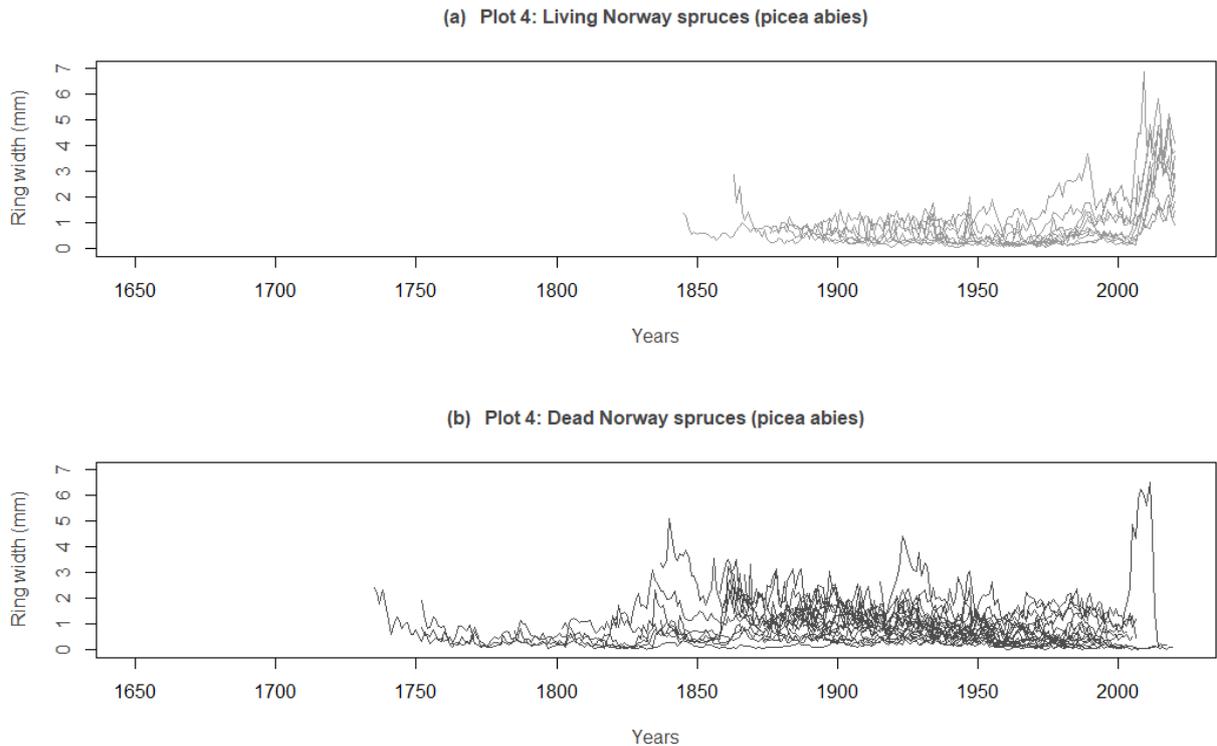
Figure 23: Time-series plots of the tree ring widths of the (a) sampled living Norway spruces and (b) dead Norway spruces in plot 4.

The sampled dead Norway spruces in plot 5 lived between 112 and 335 years (see Figure E.2). However, only one tree lived 335 years. This is likewise the oldest dead Norway spruce that has been found. The second and third oldest dead Norway spruce established in 1735 and 1738, and were found in plot 4 and 5. All the other living and dead Norway spruces in plot 5 established between 1830 and 1881 (see Figure E.3). As in plot 4, there was an increase in growth of the living Norway spruces and a decrease in growth of the dead Norway spruces after 2000 (see Figure 24). The time-series plots of the sampled Norway spruces of plot 1 to 3 can be found in Figures H1-H3.

(a) Plot 5: Living Norway spruces (picea abies)

(b) Plot 5: Dead Norway spruces (picea abies)
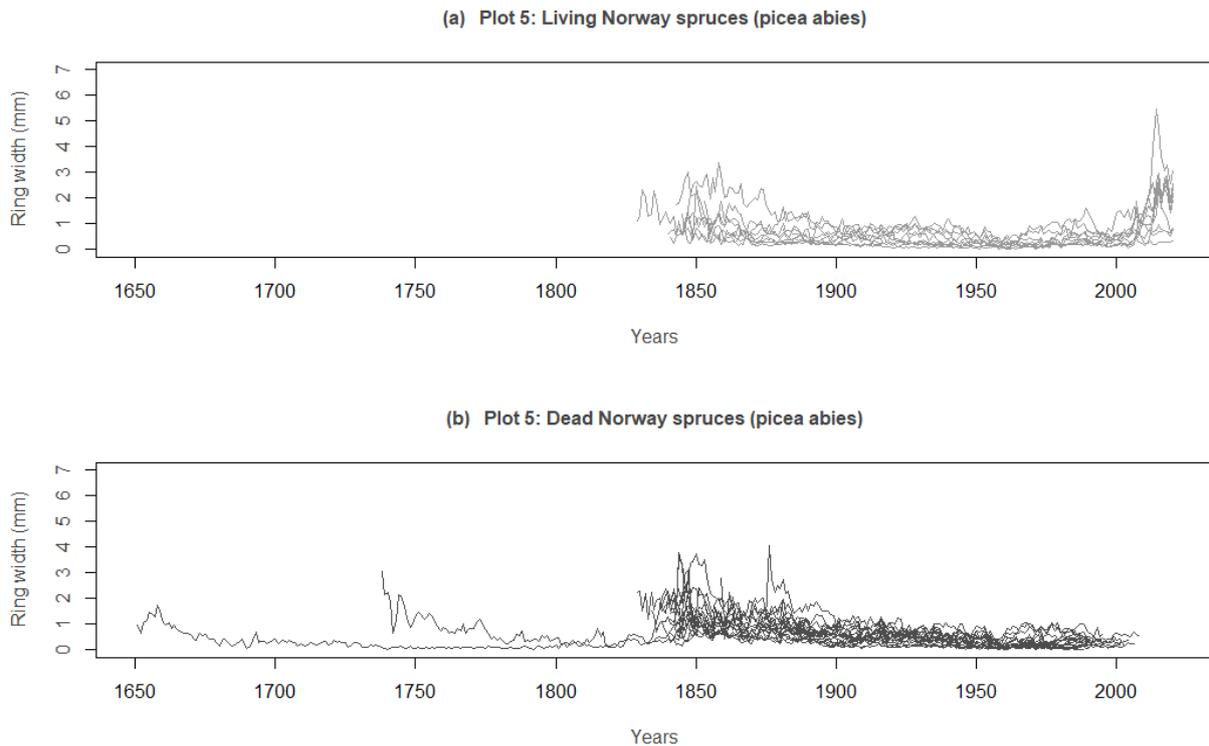
Figure 24: Time-series plots of the tree-ring widths of the (a) sampled living Norway spruces and (b) dead Norway spruces in plot 5.

To investigate whether the lifespan of the dead mountain pines respectively Norway spruces differed, the response variable of the linear model (LM) was lifespan and the independent variables were (1) early growth, (2) DBH, (3) plots, (4) number of neighbouring trees, (5) mean slope, and (6) sphagnum cover. All possible models with six independent variables were fitted for both of the two tree species separately. The AICc was calculated from the six best performing models. Out of these six models the best performing model is presented. Before the two best performing models are shown, the distribution of the response variable lifespan is described by time-series plots which show the tree-ring widths of the sampled tree species.

a   Mountain pine (*Pinus montana*)

The best performing model of the analysis of the mountain pines was model 5 (see Table 3). It indicated an effect between the response variable lifespan and the independent variables (1) DBH and (2) early growth. Accordingly, the variables (1) plot, (2) slope, (3) number of neighbouring trees, and (4) sphagnum cover did not seem to have a strong influence on the lifespan of the sampled dead mountain pines of plot 1 to 3.

Table 3: Model comparison with the p-value, AICc, and adjusted R^2 of the mountain pines. The response variable is lifespan.

Model	Variables	p-value	adjusted R^2	AICc
1	DBH + early growth + plot + slope + neighbours + sphagnum	0.1212	0.1187	519.67
2	DBH + early growth + plot + slope + neighbours	0.01347	0.1844	507.80
3	DBH + early growth + plot + slope	0.008781	0.2025	504.98
4	DBH + early growth + plot	0.004404	0.2127	502.74
5	**DBH + early growth**	**0.001572**	**0.204**	**500.44**
6	DBH	0.004976	0.1327	503.50

Notes: These are the six best performing linear models (LM) of the analyses of the lifespan of the dead mountain pines. The model with the lowest p-value and AICc, and the highest adjusted R^2 was the best performing model and is marked in bolt.

The relationship between the lifespan and DBH was positive. If the DBH increased by 1 cm, the lifespan increased by 3.6 years. The relationship between the lifespan and the early growth was negative. If the early growth increased by 1 mm, the lifespan decreased by 30.3 years. The significant p-values of the intercept and the two independent suggest to reject the null hypothesis.

Table 4: Details of Model 5 (lifespan ~ DBH + early growth) of the mountain pines

Parameters	Estimate	Standard Error	t-value	p-value	
(Intercept)	89.767	24.205	3.709	0.000540	***
DBH	3.620	1.003	3.608	0.000733	***
Early growth	-30.318	13.063	-2.321	0.024583	*

Notes: Levels of significance of the p-value: . $p < .1$, * $p < .05$, ** $p < .01$, *** $< .001$

The lifespan of the sampled dead mountain pines was affected by the DBH and early growth. On one the hand, the dead mountain pines with a higher DBH had a longer lifespan than those with a smaller DBH (see Figure 25a). On the other hand, the dead mountain pines that grew slower at the beginning of their life, had a longer lifespan than those that grew faster at the beginning of their life (see Figure 25b).
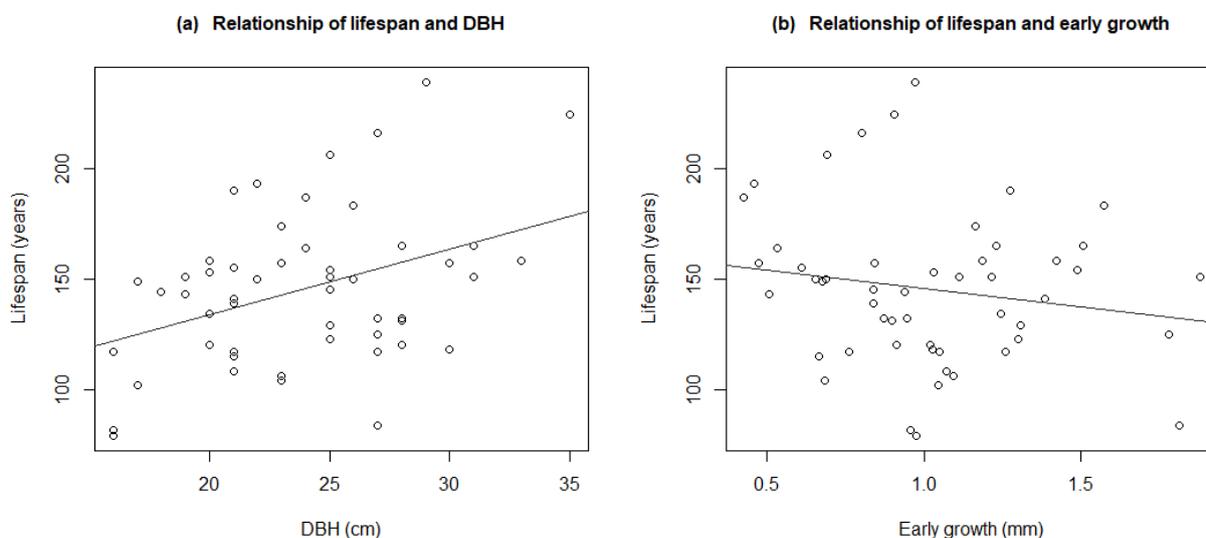
Figure 25: Relationship of the response variable lifespan and the independent variables (a) DBH and (b) early growth. Each point in each of the two plots represent one of the 51 sampled dead mountain pines. The regression line shows the relationship between the response and the independent variables.

b   Norway spruce (*Picea abies*)

The best performing model of the analysis of the Norway spruces was model 2 (see Table 5). In this model, all independent variables were included, except for the variables plot and slope. The lifespan of the sampled dead Norway spruces was thus influenced by (1) early growth, (2) DBH, (3) number of neighbouring trees, (4) sphagnum cover, and (5) plots.

Table 5: Model comparison with the p-value, AICc, and adjusted R^2 of the Norway spruces. The response variable is lifespan.

Model	Independent variables	p-value	adjusted R^2	AICc
1	early growth + DBH + neighbours + sphagnum + plot + slope	0.0001304	0.5209	422.02
2	early growth + DBH + neighbours + sphagnum + plot	4.879×10^{-5}	0.5355	418.25
3	**early growth + DBH + neighbours + sphagnum**	**3.594×10^{-5}**	**0.5252**	**416.82**
4	early growth + DBH + neighbours	4.042×10^{-5}	0.4234	417.06
5	early growth + DBH	5.084×10^{-5}	0.3823	418.29
6	early growth	0.001861	0.2071	426.87

Notes: These are the six best performing linear models (LM) of the analyses of the lifespan of the dead Norway spruces. The model with the lowest p-value and AICc, and the highest adjusted R^2 was the best performing model. This model is marked in bold.

The relationship of the lifespan and early growth is negative (see Table 6). This means that if the early growth increases by 1 mm, the lifespan decreases by 61.8 years. The DBH is positively associated to the lifespan. If the DBH increased by 1 cm, the lifespan increased by 2.4 years. The lifespan is negatively related to the number of neighbouring trees and the sphagnum densities. When the number of neighbouring trees increased by one tree, the lifespan decreased by 5.4 years. However, the sphagnum cover of 50-75% (category 3) did not influence the lifespan of the Norway spruces as negatively as the other three sphagnum categories. In addition, the dead Norway spruces in plot 5 had, on average, a 21.3 years longer lifespan than the dead Norway spruces in plot 4. The significant p-value of the (1) intercept, (2) early growth and (3) DBH, (4) number of neighbouring trees, (5) sphagnum category 1 (0-25%) and category 4 (75-100%) suggest to reject the null hypothesis.

Table 6: Details of Model 3 (lifespan ~ early growth + DBH + neighbours + sphagnum) of the Norway spruces

Parameters	Estimate	Standard Error	t-value	p-value	
(Intercept)	240.7325	40.9850	4.995	2.18×10^{-5}	***
Early growth	-61.7912	13.8205	-4.471	0.000103	***
DBH	2.4042	0.8891	3.457	0.002587	***
Neighbours	-7.2037	2.6703	-2.063	0.003323	**
Sphagnum1	-49.2771	15.9861	-3.314	0.002696	**
Sphagnum2	-31.9555	25.0262	-1.591	0.215405	
Sphagnum3	-1.3057	41.6953	-0.091	0.974856	
Sphagnum4	-60.71	29.5590	-1.929	0.049591	*

Notes: The reference level of the factor sphagnum is category zero (0% sphagnum 1 m around the sampled dead Norway spruce).

Levels of significance of the p-value: . $p < .1$, * $p < .05$, ** $p < .01$, *** $< .001$

Norway spruces in plot 4 and 5 that reached a higher lifespan (1) grew slower at the beginning of their life, (2) had a higher DBH, (3) had less neighbouring trees, and (4) had neither much nor little sphagnum around themselves (see Figure 26).
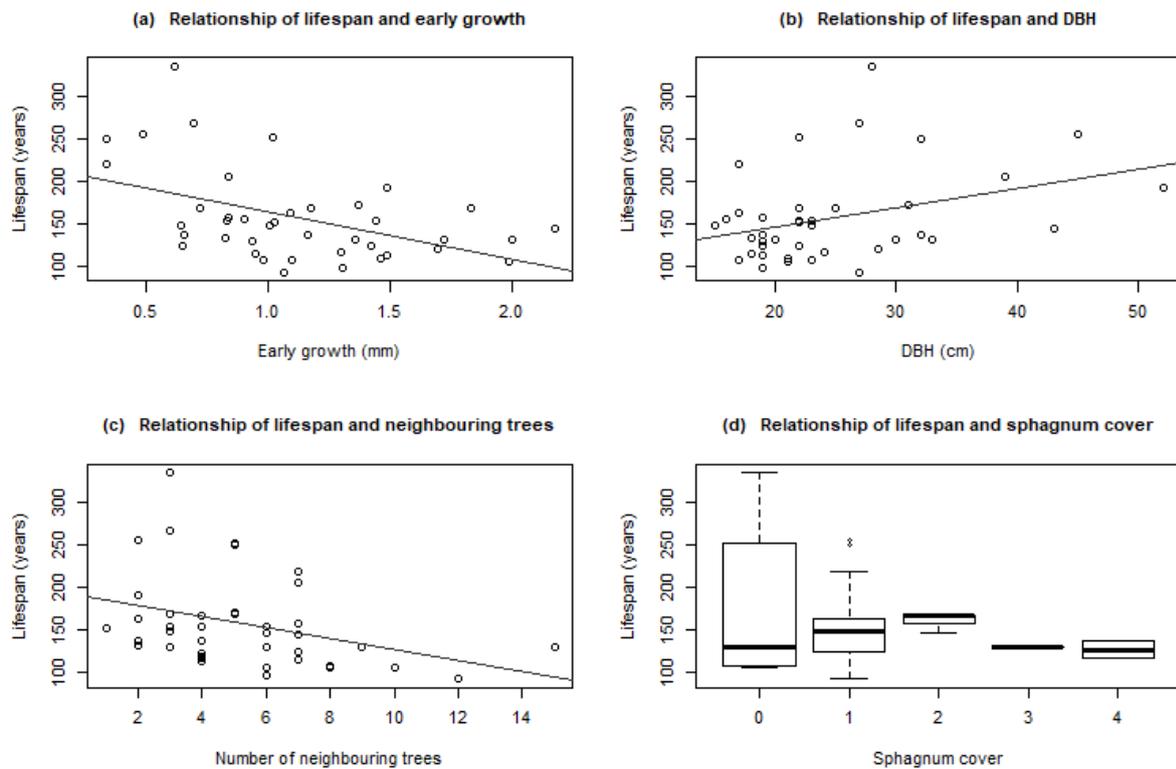
Figure 26: Relationship of the response variable lifespan and the independent variables (a) mean growth, (b) DBH, (c) number of neighbouring trees, and (d) sphagnum cover. Each point of the plots a-c represent one of the 40 sampled dead Norway spruces. The regression line shows the relationship between the two variables. Each boxplot of the plot (d) shows one of the five category of the factorial variable sphagnum cover.

Fourth research question: Why are some trees dead while others are alive?

The fourth research question, which investigates why some mountain pines and Norway spruces are dead while others are alive, is analysed with a mortality model using logistic generalised linear mixed models (logit-GLM). The response variable in both models of the two species was the condition (living or dead) and the independent variables were (1) height, (2) recent growth, (3) DBH, (4) slope, (5) number of neighbouring trees, (6) plots, and (7) sphagnum cover.

a   Mountain pine (*Pinus montana*)

The AUC of the analyses of the mountain pines in plot 1 to 3 was between 0.825 and 0.976 (see Table 7). The best performing logit-GLM of the mountain pines has an AUC of 0.844 and includes the independent variables (1) height and (2) number of neighbouring trees.

Table 7: Comparison of the mortality models with the AUC and AICc of the mountain pines

Model	Independent variables	AUC	AICc
1	height + neighbours + recent growth + DBH + slope + lifespan + plot + sphagnum	0.876	90.77
2	height + neighbours + recent growth + DBH + slope + lifespan + plot	0.876	82.84
3	height + neighbours + recent growth + DBH + slope + lifespan	0.864	79.57
4	height + neighbours + recent growth + DBH + slope	0.862	77.32
5	height + neighbours + recent growth + DBH	0.853	75.57
6	height + neighbours + recent growth	0.844	73.90
7	**height + neighbours**	**0.843**	**73.58**
8	height	0.825	73.60

Notes: These are the eight best performing generalised mixed models (GLM) of the analyses of the lifespan of the mountain pines. The response variable was the condition (living = 0 or dead = 1), of which the condition living was set as the reference level. The independent variables were the (1) height, (2) number of neighbouring trees, (3) recent growth, (4) DBH, (5) slope, (6) lifespan, (7) plot, and (8) sphagnum cover. The model with the lowest AICc value was the best performing model. This model is marked in bold.

With an increase of the height by 1 m the mortality probability decreased by 0.51 (see Table 8). and increase of the number of neighbouring trees by one and 0.26. The low p-value of height was the only significant value and had the greatest influence on the mortality of the mountain pines in plot 1 to 3.

Table 8: Details of the Model 7 (condition ~ height + neighbours) of the mountain pines.

Parameters	Estimate	Standard Error	z-value	p-value	
(Intercept)	8.262	1.899	4.352	1.35×10^{-5}	***
Height	-0.514	0.137	-3.749	0.000177	***
Neighbours	-0.260	0.181	-1.439	0.150119	

The larger and the fewer neighbouring trees the samples dead mountain pines in plot 1 to 3 had, the lower was the mortality probability (see Figure 27).

Figure 27: Relationship of the response variable condition (living and dead) and the independent variable (a) height and (b) number of neighbouring trees.

b   Norway spruce (*Picea abies*)

The models of the Norway spruces of plot 4 to 5 had AUC values between 0.944 and 0.989 (see Table 9). The highest AUC value of 0.989 had model 1. However, this model has one of the highest AICc value and thus did not get selected as the best performing model. The model with the lowest AICc value is model 6, of which the AUC value of 0.982 is also rated as high. Model 6 included the independent variables (1) recent growth, (2) neighbouring trees, and (3) sphagnum cover.

Table 9: Comparison of the mortality models with AUC and AICc of the Norway spruces.

Model	Independent variables	AUC	AICc
1	recent growth + neighbours + sphagnum + DBH + lifespan + plot + slope + height	0.989	56.43
2	recent growth + neighbours + sphagnum + DBH + lifespan + plot + slope	0.988	54.10
3	recent growth + neighbours + sphagnum + DBH + lifespan + plot	0.985	53.33
4	recent growth + neighbours + sphagnum + DBH + lifespan	0.986	54.70
5	recent growth+ neighbours + sphagnum + DBH	0.981	52.38
6	**recent growth + neighbours + sphagnum**	**0.982**	**50.14**
7	recent growth + neighbours	0.944	50.74
8	recent growth	0.95	54.90

Notes: These are the eight best performing generalised mixed models (GLM) of the analyses of the lifespan of the Norway spruces. The response variable was the condition (living = 0 or dead = 1), of which the condition living was set as the reference level. The independent variables were the (1) recent growth, (2) number of neighbouring trees, (3) sphagnum cover, (4) DBH, (5) lifespan, (6) plot, (7) slope, and (8) height. The model with the lowest AICc value was the best performing model. This model is marked in bold.

If the recent growth increases by 1 mm the mortality probability decreases by 3.43 (see Table 10). If although the number of neighbouring trees increases by one the mortality probability increased by 0.66. The more the Norway spruces were covered by sphagnum, the lower was the mortality probability. The lowest mortality probability had the sphagnum cover category three (50-75%) with -5.80 followed by sphagnum cover category four (75-100%) with -1.10, and sphagnum cover category two (25-50%) with -0.57. The sphagnum cover categories one and zero increased the mortality probability.

Table 10: Details of the Model 6 (condition ~ recent growth + neighbours + sphagnum) of the Norway spruces.

Parameters	Estimate	Standard Error	z-value	p-value	
(Intercept)	1.7946	1.3767	1.304	0.192380	
Recent growth	-3.4304	0.9062	-3.786	0.000153	***
Neighbours	0.6656	0.2377	2.800	0.005110	**
Sphagnum1	0.3905	1.3795	0.283	0.777128	
Sphagnum2	-0.5796	1.6166	-0.359	0.719934	
Sphagnum3	-5.8032	2.4450	-2.373	0.019934	*
Sphagnum4	-1.1022	1.9750	-0.558	0.576782	

The sampled living Norway spruces of plot 4 to 5 had (1) a higher recent growth, (2) less neighbouring trees, and (3) a higher sphagnum cover than the dead Norway spruces (see Figure 28).
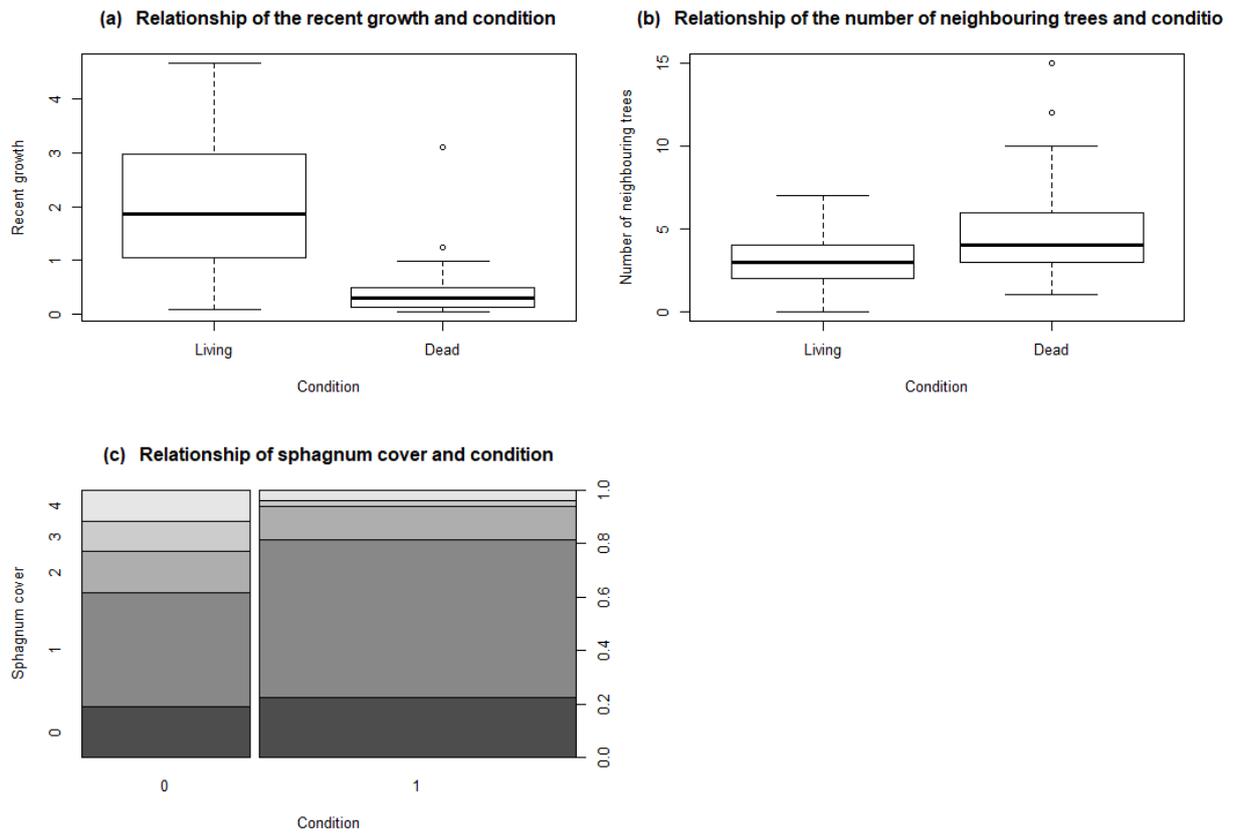
Figure 28: Relationship of the response variable condition (living and dead) and the independent variable (a) recent growth, (b) number of neighbouring trees, and (c) sphagnum cover.

4 DISCUSSION

In the Entlebuch biosphere reserve, the growth of the sampled living mountain pines and Norway spruces decreased significantly between 2000 and 2005, despite rising monthly mean temperatures. Tree mortality in the Entlebuch biosphere reserve was strongly influenced by the summer drought of 2003. The majority of sampled dead mountain pines and Norway spruces had a lifespan between 100 and 200 years. The dead mountain pines and Norway spruces that grew slowly at the beginning of their lives had the longest lifespan. The mortality probability of mountain pines decreased with increasing height and more neighbouring trees, whereas the mortality probability of the Norway spruces decrease with an increasing recent growth, fewer neighbouring trees and increasing sphagnum cover.

The results of the first research question, which analysed the influence of the temperature and precipitation on tree growth, only partially confirm the hypotheses that high temperatures and more precipitation in the growth season enhances tree growth. The living mountain pines in plot 1 to 3 was positively influenced by high snow accumulation in current January and low precipitation in current September. The positive correlation is the result of high snow accumulation that provide isolation during the cold winter months. In spring, the runoff of water during the snow melting supplies the living mountain pines with water that favours their growth. In contrast, the growth of the Norway spruces in plot 4 to 5 showed no common pattern. Previous studies on tree growth in peatbogs did as well not reveal a common pattern as tree growth in peatbog ecosystems is species- and site-specific (Edvardsson & Hansson 2015; Linderholm et al. 2002). This leads to the assumption that trees in peatbogs react differently to current climate fluctuations as they used to in the past (Speer 2010). However, upcoming studies should obtain more robust response function results by using ten to twenty instead of six to ten living trees.

The second research question, which investigated when the sampled mountain pines and Norway spruces in the Entlebuch biosphere reserve died, showed that the mortality of mountain pines and Norway spruces was the highest in 2003 and 2004. Although the present study only included standing trees with a low degree of decay, these findings clearly indicate that most of the tree species died due to the drought-induced stress during and after the summer 2003. A long term study revealed a clear pattern from the one century-long data set, namely that since 1960, tree mortality on mountain pines and Norway spruces increased significantly in Switzerland (Etzold et al. 2019). As in this study, especially the summer drought of 2003 damaged several forests in Switzerland (Beniston 2004; Etzold et al. 2019). All over the world drought-induced stress after heatwaves and high summer temperatures had led to increasing tree mortality in the 21th century (Allen et al. 2010; Greenwood et al. 2017; Williams et al. 2012).

The third research question, which examined the lifespan of the dead trees, revealed that the slow-growing dead trees of both species had a longer lifespan than the fast-growing dead trees. In addition, the lifespan of both species increased slightly with an increasing DBH: Based on these findings, the hypothesis can be accepted: Mountain pines and Norway spruces growing on peatbogs behave the same as the mountain pines and Norway spruces growing outside the peatbog (Bigler 2016; Castagneri et al. 2012; Rötheli et al. 2011). Moreover, the best fitting model showed that dead Norway spruces with fewer neighbouring trees had a higher lifespan. This is in line with various studies, in which the analyses showed that competition is one of the main triggers for the mortality of Norway spruces (Schmid et al.

2006, Peltoniemi & Mäkipää 2011). Due to the decreasing number of neighbouring trees, the light conditions improved, allowing for more light to be absorbed which influences growth and thus increases the lifespan of the surviving Norway spruces (Das et al. 2011; Schmid et al. 2006). For the dead Norway spruces, the lifespan additionally increased in case they had neither much nor little sphagnum cover. Thus, the hypothesis can only be partially accepted as the life span does not increase with decreasing sphagnum cover as previous studies (e.g., Dietze & Moorcroft 2011; Pawlik et al. 2013; Toledo et al. 2011) on vegetation and its influence on tree mortality predicted. This is probably mainly due to the different sphagnum mosses which grow on peatbog and seem to influence trees in a different way than other vegetation. As the energy exchange of the surface of peatbogs varies widely among different peatbog types (Alekseychik et al. 2018), I suspect that the sphagnum mosses and Norway spruces have a special interaction with each other. The sphagnum mosses may moisture the shallow-rooted Norway spruces in dry months. The slope did not seem to have influenced the growth of the sampled mountain pines and Norway spruce significantly. In the study of Toledo et al. 2011, the soil, slope and vegetation also did not significantly influence tree mortality.

The fourth research question, which investigated why some mountain pines and Norway spruces are dead while others are still alive, showed that the mortality probability of the mountain pines decreased with increasing height and more neighbouring trees. The mortality probability of the Norway spruces decrease with an increasing recent growth, fewer neighbouring trees and increasing sphagnum cover. This results suggest that the mortality probability is highly side- and species-specific and would need further investigations in order to come up with a final conclusion.

Apart from the investigated influences on tree mortality in the Entlebuch biosphere reserve, several other environmental impacts such as interactions with peat mosses and other plant species, animals, and insects might have additionally influenced tree mortality in peatbogs (Cailleret et al. 2019; Fritts 1976). With increasing temperature especially bark beetles outbreaks can cause huge forest damages (Raffa et al. 2015). Much of the conifer mortality in the 2000s was caused by bark-beetle attack (Williams et al. 2012). In Switzerland, bark beetle outbreaks on Norway spruces have increased since 2000 due to drought-induced stress and were significantly high during summer 2003 (Stadelmann et al. 2013, Stadelmann et al. 2014). Bark beetles do not usually kill their host but attack weakened trees whose defence mechanism no longer functions due to environmental or endogenous stress which then leads to death (Jonasova & Prach 2004; Raffa et al. 2015). In plot 4, bark beetle infested living and dead Norway spruces were detected but no samples of these discoveries were taken (see Figures I.1 and I.2). Given that the majority of the Norway spruces died in 2003, such bark beetle infestations are also likely to have had a considerable influence on the mortality of Norway spruces in the Entlebuch biosphere reserve.

If the balance of the trees in terms of the environment is disrupted, it is more likely that these trees are weakened and get diseases (Manion 1981). In a study on the spread of the brown spot disease on trees in Switzerland, the spread of fungal species on mountain pines and Norway spruces was detected in the Entlebuch biosphere reserve (Beenken et al. 2018). Such fungal infestations have not been seen on mountain pines and Norway spruces during summer 2020 at the sampling sites 1 to 3 but may have had an impact on the trees weakened condition. Two study of mountain pines in the Swiss National Park showed that the majority of the dead mountain pines were infected by different root diseases (Cherubini

et al. 2002; Dobbertin et al. 2001). These root diseases decreased the growth of the mountain pines for several decades or directly infected and killed the trees (Cherubini et al. 2002). In this study, no root samples were taken from the dead trees. As the growth of the sampled mountain pines and as well Norway spruces dropped suddenly in some years, this may indicate fungal and root diseases. This assumption would need to be investigated in more detail in future studies in the Entlebuch biosphere reserve.

As the trees in the Entlebuch biosphere reserve were exposed to various biotic and abiotic factors such as competition with neighbouring trees, sphagnum cover, bark beetle infestation, pathogens and the hydrology of the peatbog, I suspect that these trees will be further weakened and that future summer droughts might have an even stronger impact on tree mortality. Many common tree species in Switzerland and all over Europe became more vulnerable to extreme summer droughts and heat waves (Beniston 2004; Etzold et al. 2019; Schuldt et al. 2020). The summer drought of 2003 can be seen as an example for future summers in the coming decades (Beniston 2004). However, it should be noted that several mechanisms can cause tree mortality during drought (McDowell et al. 2008) such as the nutrient availability before droughts which are essential for the survival of a tree after the drought-induced stress (Gessler et al. 2017).

The tree mortality signalizes that the balance of the very sensitive peat moss forest is disturbed. Peatbog ecosystems are very sensitive to changes in the climate (Holden et al. 2007; Tarnocai 2006) because the upper peat layers depend primarily on precipitation, temperature, and evapotranspiration (Linderholm & Leine 2004). Peatbogs appear in regions where the climate is changing faster than anywhere else on earth (Dise 2009; Heijmans et al. 2013; Joosten 2017). Especially low water tables caused by climate change and droughts may increase the occurrence of trees and other vascular plants and lead to a shift in the dominant Sphagnum species (Breeuwer et al. 2009; Helbig et al. 2020; Minayeva & Sirin 2012; Riutta et al. 2007). This changes could reduce the productivity of the peat mosses (Bragazza et al. 2012). However, as moisture is a limiting factor for trees (Edvardsson & Hansson 2015), a rise in the water table in peat moss forests would mean that the roots of the trees would assimilate fewer nutrients, which in turn would weaken them (Edvardsson 2015; Linderholm & Leine 2004). How and whether these changes will positively or negatively affect peat moss forests in the future are important questions for future researches.

Despite the insights gained in this study, many research gaps remain on tree mortality in peatlands. For further studies I suggest including water level measurements of the peatbogs so that it can be recognized whether tree mortality in central Switzerland depends on the hydrology of peatbogs as well. Moreover, I recommend for further studies to sample tree cores of other peat moss forests in Switzerland where tree mortality has not yet occurred in order to detect early warning signals more rapidly. A better understanding of the tree mortality in peatbogs can help forest authorities, biosphere reserve managers, researchers, and policy makers to identify early warning signals. The discussed results of this study have shown that both tree species are vulnerable and can no longer defend themselves against environmental influences. This fact underlines the urgent need for future researches that examines further biotic and abiotic influences on tree mortality in peatbogs.

5 ACKNOWLEDGEMENTS

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7 APPENDIX

A *Plot selection*

Table A.1: All 10 plots and their center coordinates and elevation. The chosen plots are marked in bold.

Plot numbers	Chosen plots	Centrum Coordinates (CH1903)		Elevation (m) (100 m radius around the centrum coordinate)
		x-coordinate	y-coordinate	
1	**Plot 1**	**642686**	**184705**	**1,358.3 – 1,350.4**
2	**Plot 2**	**643818**	**184582**	**1,467.0 – 1,467.8**
3		643851	184250	1,495.7 – 1,496.8
4	**Plot 3**	**643237**	**183787**	**1,446.5 – 1,441.1**
5		645921	183939	1,454.1 – 1,457.2
6	**Plot 4**	**642006**	**183824**	**1,357.5 – 1'366.0**
7		641806	183752	1,352.7 – 1,362.6
8	**Plot 5**	**641975**	**184450**	**1,272.9 – 1,282.9**
9		642217	184308	1,301.4 – 1,303.9
10		642321	184084	1,315.8 – 1,321.2
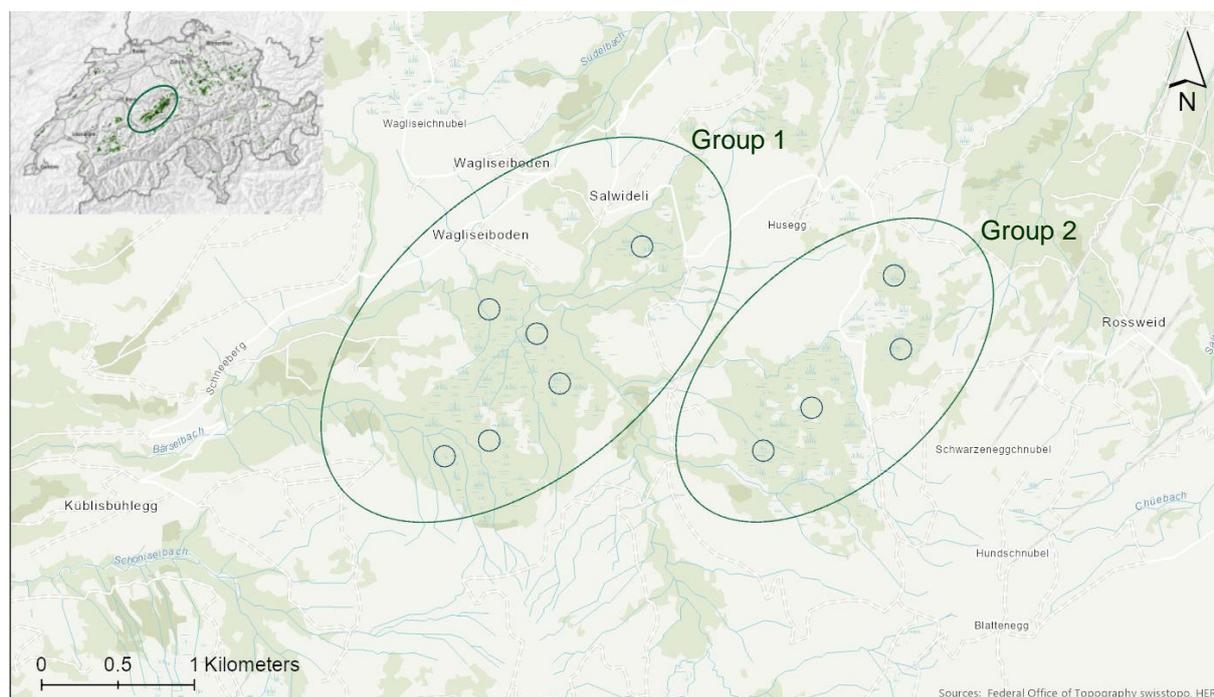
Figure A.2: The location of all 10 plots where tree mortality in the Entlebuch biosphere reserve is present. From the first group, three of the six possible sampling sites were selected. From the second group, two of the four possible sampling sites were selected.

B Correlation of the time-series by segments

Table B.1: COFECHA Output of the correlations of the time-series by segments of all mountain pines

```
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Correlations of  50-year dated segments, lagged  25 years
Flags:  A = correlation under    .3281 but highest as dated;  B = correlation higher at other than dated position
```

Seq	Series	Time_span	1775 1824	1800 1849	1825 1874	1850 1899	1875 1924	1900 1949	1925 1974	1950 1999	1975 2024
1	p1_lt1	1890 2020					-.15B	-.17B	-.13B	-.12B	-.10B
2	p1_lt3	1902 2020						.42	.46	.38	.33A
3	p1_lt5	1838 2020			-.26B	-.29B	-.34B	-.20B	.19B	.33	.11B
4	p1_lt8	1891 2020					-.10B	-.32B	-.27B	-.05B	.05B
5	p1_lt9	1904 2020						.29B	.42	.33A	.22B
6	p1_lt10	1919 2020						.55	.52	.34B	.19A
7	p1_dt11	1883 2002					.47	.32B	.38	.62	.56
8	p1_dt13	1921 2004						.39	.28B	.20B	.08B
9	p1_dt14	1890 2004					.23B	.49	.49	.44	.37
10	p1_dt15	1897 2004					.41	.45	.52	.43	.35
11	p1_dt16	1886 2002					.33A	.44	.45	.32A	.38
12	p1_dt17	1877 2001					.63	.65	.52	.45	.43
13	p1_dt18	1852 1992				-.09B	.14B	.34	.28A	.36	
14	p1_dt19	1802 1952		.60	.60	.41	.31A	.20B	.24B		
15	p1_dt20	1873 2004				.17B	.20B	.68	.68	.38	.27A
16	p1_dt21	1832 2018			-.20B	-.13B	.03B	.15B	.31A	.22B	.14B
17	p1_dt22	1925 2006							.44	.58	.35
18	p1_dt23	1878 1983					.13B	.36	.41	.30B	
19	p1_dt24	1855 2005				.22B	.44	.69	.72	.50	.44
20	p1_dt25	1870 2003				.26A	.39	.33A	.50	.46	.38
21	p1_dt26	1818 2000		.67	.66	.54	.29A	.15B	-.03B	-.06B	-.04B
22	p1_dt27	1814 2003		.68	.67	.66	.54	.54	.58	.46	.29A
23	p1_dt28	1867 1986				.24A	.29A	.33	.34	.33B	
24	p1_dt29	1873 2001				.33	.34	.55	.60	.36	.35
25	p1_dt30	1872 2003				.28A	.29A	.39	.50	.43	.37
26	p2_lt31	1838 2020			.13B	.14B	.52	.35	.41	.59	.49
27	p2_lt32	1895 2020					.40	.43	.62	.48	.34
28	p2_lt33	1901 2020						.34	.40	.20B	.13B
29	p2_lt34	1892 2020					.58	.60	.72	.26B	.13B
30	p2_lt35	1923 2020						.63	.66	.59	.42
31	p2_lt37	1854 2020				.21B	.25B	.43	.40	.47	.54
32	p2_lt38	1851 2020				.48	.26B	.23B	.51	.54	.55
33	p2_lt39	1875 2020					.38	.41	.48	.41	.25A
34	p2_lt40	1813 2020		.47	.53	.64	.50	.46	.50	.37	.28A
35	p2_dt41	1902 2005						.49	.64	.51	.42
36	p2_dt42	1890 2006					.31A	.52	.62	.59	.61
37	p2_dt43	1858 2006				.21B	.50	.55	.60	.43	.37
38	p2_dt44	1864 2006				.32A	.43	.50	.48	.37	.34
39	p2_dt45	1806 1969		.43	.40	.23B	.26A	.11B	.22A		
40	p2_dt46	1877 2007					.28B	.53	.45	.38	.46
41	p2_dt47	1791 1996	-.30B	-.23B	-.16B	-.07B	.26A	.32A	.06B	.02B	
42	p2_dt48	1844 2001			.53	.45	.19B	.47	.45	.41	.33
43	p2_dt49	1846 2010			.31A	.27A	.18B	-.01B	.18B	.25B	.24B
44	p2_dt50	1925 2003							.46	.40	.37
45	p2_dt51	1791 1943	.41	.67	.44	.40	.35	.03B			
46	p2_dt53	1864 2002				.34	.43	.39	.50	.55	.48
47	p2_dt54	1852 2005				.40	.39	.46	.48	.38	.40
48	p2_dt55	1861 2004				.29A	.41	.58	.72	.58	.58
49	p2_dt56	1788 2003	-.02B	.40	.57	.57	.54	.39	.54	.58	.54
50	p2_dt57	1765 2003	.19B	.40	.54	.40	.48	.09B	-.10B	-.08B	-.23B
51	p2_dt58	1794 2017	.54	.59	.59	.63	.38	.52	.57	.52	.58
52	p2_dt59	1887 2004					.30A	.47	.72	.61	.54
53	p3_lt61	1854 2020				.48	.38	.34	.54	.34	.04B
52	p2_dt59	1887 2004					.30A	.47	.72	.61	.54
53	p3_lt61	1854 2020				.48	.38	.34	.54	.34	.04B
54	p3_lt63	1859 2020				.51	.41	.47	.52	.40	.36
55	p3_lt64	1875 2020					.34	.54	.50	.37	.19B
56	p3_lt65	1881 2020					.42	.31B	.16B	.25B	.43
57	p3_lt66	1815 2020		.56	.54	.35	.34	.59	.37	.31A	.45
58	p3_lt67	1854 2020				.54	.42	.35B	.47	.51	.27A
59	p3_lt68	1919 2020						.24A	.14B	.03B	.38
60	p3_lt69	1789 2020	.21A	.36	.63	.39	.29A	.53	.39	.32A	.30A
61	p3_lt70	1949 2020							.29A	.27A	.22B
62	p3_dt75	1848 2004			.51	.51	.63	.69	.43	.26A	.29B
63	p3_dt76	1848 2004			.66	.65	.48	.46	.52	.52	.44
64	p3_dt77	1900 2001						.39	.41	.34	.35
65	p3_dt78	1812 2004		.43	.35	.28A	.21B	.38	.45	.39	.36
66	p3_dt79	1882 2004					.58	.61	.60	.58	.47
67	p3_dt80	1859 2003				.49	.44	.61	.54B	.47	.48
68	p3_dt81	1903 2019						.30A	.70	.40	.28B
69	p3_dt82	1851 2015				.72	.70	.62	.59	.61	.62
70	p3_dt83	1830 2003			.54	.50	.46	.72	.60	.56	.46
71	p3_dt84	1854 2003				.52	.39	.36	.46	.51	.48
72	p3_dt85	1853 2002				.57	.41	.52	.65	.58	.49
73	p3_dt86	1845 2002			.60	.57	.41	.48	.44B	.52	.53
74	p3_dt89	1846 1996			.19A	.28A	.55	.71	.79	.41	
75	p3_dt90	1848 2002			.24A	.22A	.23B	.43	.34	.28A	.18B
Av segment correlation			.17	.46	.40	.36	.35	.40	.44	.38	.34

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Table B.2: COFECHA Output of the correlations of the time-series by segments of all Norway spruces

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Correlations of  50-year dated segments, lagged  25 years
Flags:  A = correlation under   .3281 but highest as dated;  B = correlation higher at other than dated position

Seq Series  Time_span   1725 1750 1775 1800 1825 1850 1875 1900 1925 1950 1975
                        1774 1799 1824 1849 1874 1899 1924 1949 1974 1999 2024
--- -------- ---------- ---- ---- ---- ---- ---- ---- ---- ---- ---- ---- ---- .
   1 p1_lt2    1878 2020                                  .53  .39  .41  .42  .47
   2 p1_lt4    1907 2020                                       .12B .40B .25B .07B
   3 p1_lt6    1856 2020                             -.07B .04B .14B .12B-.05B-.10B
   4 p1_lt7    1890 2020                                  -.07B .05B .09B-.02B-.08B
   5 p1_dt12   1901 2003                                       .19A .29B .45  .43
   6 p2_lt36   1934 2020                                            .40  .45  .25A
   7 p2_dt52   1791 1990             .06B .16B .05B .03B .00B .07B .26B .19B
   8 p2_dt60   1841 2006                        .14B .15B .10B .14B .45  .14B .00B
   9 p3_lt62   1866 2020                             .13B .17B .18A .30B .42  .42
  10 p3_dt71   1848 2003                        .20B .19B .05B .14B .18B .13B .10B
  11 p3_dt72   1851 2001                             .07B .21A .41  .30A .08B .11B
  12 p3_dt73   1872 2003                             .12B .13B .29B .04B-.01B-.01B
  13 p3_dt74   1902 2000                                       .10B .25B .30B .30B
  14 p3_dt87   1881 2002                                  .20B-.07B .08B .17B .09B
  15 p3_dt88   1857 2003                             .00B .01B .21B .25B .27A .24B
  16 p4_lt91   1886 2020                                  -.12B-.11B .24B .48  .61
  17 p4_lt92   1881 2020                                  .51  .60  .61  .56  .55
  18 p4_lt93   1845 2020                             -.28B-.31B .10B .29B .24B .37  .41
  19 p4_lt94   1893 2020                                  -.17B-.18B .19B .31A .58
  20 p4_lt95   1927 2020                                            -.16B .16B .60
  21 p4_lt96   1876 2020                                  -.10B-.18B .31B .54  .51
  22 p4_lt97   1863 2020                             .47  .29A .30B .49  .51  .53
  23 p4_lt98   1956 2020                                                 -.01B .27B
  24 p4_lt99   1929 2020                                            .01B .21B .67
  25 p4_lt100  1901 2020                                       -.25B .03B .41  .56
  26 p4_dt101  1785 2003        .00B .13B .09B .00B .45  .42  .25A-.09B-.25B
  27 p4_dt120  1858 1981                             .07B .34  .46  .49  .41
  28 p4_dt102  1752 2000        .15B .31A .22B .02B .31A .42  .42  .45  .43  .44
  29 p4_dt103  1802 2006             .28A .39  .38  .59  .57  .46  .37  .17B
  30 p4_dt104  1735 2001   -.04B-.16B .12B .03B-.05B .01B-.07B-.01B .36  .45  .48
  31 p4_dt105  1752 2006        .09B .26A .16B .03B .32A .43  .40  .32B .24B .16B
  32 p4_dt106  1867 2003                             .00B .14B .47  .54  .37  .37
  33 p4_dt107  1815 2005                   -.03B .13B .42  .50  .42  .52  .65  .53
  34 p4_dt108  1888 1993                                  .43  .37  .06B-.22B
  35 p4_dt109  1837 1984                             .47  .57  .61  .52  .36  .20B
  36 p4_dt110  1885 2013                                  .33  .22B .33  .32A .24B
  37 p4_dt111  1837 1980                             .00B .06B .38  .29B .29A .34
  38 p4_dt112  1862 1980                             -.03B-.03B .33  .40  .45
  39 p4_dt113  1926 2017                                            -.14B .12B .34
  40 p4_dt114  1875 1982                                  .48  .56  .17B .12B
  41 p4_dt115  1897 1993                                  .23B .23B .00B .21B
  42 p4_dt116  1915 2019                                       .30A .27B .20B .27A
  43 p4_dt117  1859 1988                             .05B .27A .42  .30B .26B
  44 p4_dt118  1884 1999                                  .36  .28A .26A .28B
  45 p4_dt119  1874 2003                             .20B .19B .14B .41  .39  .34
  46 p5_lt121  1848 2020                        .22B .24B .43  .41  .57  .72  .60
  47 p5_lt122  1881 2020                                  .20B .15B .06B .24B .54
  48 p5_lt123  1840 2020                        .44  .40  .37  .39  .43  .51  .72
  49 p5_lt124  1841 2020                        .38  .52  .39  .37B .60  .59  .23A
  50 p5_lt125  1846 2020                        .09B .16B-.17B-.23B .13B .42  .27B
  51 p5_lt126  1829 2020                        .20A .16B .33B .46  .50  .43  .28B
  52 p5_lt127  1845 2020                        -.20B-.11B .03B-.10B-.07B .22B .56
  53 p5_lt128  1863 2020                             .26B .23B .20B .08B .17B .45
  54 p5_lt129  1843 2020                        .54  .48  .50  .61  .60  .56  .66
  55 p5_lt130  1853 2020                             .53  .43  .39  .57  .67  .51
  56 p5_dt131  1840 2006                        .26A .38  .55  .62  .18B-.03B-.17B
  57 p5_dt132  1844 2000                        .36  .38  .55  .51  .15B-.18B-.20B
  58 p5_dt133  1838 2008                        .37  .35  .34  .40  .46  .41  .33
  59 p5_dt134  1859 1995                             .31A .41  .17B .07B .27B
  60 p5_dt135  1837 2004                        .50  .34B .46  .58  .54  .46  .50
  61 p5_dt136  1843 1995                        .45  .44  .56  .63  .68  .59
  62 p5_dt137  1838 1991                        .40  .54  .42  .33A .18B .07B
  63 p5_dt138  1844 1990                        .42  .36  .48  .42  .42  .33A
  64 p5_dt139  1881 1995                             .43  .54  .64  .70
  65 p5_dt140  1843 1994                        .65  .69  .66  .66  .48  .28B
  66 p5_dt141  1879 2001                             .44  .37  .58  .65  .63
  67 p5_dt142  1841 2003                        .61  .69  .60  .55  .72  .65  .57
  68 p5_dt143  1853 1984                             .51  .43  .57  .60  .56
  69 p5_dt144  1841 1988                        .31A .59  .55  .34  .44  .17B
  70 p5_dt145  1833 1985                        .52  .45  .67  .75  .68  .68
  71 p5_dt146  1834 2001                        .36  .25B .37  .56  .39  .08B .10B
  72 p5_dt147  1829 1958                        .40  .49  .49  .23B .22B
  73 p5_dt148  1651 1985   -.02B-.12B-.22B-.02B .00B .24B .60  .58  .25B-.05B
  74 p5_dt149  1738 1988   .01B-.08B-.18B-.05B .21A .29A .26A .07B .05B .04B
  75 p5_dt150  1875 1986                             .15B .29A .33B .34
Av segment correlation  -.02 -.02  .05  .10  .26  .27  .31  .31  .32  .31  .33
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C   *Tree-ring chronologies of each tree species and their condition (living and dead)*
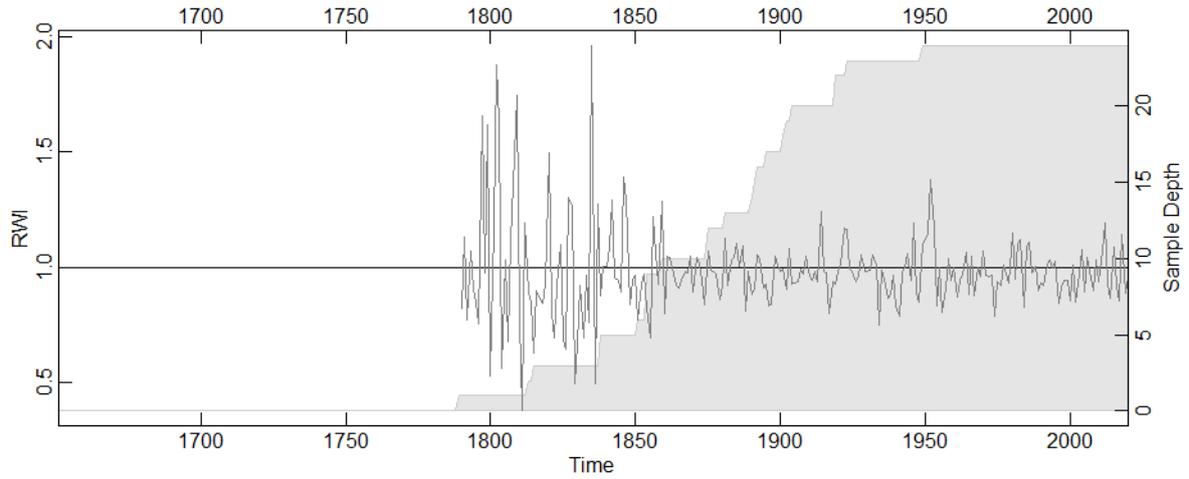
Figure C.1: Tree-ring chronologies of the annual growth of all 24 living mountain pines of plot 1-3. RWI is the ring width index and the sampling depth represents the number of tree samples.
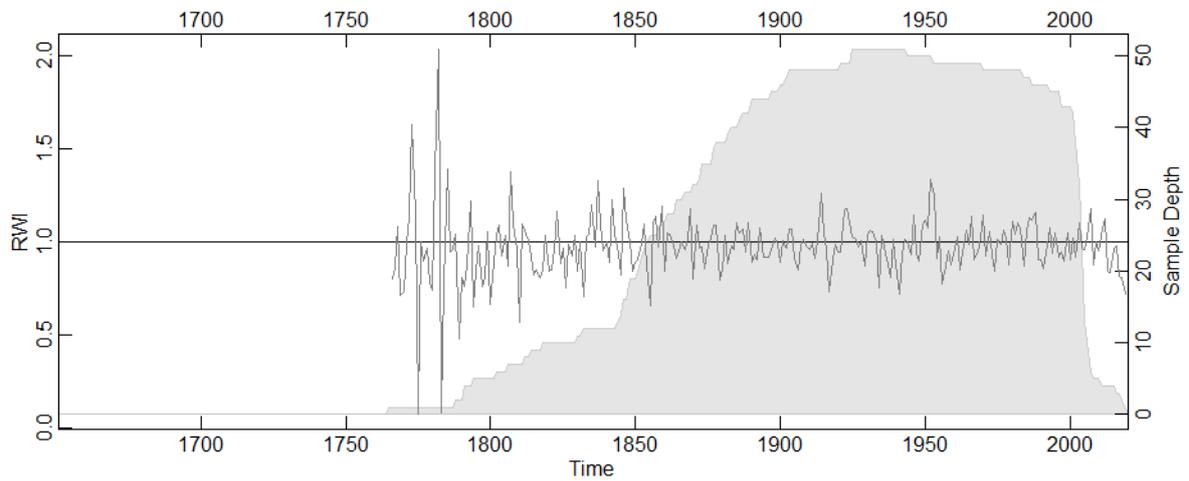
Figure C.2: Tree-ring chronologies of the annual growth of all 51 dead mountain pines of plot 1-3. RWI is the ring width index and the sampling depth represents the number of tree samples.
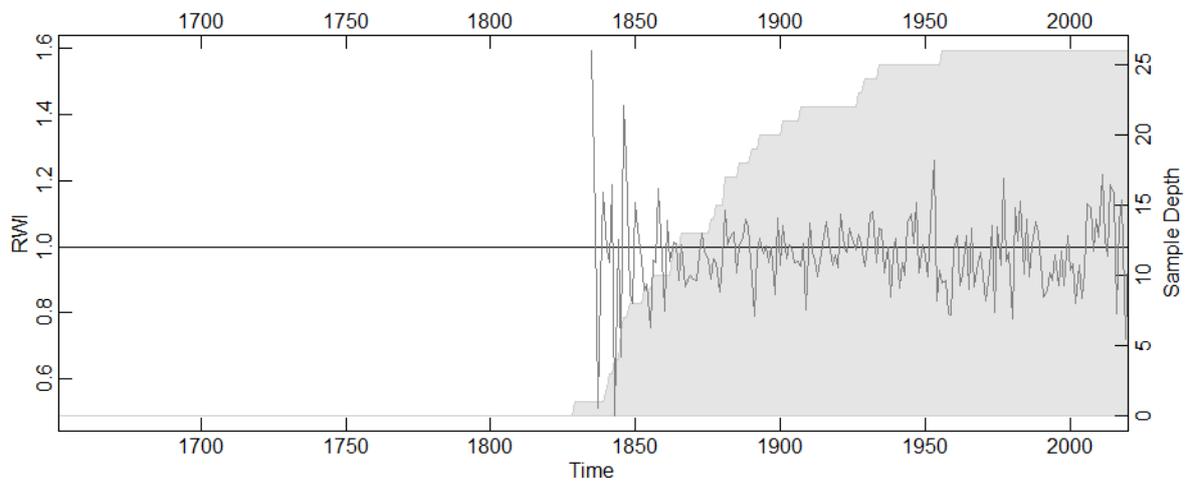
Figure C.3: Tree-ring chronologies of the annual growth of all 26 living Norway spruces of plots 1-5. RWI is the ring width index and the sampling depth represents the number of tree samples.
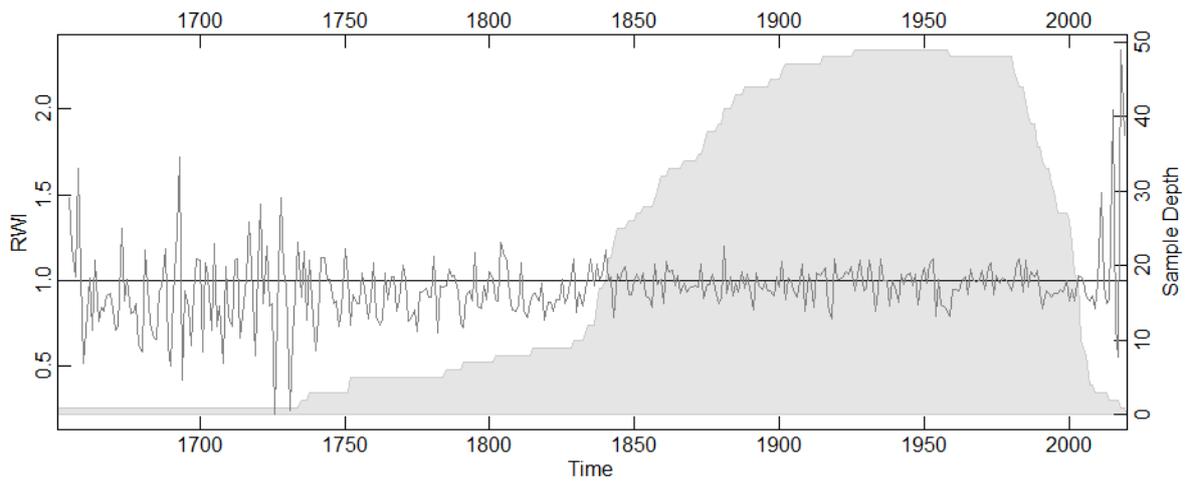
Figure C.4: Tree-ring chronologies of the annual growth of the 49 living Norway spruces of plots 1-5. RWI is the ring width index and the sampling depth represents the number of tree samples.
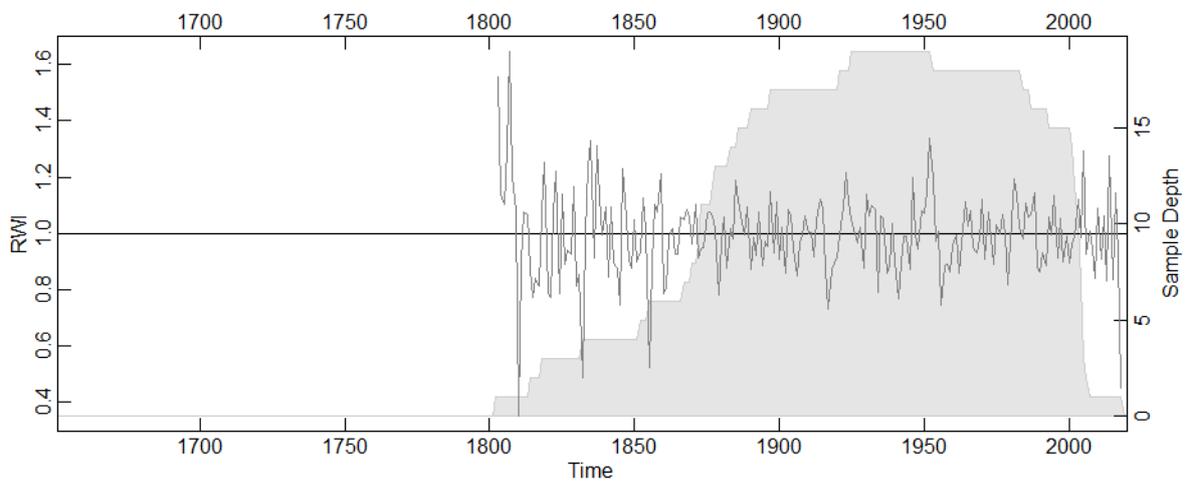
Figure C.5: Tree-ring chronologies of the annual growth of the 19 dead mountain pines of plot 1. RWI is the ring width index and the sampling depth represents the number of tree samples.
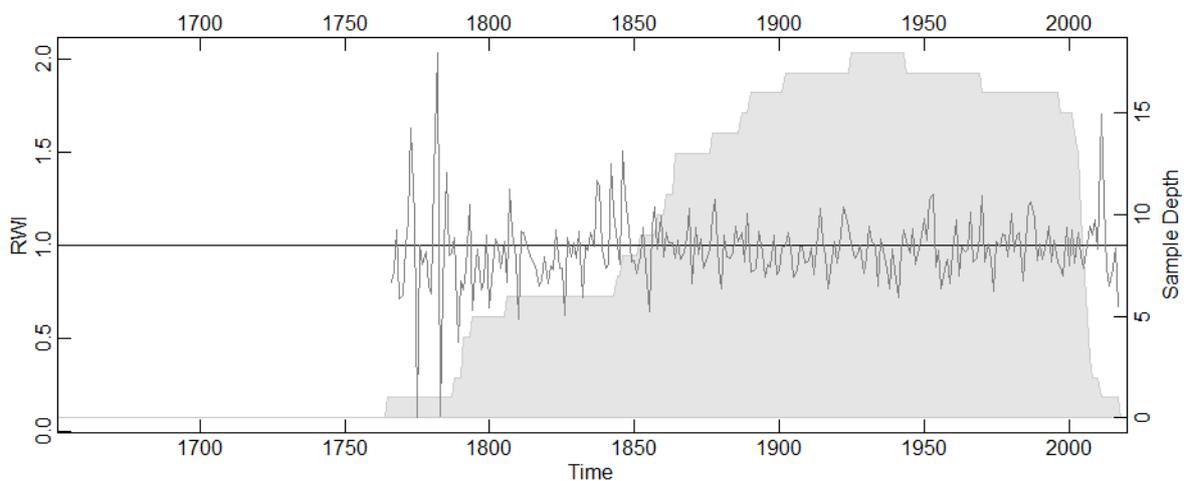
Figure C.6: Tree-ring chronologies of the annual growth of the 18 dead mountain pines of plot 2. RWI is the ring width index and the sampling depth represents the number of tree samples.
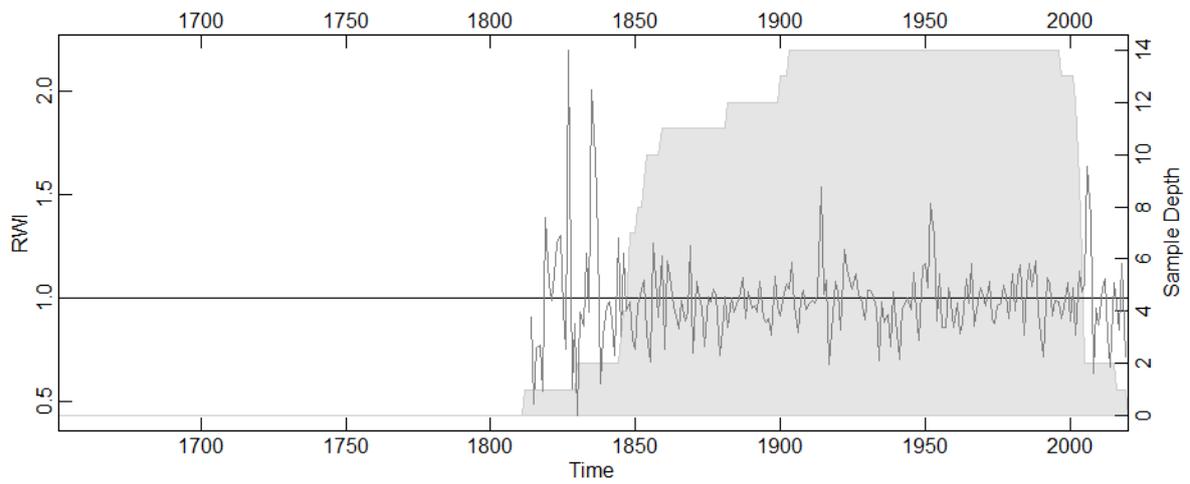
Figure C.7: Tree-ring chronologies of the annual growth of the 14 dead mountain pines of plot 3. RWI is the ring width index and the sampling depth represents the number of tree samples.
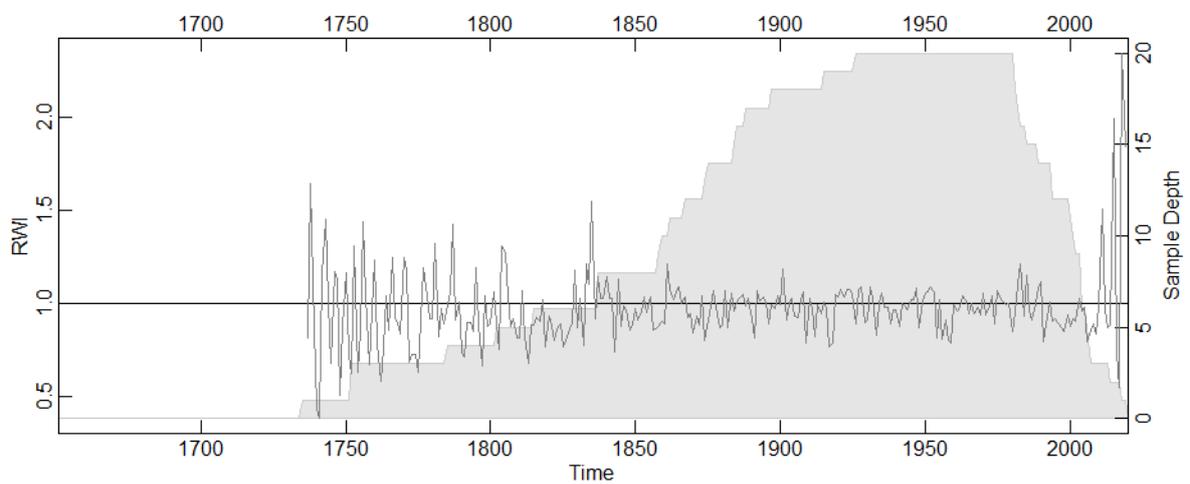
Figure C.8: Tree-ring chronologies of the annual growth of the 20 dead Norway spruces of plot 4. RWI is the ring width index and the sampling depth represents the number of tree samples.
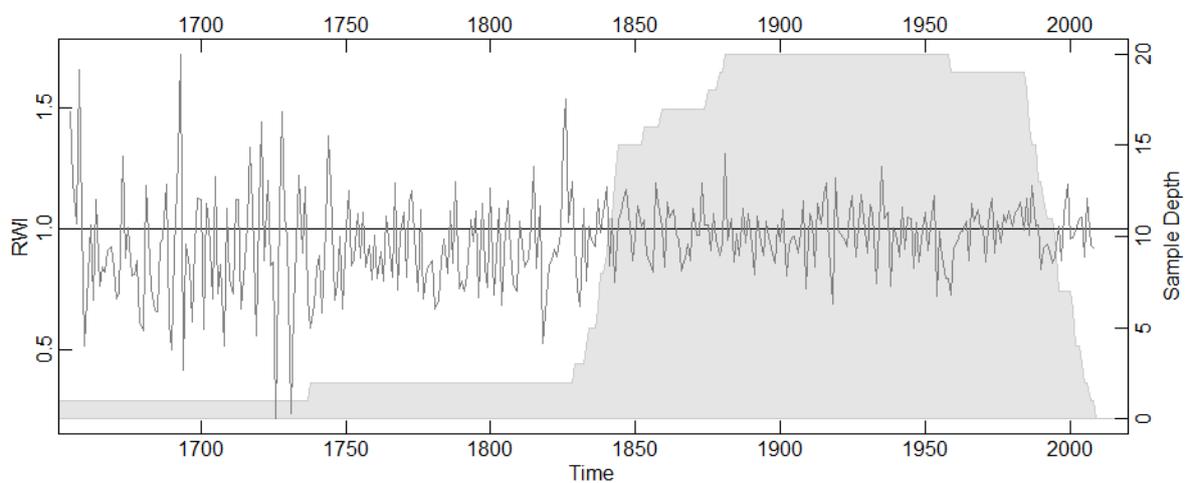
Figure C.9: Tree-ring chronologies of the annual growth of the 20 dead Norway spruces of plot 5. RWI is the ring width index and the sampling depth represents the number of tree samples.

D *Correlation of the dependent and independent variables*

(a) Relationship of lifespan and neighbouring trees　　　　**(b) Relationship of lifespan and CI**
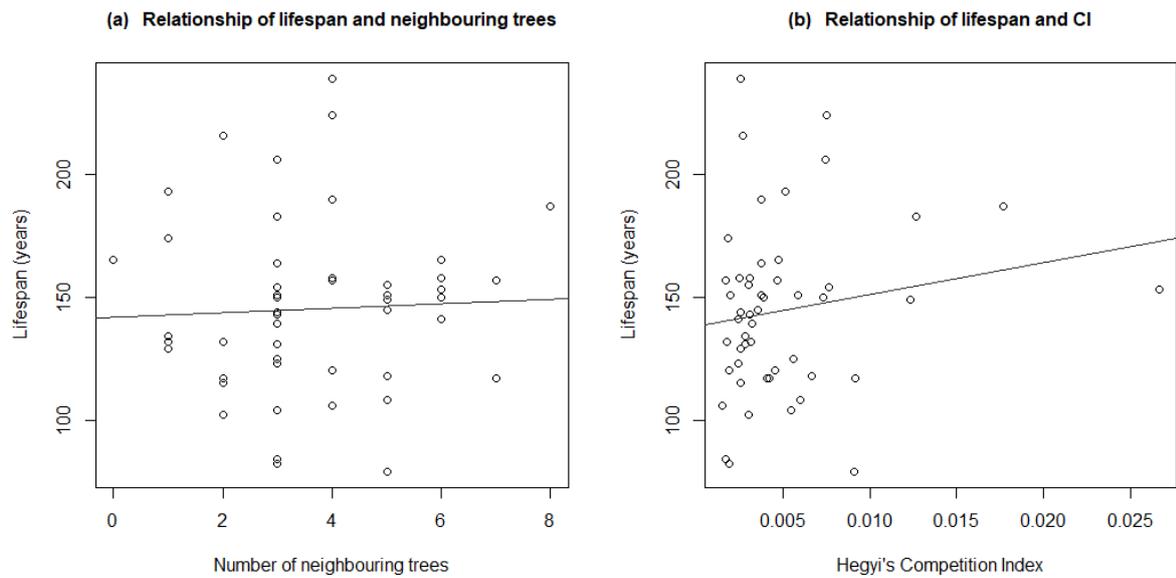
Figure D.1: Relationship of the lifespan and (a) neighbouring trees and (b) the Hegyi's Competition Index of all dead Norway spruces. The points represent in both plots the 51 sampled dead mountain pines. The two regression lines show on both plots the positive linear relationship between lifespan and neighbouring trees, respectively competition.

(a) Relationship of lifespan and neighbouring trees　　　　**(b) Relationship of lifespan and CI**
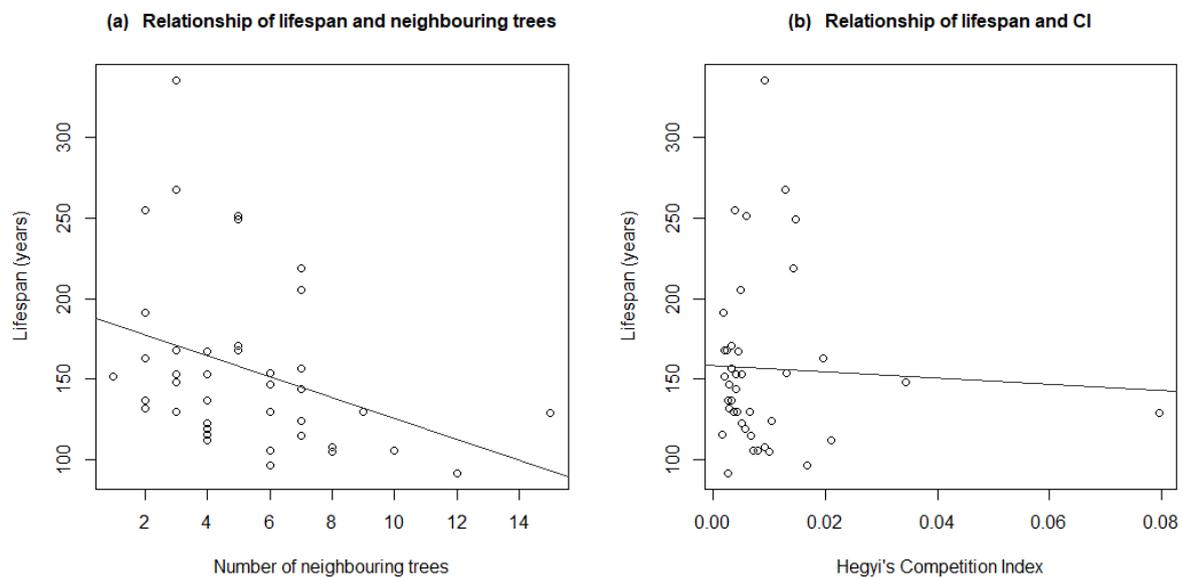
Figure D.2: Relationship of the lifespan and (a) neighbouring trees and (b) the Hegyi's Competition Index of all dead mountain pines. The points represent in both plots the 49 sampled dead Norway spruces. The two regression lines show on both plots the negative linear relationship between lifespan and neighbouring trees, respectively competition.

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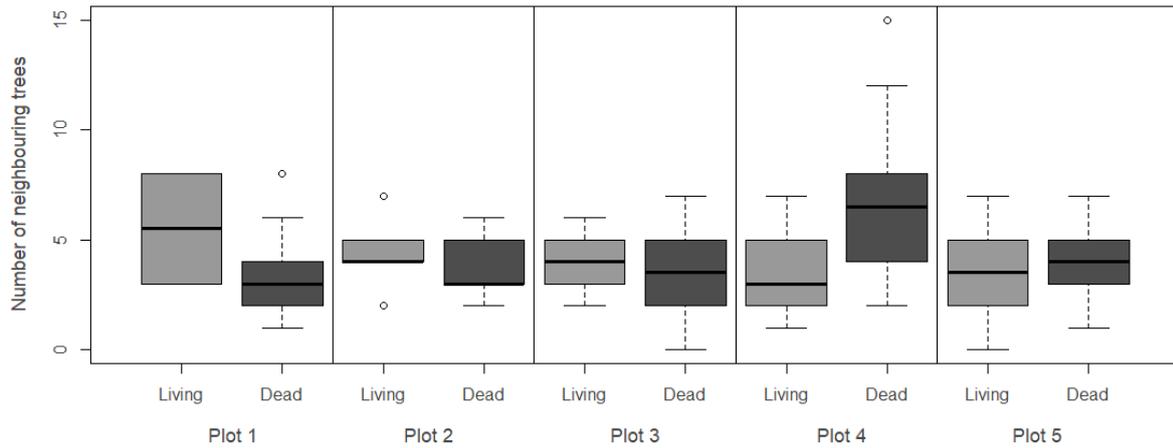
Notes: Living and dead mountain pines have between zero and eight neighbouring trees. The median of all sampled living mountain pines is four and the median of all sampled dead mountain pines is three. Only plot 1 is out of line, as the sampled living mountain pines have on average twice as many neighbouring trees than the sampled dead mountain pines. The median of the all the sampled dead Norway spruces is three. The number of neighbouring trees differs slightly more among the Norway spruces. This difference is mainly caused by the dead Norway spruces in plot 5. With fifteen neighbouring trees, the dead Norway spruces have more than twice as much neighbouring trees than the living Norway spruces with seven neighbouring trees.

Figure E.1: Boxplot of the number of neighbouring trees of the sampled mountain pines (plot 1-3) and sampled Norway spruces (plot 4-5)
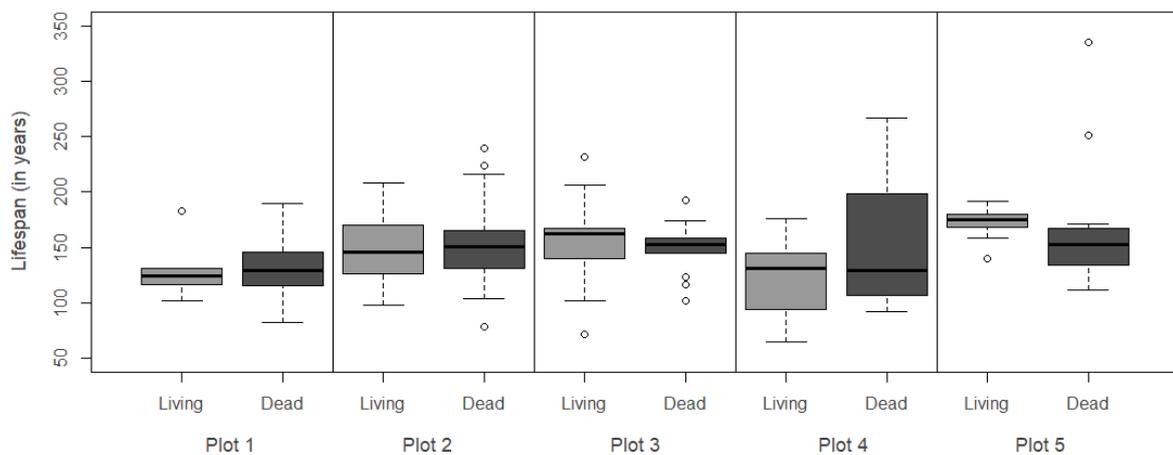
Notes: The oldest sampled dead mountain pine lived 239 years and was found in plot 2. The oldest sampled Norway spruce lived 335 years and was found in plot 4. The youngest sampled dead mountain pines and Norway spruces lived approximately 85 years and were found in plot 1, plot 2, and plot 5.

Figure E.2: Boxplot of the lifespan of the sampled mountain pines (plot 1-3) and sampled Norway spruces (plot 4-5)
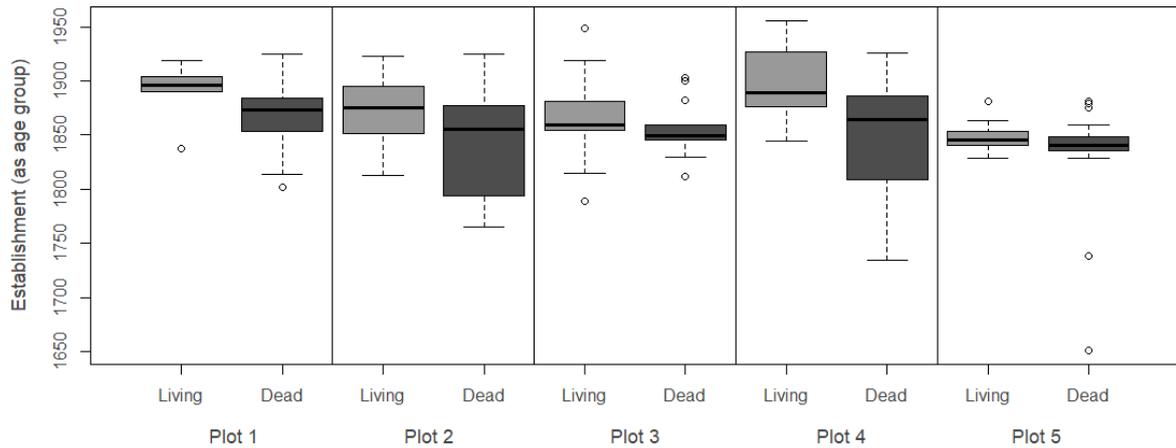
Figure E.3: Boxplot of the establishment of the sampled mountain pines (plot 1-3) and sampled Norway spruces (plot 4-5). The sampled mountain pines established between 1765 and 1949 and the Norway spruces between 1651 and 1956. The oldest sampled dead mountain pine lived 239 years and was found in plot 2. The oldest sampled Norway spruce lived 335 years, was established in 1651, and was found in plot 4. The youngest sampled dead mountain pines and Norway spruces lived approximately 85 years, were established in 1925/1926, and were found in plot 1, plot 2, and plot 5.
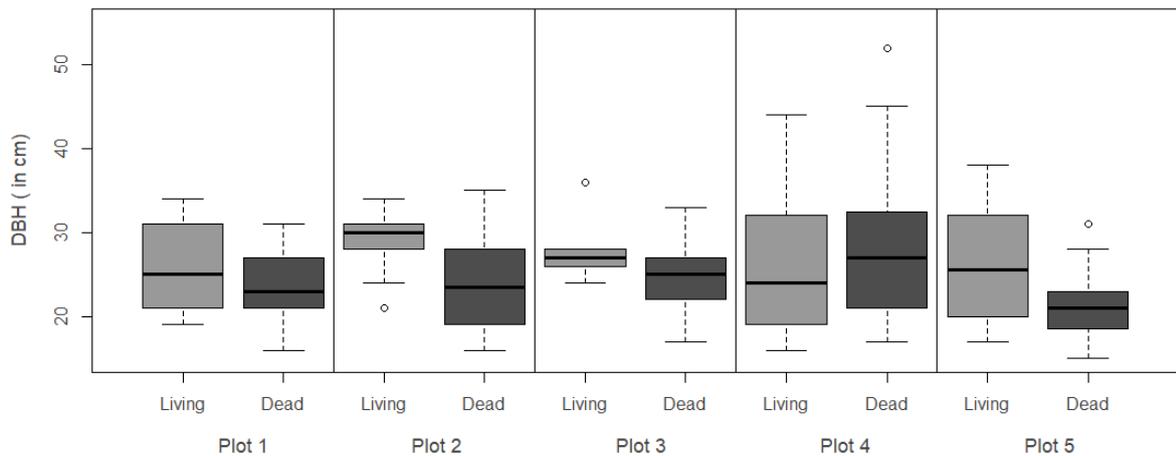
Figure E.4: Boxplot of the DBH of the sampled mountain pines (plot 1-3) and sampled Norway spruces (plot 4-5). The DBH of the sampled living mountain pines lies between 19 cm and 36 cm (19 cm < living MP < 36 cm | Ø 27.54 cm) and the DBH of the sampled dead mountain pines between 16 cm and 35 cm (16 cm < dead MP < 35 cm | Ø 23.86 cm). The DBH of the sampled living Norway spruces lies between 15 cm and 44 cm (15 cm < living NS < 44 cm | Ø 25.65 cm) and the sampled dead Norway spruces between 15cm and 52 cm (15 cm < dead NS < 52 cm | Ø 24.40 cm.

(a) Plot 1: Sphagnum density of the mountain pines (pinus montana)

(b) Plot 2: Sphagnum density of the mountain pines (pinus montana)

(c) Plot 3: Sphagnum density of the mountain pines (pinus montana)

(d) Plot 4: Sphagnum density of the Norway spruces (picea abies)

(e) Plot 5: Sphagnum density of the Norway spruces (picea abies)
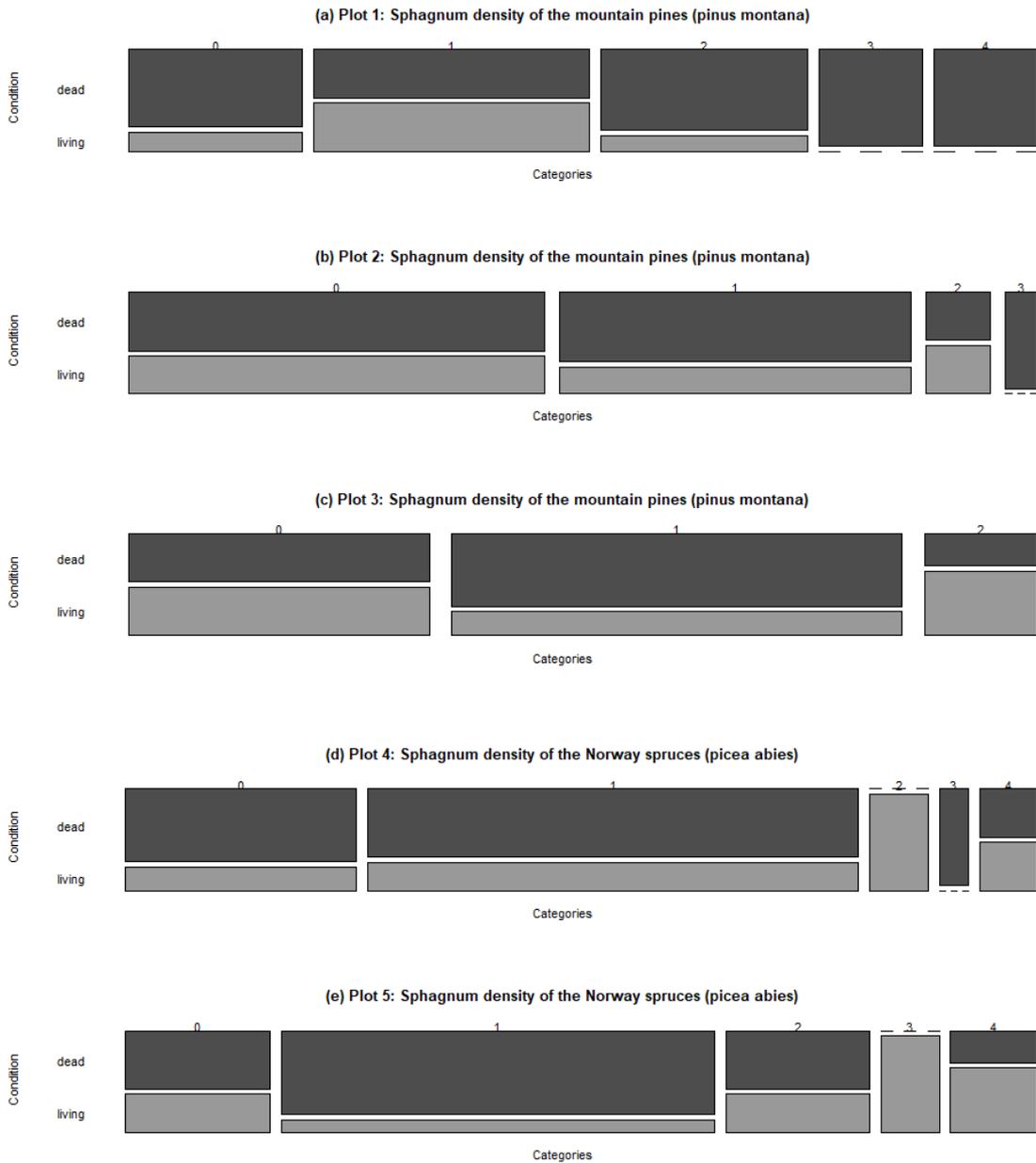
Figure E.5: Mosaic plot of the sphagnum cover of the sampled mountain pines (plot 1-3) and sampled Norway spruces (plot 4-5). The sphagnum cover (one meter around the trees) was low in all plots (see Figures D7 a-e). Category one (0-25% sphagnum cover) is the most frequent in all plots whereas category tree (50-75%) and four (75-100%) are both equally rare. The sampled dead mountain pines of plot 1 have compared to plot 2 and plot 3 the highest sphagnum cover. Contrary, have the mountain pines in plot 3 the lowest sphagnum cover. The living Norway spruces in plot 4 and plot 5 have a higher sphagnum cover than the dead Norway spruces in these plots. However, no clear pattern can be identified.
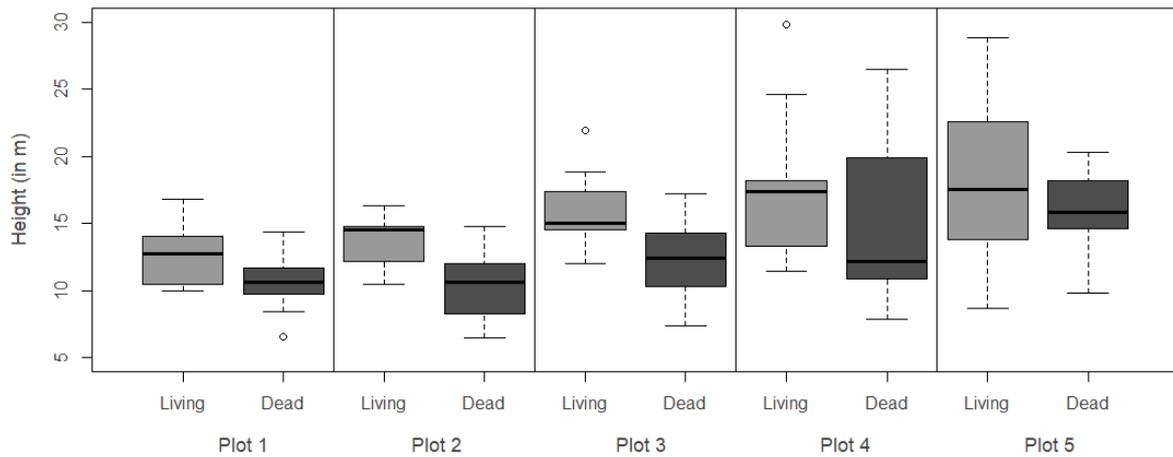
Figure E.6: Boxplot of the height of the sampled mountain pines (plot 1-3) and sampled Norway spruces (plot 4-5). The height of all the sampled living mountain pines (10 m < living MP < 21.9 m | Ø 14.33 m) were higher than the sampled dead mountain pines (6.5 m < dead MP < 17.2 m | Ø 11.01 m).The sampled living Norway spruces (7 m < living NS < 29.8 m | Ø 16.79 m) were also higher than the sampled dead Norway spruces (7.2 m > dead NS < 26.5 m | Ø 14.44 m).

F   Response function
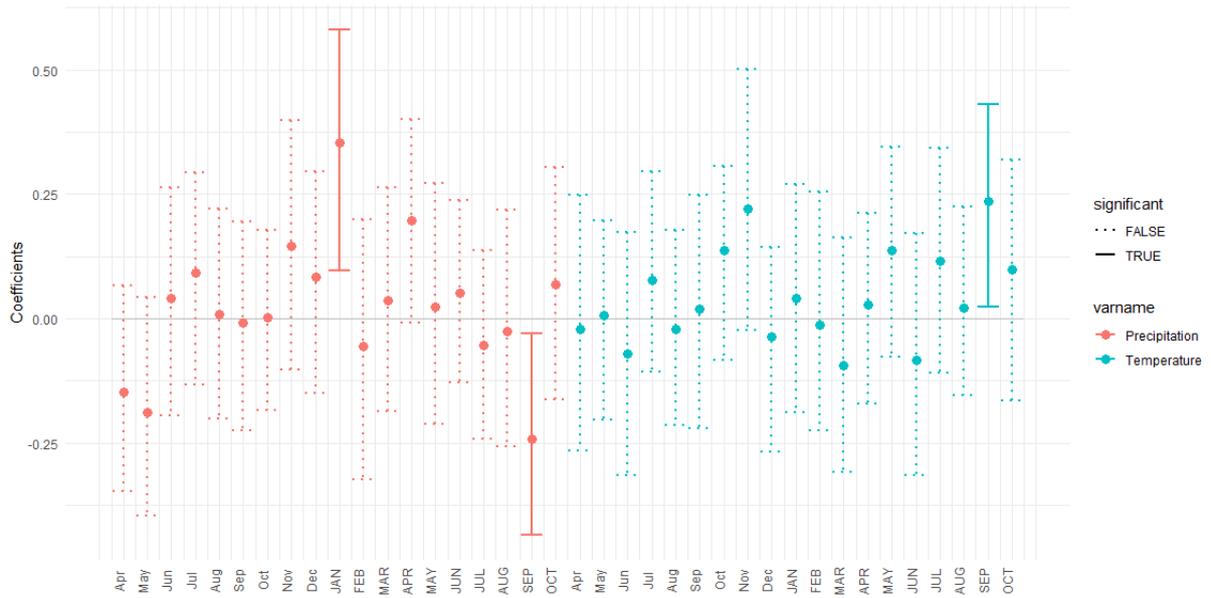
Figure F.1: Response function of the 24 living mountain pines, total precipitation and mean temperature in the Entlebuch biosphere reserve. See also legend description of Figure 7.
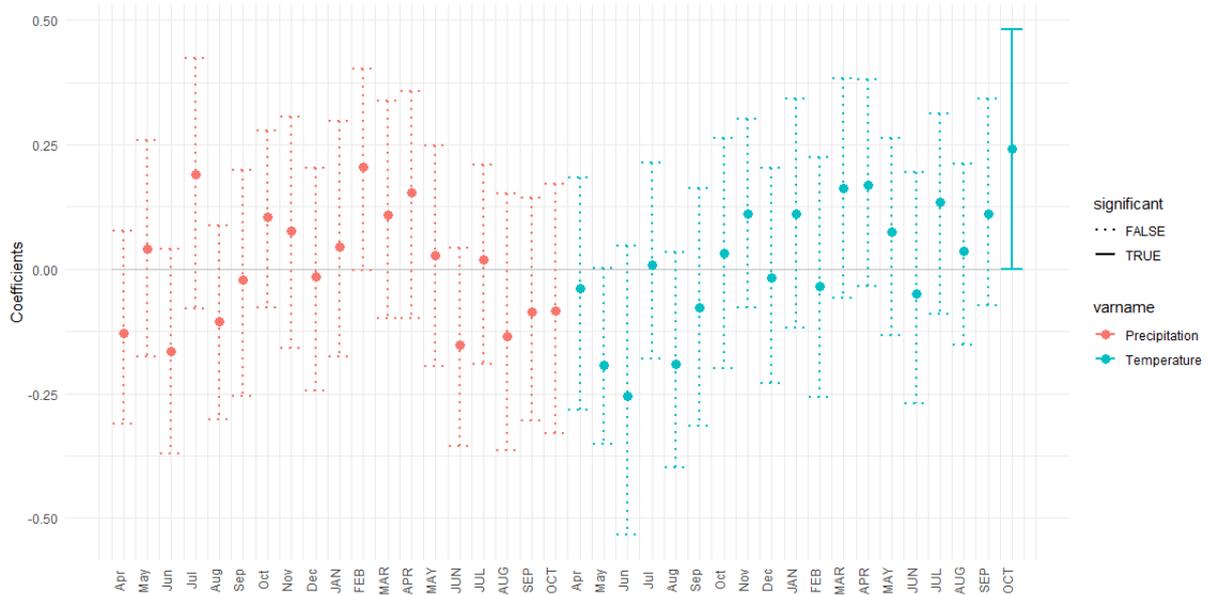
Figure F.2: Response function of the 26 living Norway spruces, total precipitation and mean temperature in the Entlebuch biosphere reserve See also legend description of Figure 7.
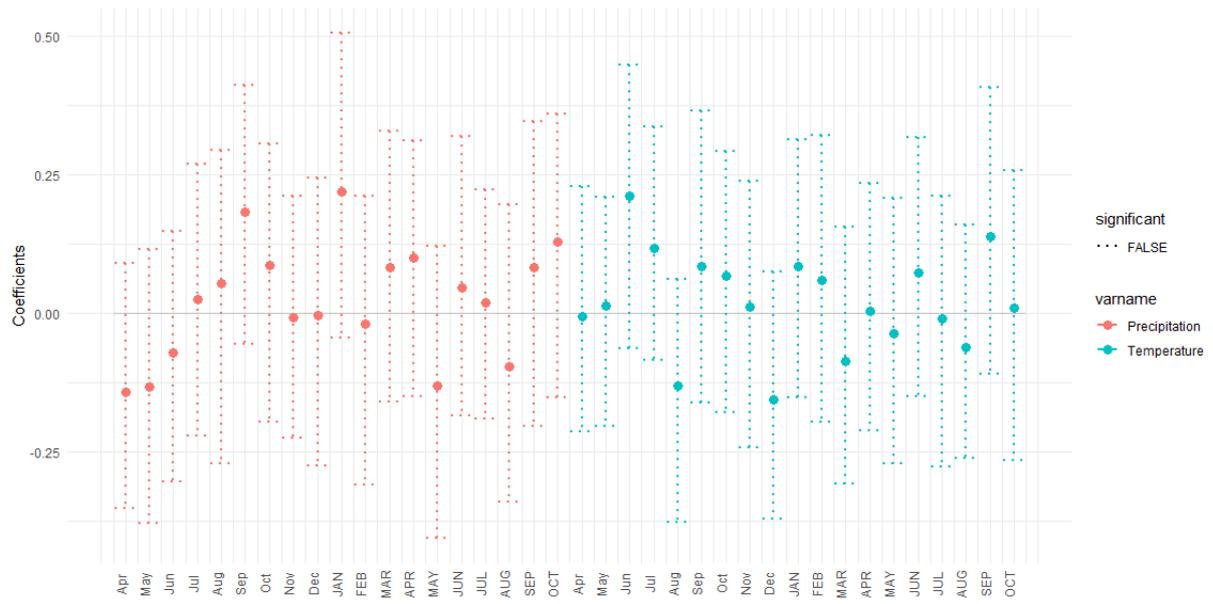
Figure F.3: Response function of the 6 living Norway spruces in the Entlebuch biosphere reserve in plot 1-3. See also legend description of Figure 7.
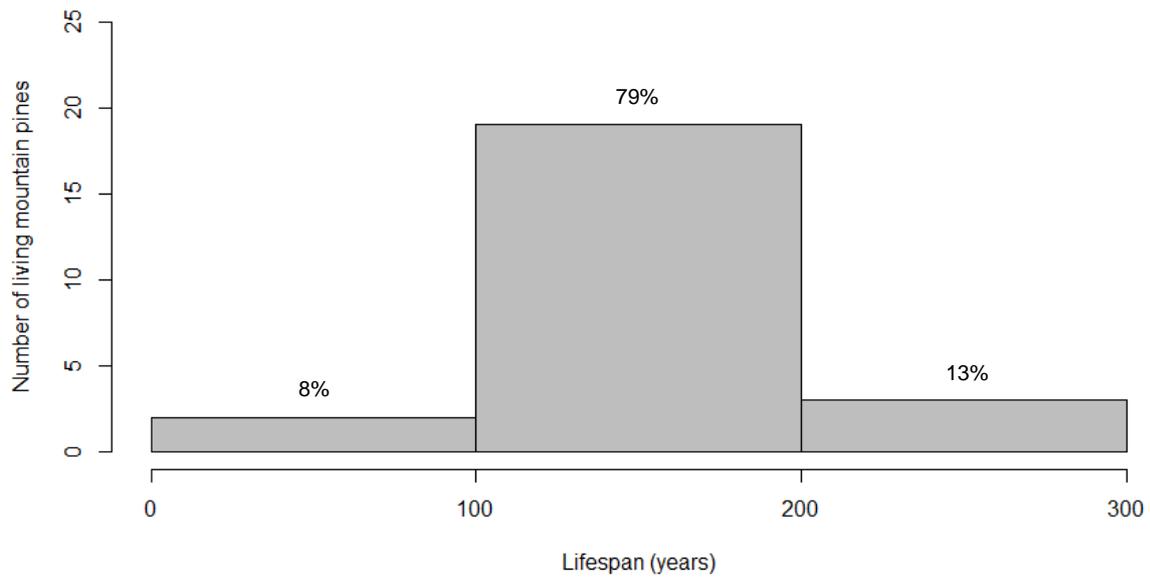
Figure G.1: Histogram of the lifespan of all sampled living mountain pines of plot 1-3.
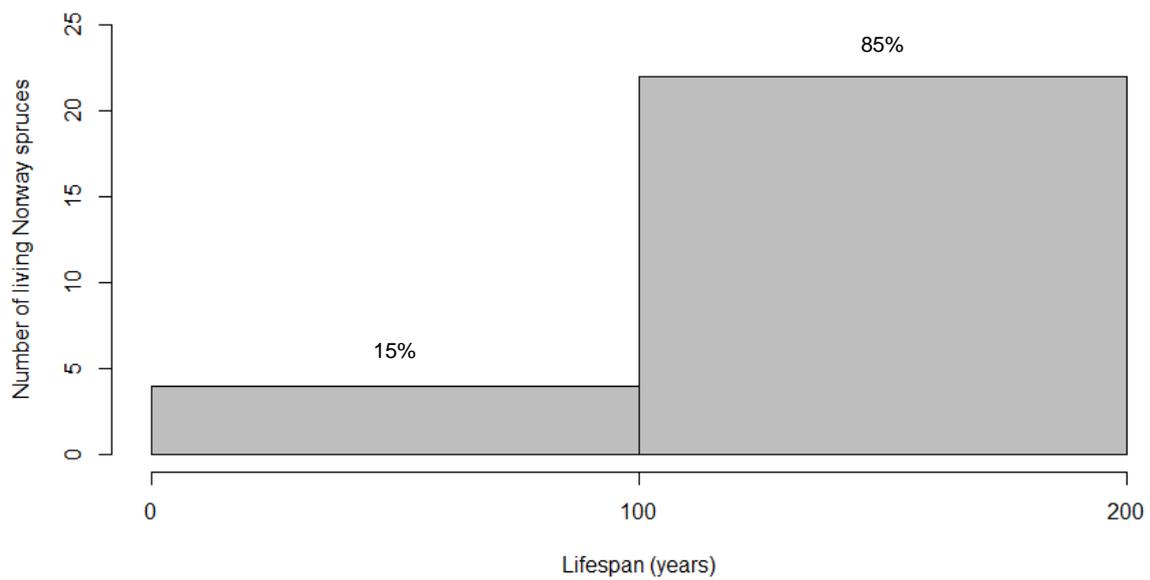
Figure G.2: Histogram of the lifespan of all sampled living Norway spruces of plot 4-5.

H Time-series plots of the tree-ring widths

(a) Plot 1: Living Norway spruces (picea abies)

(b) Plot 1: Dead Norway spruces (picea abies)
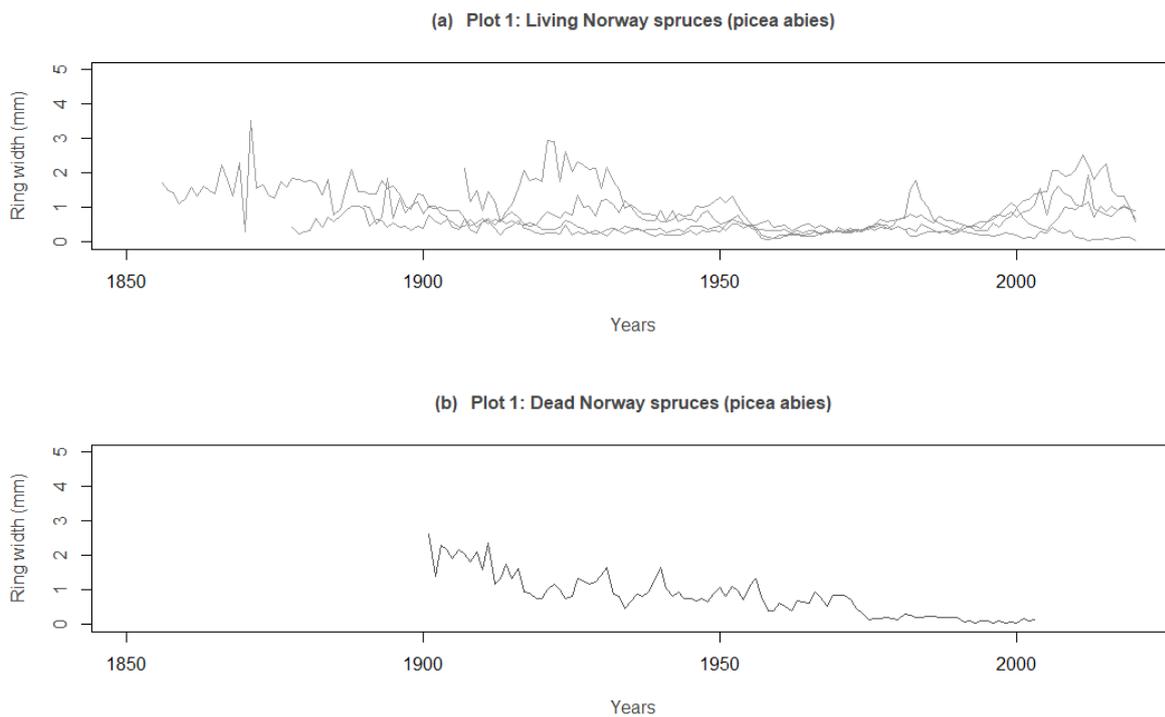
Figure H.1: Time-series plots of the tree-ring widths of the (a) sampled living Norway spruces and (b) dead Norway spruces in plot 1

(a) Plot 2: Living Norway spruces (picea abies)

(b) Plot 2: Dead Norway spruces (picea abies)
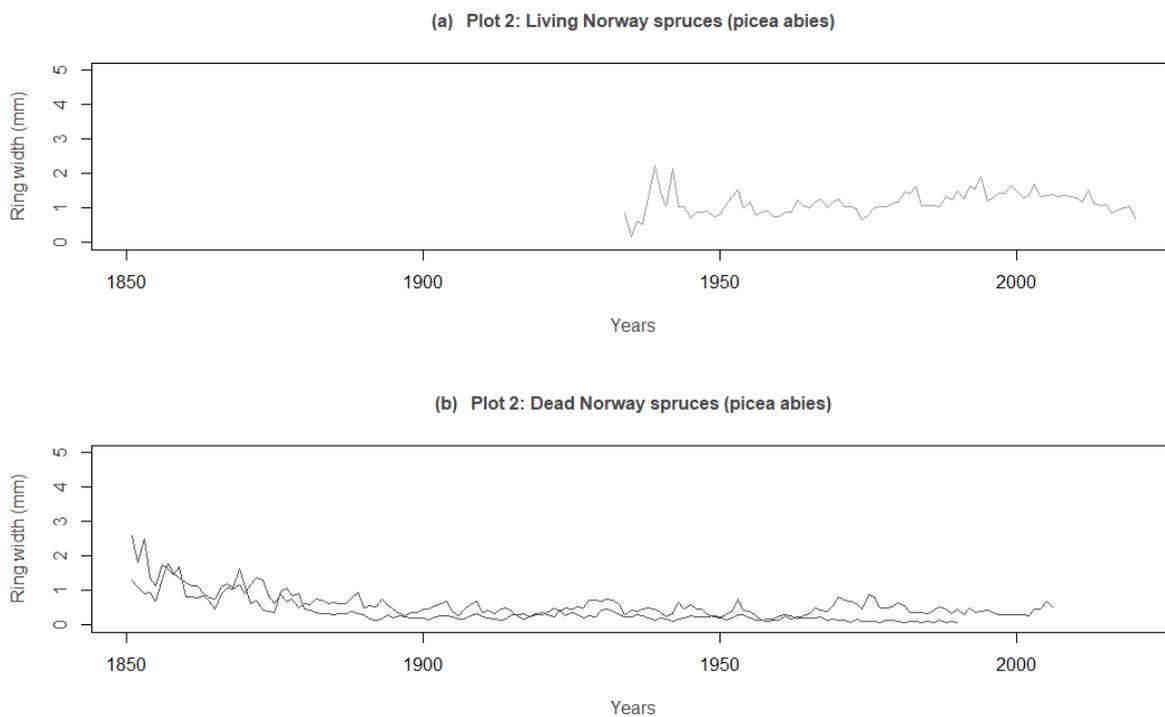
Figure H.2: Time-series plots of the tree-ring widths of the (a) sampled living Norway spruces and (b) dead Norway spruces in plot 2

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(a) Plot 3: Living Norway spruces (picea abies)

(b) Plot 3: Dead Norway spruces (picea abies)s
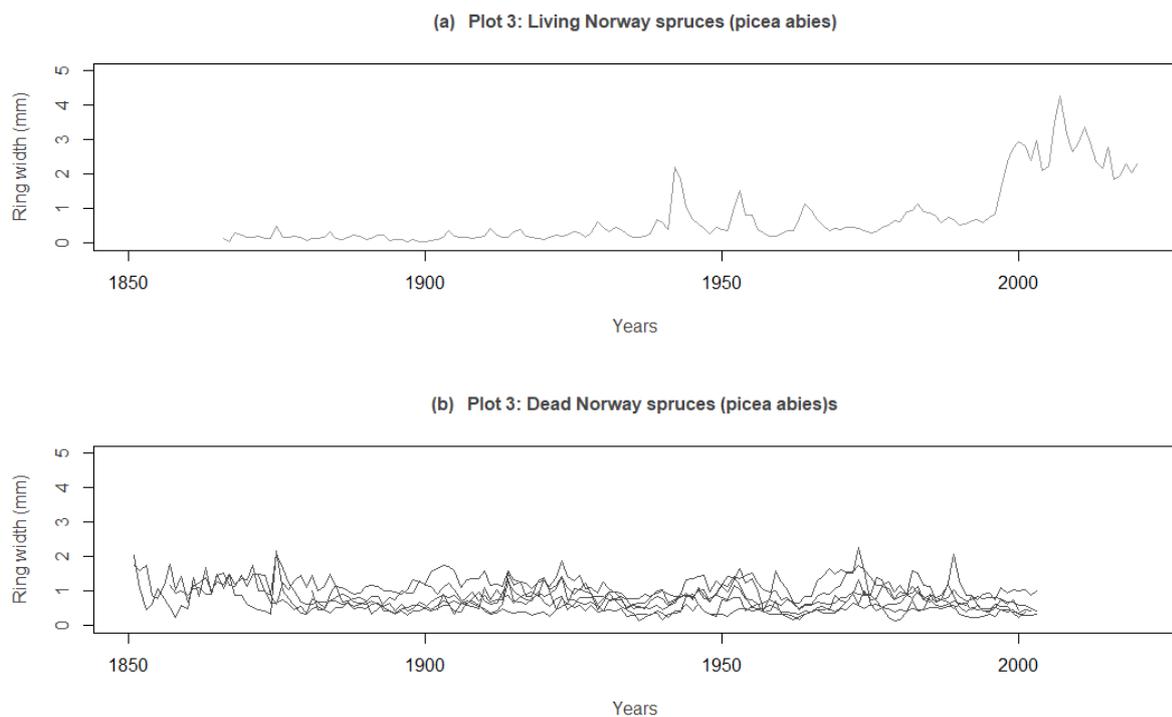
Figure H.3: Time-series plots of the tree-ring widths of the (a) sampled living Norway spruces and (b) dead Norway spruces in plot 3
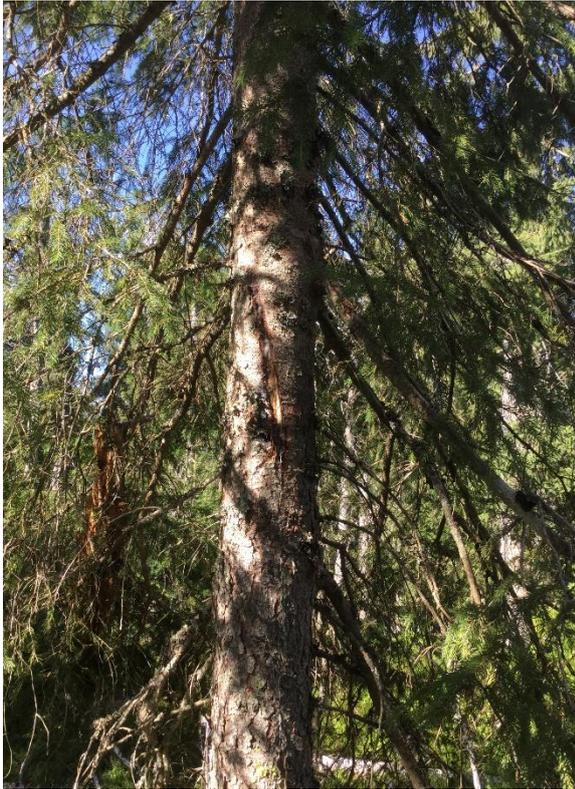
Figure I.1: Bark beetle infested living Norway spruce in plot 4

Figure I.2: Bark beetle infested dead Norway spruce in plot 4