Vegetation succession dynamics at the Alpine timber-line ecotone in the Grindelwald region (Northern Swiss Alps)

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Table of Contents

List of Figures

List of Tables

Ph. D. Sarah C. Strähl

Abstract

This Ph. D. study investigates the importance of vegetation mappings (as proposed by Braun-Blanquet, 1964), in differentiating the type of dynamics of vegetation succession (non-disturbed/naturally determined vs. disturbed/anthropo-zoogenically determined) taking place in a newly forested surface at the Alpine timber line in the Grindelwald region. Non-disturbed and disturbed areas differ in their vegetation structure and phyto-diversity, as proved by previous studies. In this study we test these statements at the timber-line ecotone, which is an ecologically sensitive area and therefore well-suited for investigating changes in vegetation development, caused by non-disturbed (e.g., site conditions with intact ecological balance) and disturbed (e.g., site conditions with disturbed ecological balance) processes. For this purpose, we have chosen a site located in the region of Grindelwald that has shown the largest increases in forest cover at the timber line over the past 100 years.

Our results show that phyto-diversity is more meaningful than plant structure when determining a surface area of progressing forest vegetation at the timber-line ecotone by its non-disturbed character, in probable response to global warming.

We find a tendency for large parts of the current timber line to be anthropo-zoogenically determined, whereas non-disturbed/naturally shaped current timber line is limited to some local areas, as known from other Alpine regions. However, in the majority of studied areas the cause of current vegetation succession at the timber-line ecotone is unclear, neither attributable to the impact of possible global warming nor pasture reduction. These results reinforce the observations of previous studies that the timber line is unlike the snow line suited to showing the effects of evolutionary climate change as a global relation and that the spatial pattern of vegetation at the Alpine timber line is expected to behave non-synchronously with ongoing global climate change in the coming century.

Zusammenfassung

Diese Ph. D. Studie untersucht die Bedeutung der Vegetationskartierung nach Braun-Blanquet (1964), um innerhalb eines neu bewaldeten Gebietes entlang der Waldgrenze, natürliche von anthropo-zoogenen Einflüssen zu unterscheiden. Wie bereits aus früheren Untersuchungen bekannt, unterscheidet sich die natürliche und anthropo-zoogene Vegetationsdynamik in ihrer Pflanzenstruktur und Phytodiversität. In der vorliegenden Studie testen wir diese Aussagen im Waldgrenzökoton, welches ein ökologisch sensitives Gebiet darstellt. Deswegen ist diese Methode geeignet für Aussagen über die aktuelle Vegetationsdynamik, die von natürlichen Prozessen (z.B. Standortfaktoren mit intaktem ökologischem Gleichgewicht), von anthropo-zoogenen Prozessen (z.B. Standortfaktoren mit gestörtem ökologischem Gleichgewicht) oder einer Kombination davon entstehen. Dazu wurde ein Standort in der Region Grindelwald ausgewählt, wo sehr grosse Zunahmen von Waldflächen an der Waldgrenze seit den letzten 100 Jahren festgestellt wurden.

Die Resultate betonen die Bedeutung der Phytodiversität im Vergleich zur Pflanzenstruktur, um Bereiche fortschreitender Waldvegetation im Waldgrenzökoton zu bestimmen, die wahrscheinlich durch die globale Klimaerwärmung hervorgerufen werden.

Wir erwarten, dass grosse Bereiche der aktuellen Waldgrenze anthropo-zoogen bedingt sind, wohingegen die Proportion der natürlich geformten aktuellen Waldgrenze sich auf ein paar wenige lokale Standorte konzentriert, wie bereits bekannt aus anderen alpinen Regionen. Dennoch gibt es für die Mehrheit der untersuchten Gebiete keine klaren Ursachen als Auslöser der aktuellen Vegetationsdynamik, d.h. kann weder der globalen Klimaerwärmung noch der nachlassenden Landnutzung zuordnet werden. Somit stimmen die vorliegenden Resultate mit den Untersuchungen früherer Studien überein, welche festgestellt haben, dass die Waldgrenze nicht gleich der Schneegrenze für den globalen Zusammenhang des Klimawandels herbeigezogen werden kann und sich bei anhaltender globaler Klimaänderung auch im kommenden Jahrhundert nichtsynchron verhalten wird.

1   Introduction

1.1   Changes in the environmental conditions over the past 100 years

Over the past 100 years, global warming (ca. + 0.6 °C) has strongly affected landscape and vegetation in many regions of the Earth (IPCC 2013, 2014). The most drastic changes have been reported in high mountain ecosystems, which are more exposed to atmospheric oscillation and have therefore been identified as an important habitat for inferring primary signals of climate change (Beniston 2005, 2006). In response to climate warming, glaciers have decreased in surface area (30-40%) and lost around 50% of their original volume (Haeberli & Beniston 1998; Burga et al. 2003; Holzhauser & Zumbühl 2003; Holzhauser et al. 2005; Haeberli et al. 2007; IPCC 2013). In our study region in the Northern Swiss Alps, for example, the Lower Grindelwald Glacier (Northern Swiss Alps) has shown reductions of around 10% in surface area and of over 2 km in length over the past 150 years (Glaciological reports 1881-2009; Zumbühl et al. 2008; Figure A 3). The highest glacier area losses per decade were recorded during the period from 1985 to 1998/99, because climate warming was then most pronounced and enhanced the melt of glaciers by a factor of seven compared to the period 1850-1973 (Paul et al. 2007). As a consequence, extreme events such as landslides (Haeberli & Burn 2002) and rock falls (Gruber et al. 2004) have increased in frequency and severity (Davis et al. 2001; Beniston & Stephenson 2004; Beniston et al. 2011). In accordance with the global warming effect over the past 100 years, different plant species of the subalpine and alpine belt have migrated upslope by an average of 200 m and have caused: (a) an increase in plant species diversity on high summits, (b) a process of thermophilization of the vegetation at high elevation and (c) a change in the phyto-diversity and ecological behavior of a habitat (Braun-Blanquet 1957; Hofer 1992; Burga & Perret 1998; Carraro et al. 2001; Grabherr et al. 2001; Theurillat and Guisan 2001; Walther et al. 2001; Burga et al. 2003, 2007; Körner 2011; Gottfried et al. 2012; Pauli et al. 2012; Wipf et al. 2013). Similarly, the upslope shift of alpine treelines (approx. 30-80 m over the past 100 years) has been shown to be in direct response to global warming (Burga & Perret 1998; Harsch et al. 2009; Körner 2012). However, high mountain ecosystems, particularly the European Alps, have also been heavily affected by anthropo-zoogenic impacts. For example, during the Neolithic when settlement took place, anthropo-zoogenic impacts (e.g., cattle grazing) strongly modified the landscape of high mountain ecosystems (Burga 1988; Burga & Perret 1998, 2001a; Wick et al. 2003; Figure A 4). In this context, there are many other facets, besides only global warming, which seem to be perhaps more severe and responsible for high mountain ecosystems following an uncertain future, because not only large-scale average values of warming impact must be considered, but also the ecology – organisms, population and communities – on a regional level (Walther et al. 2002; Burga et al. 2003; Gruber & Haeberli 2007; Kullmann 2007b).

High mountain ecosystems are well-suited for inferring primary signals of climate change (Beniston 2005) because their steep thermal gradients produce a range of climatic regimes over short horizontal distances, similar to latitudinal biomes (Theurillat 1995). Elevation is one of the most fundamental determinants shaping mountain climates, because the decrease of the partial air pressure with elevation (about 1% per 100 m) leads to an adiabatic decrease of temperature (about 0.58°C per 100 m) (Körner 2003). Furthermore, the topography of high mountain ecosystems creates diverse ecological conditions within a small area and hence a wide variety of habitats suitable for plant life (Pauli et al. 2001, 2003; Walther et al. 2002). Approximately 4500 vascular plant species are found in the European Alps, which is more than a third of the entire European flora (west of the Urals) and could be affected by climate change (Theurillat et al. 1998). The European Alps are by far the best-studied high mountain areas of the world in terms of weather, climate and vegetation development and flora history, with a long tradition of floristic surveys and vegetation analysis (Ozenda 1988; Burga 1993; Lang 1994; Beniston et al. 1997; Burga & Perret 1998; Kullmann 2000; Beniston 2003, 2004, 2005, 2006; Tinner & Theurillat 2003; Tinner et al. 2003; Burga et al. 2004; Barry 2008; Aeschimann et al. 2011, 2013). Thus, a rich source of data reaching far back into the last century is available (e.g. Switzerland Heer 1884; Lüdi 1921; Hess 1923; Braun-Blanquet 1957, 1964; Welten & Sutter 1982; Walther et al. 2005a, b).

The study of plant species migration to higher elevations is relevant to understanding the effect of global climate warming because plant growth is strongly dependent on temperature (Körner 1998, 2003, 2007b; Grabherr et al. 2001). Climate warming has caused changes in: (a) plant species distribution (e.g., altitudinal shifts), (b) growing season length (e.g., changes in plant phenological cycle), and (c) phytodiversity of a habitat (e.g., changes in vegetation pattern) (Gottfried et al. 1994, 1999, 2012; Defila and Clot 2001, 2005; Grabherr et al. 2001; Menzel & Estrella 2001; Kullmann 2002; Walther et al. 2005a, b; Burga et al. 2007; Kullmann 2010). The most pronounced response of plant species to global warming has been their shift in elevation since glaciers reduction in the second half of the 19th century. Different plant species of the subalpine and alpine belt have migrated upslope by an average of 200 m as air temperatures have increased (Braun-Blanquet 1957; Hofer 1992; Kullmann 2001; Theurillat & Guisan 2001; Pauli et al. 2003b; Kullmann 2007a; Gottfried et al. 2012; Pauli et al. 2012; Wipf et al. 2013). Trends first suggested in 1957 by Braun-Blanquet, who noted increased plant species presence above 3000 m in 1947-1955 compared with 1812-1835, have been confirmed and investigated in detail by subsequent studies (Walther et al. 2005a; Burga et al. 2007). Global warming has also affected the growing season length (Walther et al. 2001; Sparks & Menzel 2002; Walther 2003). There are observations showing the onsets of spring events in Europe to have advanced by an average of 2.5 days during the decades between 1971 and 2000 (Menzel et al. 2006) and the growing season in Switzerland to have

lengthened by 13.3 days between 1951 and 1998 (Defila & Clot 2001). In response to the earlier onset of spring and the longer growing season, changes in the structure and diversity of vegetation have contributed to an increase in the plant species richness observed at several alpine summits (Theurillat & Guisan 2001; Walther et al. 2005b; Kullmann 2007a; Pauli et al. 2007, 2012). Upslope shifts in the lower altitude vegetation have, however, caused the shrinkage of nival plant species and other less competitive alpine plant species have been obliged to follow the shifting climate or have even disappeared, and thus high-mountain populations are threatened with losing their terrain and are suffering from increased habitat fragmentation (Gottfried et al. 1999; Walther et al. 2005b; Erschbamer 2006). In particular, endemic plant species must compete with plant species from lower elevations and are predicted to disappear (Burga et al. 2003). Ongoing climate warming is also being accompanied by a gradual transformation of plant communities (Gottfried et al. 2012), for instance, in the Southern Swiss Alps, where the amount of thermophilous plant species has increased in the understory of forests (Carraro et al. 2001; Walther et al. 2001).

The shift of timber lines has been used in multiple studies to analyze the impact of global warming (e.g., Burga & Perret 1998, 2001a; Körner 1998, 2003, 2007b, 2012; Kullmann 2000, 2007b; Kullmann & Öberg 2009; Grace et al. 2002; Holtmeier et al. 2003; Moiseev & Shiyatov 2003; Körner & Paulsen 2004; Van der Meer et al. 2004; Hoch & Körner 2005, 2009, 2012; Holtmeier & Broll 2005, 2007, 2010; Körner and Hoch 2006; Butler et al. 2009; Holtmeier 2009). Timber lines mark areas of marginal tree growth due to shortage of meristemic activity when shoots emerge into a cold atmosphere (sink-limitation-hypothesis, Körner 1998). Changes in timber lines can be observed on timescales of around 100 years and can be used to compare past and present climate conditions (Körner 2012). Pollen analysis (micro and macrofossil analysis) has been used to infer the altitudinal variation of timber lines over timescales of thousands of years, and to show its accordance to glacial development and climate change (Burga & Perret 1998; Tinner & Kaltenrieder 2005; Lotter et al. 2006). In the Central Alps the timber line reached its Holocene maximum average elevation approx. 8500-5500 years ago, i.e., during the Hypsithermal period, at 2450 m a.s.l. in the Swiss Central Alps, and then declined due to several climatic deteriorations between 4700 and 4000 years ago (Burga 1988; Burga & Perret 1998; Tinner & Theurillat 2003; Figure A 4). During the last 100 years, the Alpine timber line has climbed in several mountain regions in response to human impact and possibly global warming. In the Russian Ural-mountains, for example, where human impact is low, the timber line has climbed by 60-80 m in the South Ural and 20-40 m in the Polar Ural (Devi et al. 2008; Hagedorn et al. 2014). In the Swiss Alps, however, large areas have been affected by wood clearing due to land-use changes such as pasture and mining activity. During the late Holocene, 4500 years ago, and also during the Bronze Age, the Alpine timber line retreated to 300-400 m below its maximum Holocene position (Hegg 1984a, b; Burga 1988; Burga & Perret 1998;

Tinner & Theurillat 2003; Wick et al. 2003; Perret 2005; Heiri et al. 2006; Figure A 4). South-facing slopes with a smooth topography have been most strongly influenced by human impact. The present elevation of the timber line in the northern Swiss Alps, at 1800-2000 m a.s.l., is mainly determined by mechanisms of anthropo-zoogenical effects (e.g., cattle grazing & browsing, wood clearing) that shape the distribution of the timber line (Burga & Perret 2001a). It therefore no longer reaches its potential maximum elevation, but is determined by the plant physiology, topography, morphodynamics and local climate of the region (Holtmeier 2009). Changes in the elevation of Alpine timber lines are, in this context, often caused more by forest ingrowth into abandoned areas that are poorly accessible, and less by climate warming (Tasser & Tappeiner 2002; Tinner et al. 2003; Gehrig-Fasel et al. 2007; Tasser et al. 2007).

1.2 Study region and main objective

The motivation of this Ph. D. thesis is to extend the findings of my master thesis (Strähl 2006) for two reasons: First, to further investigate how differences in the vegetation structure and phyto-diversity at the timber-line ecotone of the Lauterbrunnen valley (see Tables A 45-48) reveal different dynamics of vegetation succession caused by natural or anthropo-zoogenic processes, and second, to understand the dynamics of vegetation succession on a local level where trees and other plant species develop. My research project shows the importance of vegetation mappings prescribed by Braun-Blanquet (1964) in understanding the potential impact of global warming on a subalpine ecosystem at the scale where trees and other plant species develop.

Our research question and thesis are: Can the impacts of changes in land-use activity or climate change be differentiated by means of vegetation mappings according to Braun-Blanquet (1964)?

For the purpose of this current study, we chose the region of Grindelwald, since it neighbors the Lauterbrunnen valley, and therefore its landscape is similar in its genesis and anthropo-zoogenic influences, and thus, well-suited to extending the findings of my master thesis. Furthermore, the region of Grindelwald (Northern Swiss Alps) provides a large amount of detailed data analysis from previous investigations (Kienholz 1977; Holzhauser & Zumbühl 2003; Holzhauser et al. 2005; Zumbühl et al. 2008). Data includes: (1) climate change data reaching back to the Holocene, (2) a detailed map of natural hazards in mountainous regions, and (3) the oldest reliable geo-referenced map in the Alps (Bundesamt für Landestopographie 1899). Moreover, Grindelwald's geological and glacial history, as well as current landscape-forming processes, have produced a large set of complex landscape features (Collet et al. 1938), where the pattern of soils and vegetation are not only determined by global effects responding to climate conditions, but also by local effects responding to the changing bedrock components. In addition, the Grindelwald region has been modified by human land-use practices (Naegeli-Oertle 1986) and areas of timber line that have advanced in response to global warming may not be frequent. Our study site was selected between Alpiglen (1616 m a.s.l.) and Kleine Scheidegg (2061 m a.s.l.) because it has shown one of the largest proportions of forest cover increases at the timber line over the past 100 years (Providoli & Kuhn 2012; Figure 1).

1.2.1 Study region

Geographic overview: The study region is located near the village of Grindelwald (46°37'33''N, 8°02'00''E / 1050 m a.s.l., Northern Swiss Alps) and belongs to the world heritage site of the Jungfrau Region, surrounded by the famous mountain peaks of the Eiger (3970 m a.s.l.), Mönch (4107 m a.s.l.) and Jungfrau (4158 m a.s.l.). The community covers more than 17,000 ha and has a population of around 4000 inhabitants. More than half of the community area is considered as unproductive (glaciers, rocks etc.) and almost one third of it is agricultural land (Liechti et al., in prep.; SFSO 2014). The western boundary of the research area is near Kleine Scheidegg (2061 m a.s.l.) and the eastern boundary is near Alpiglen (1616 m a.s.l.). The study region covers a surface of around 4 km^2 (Figure 1).
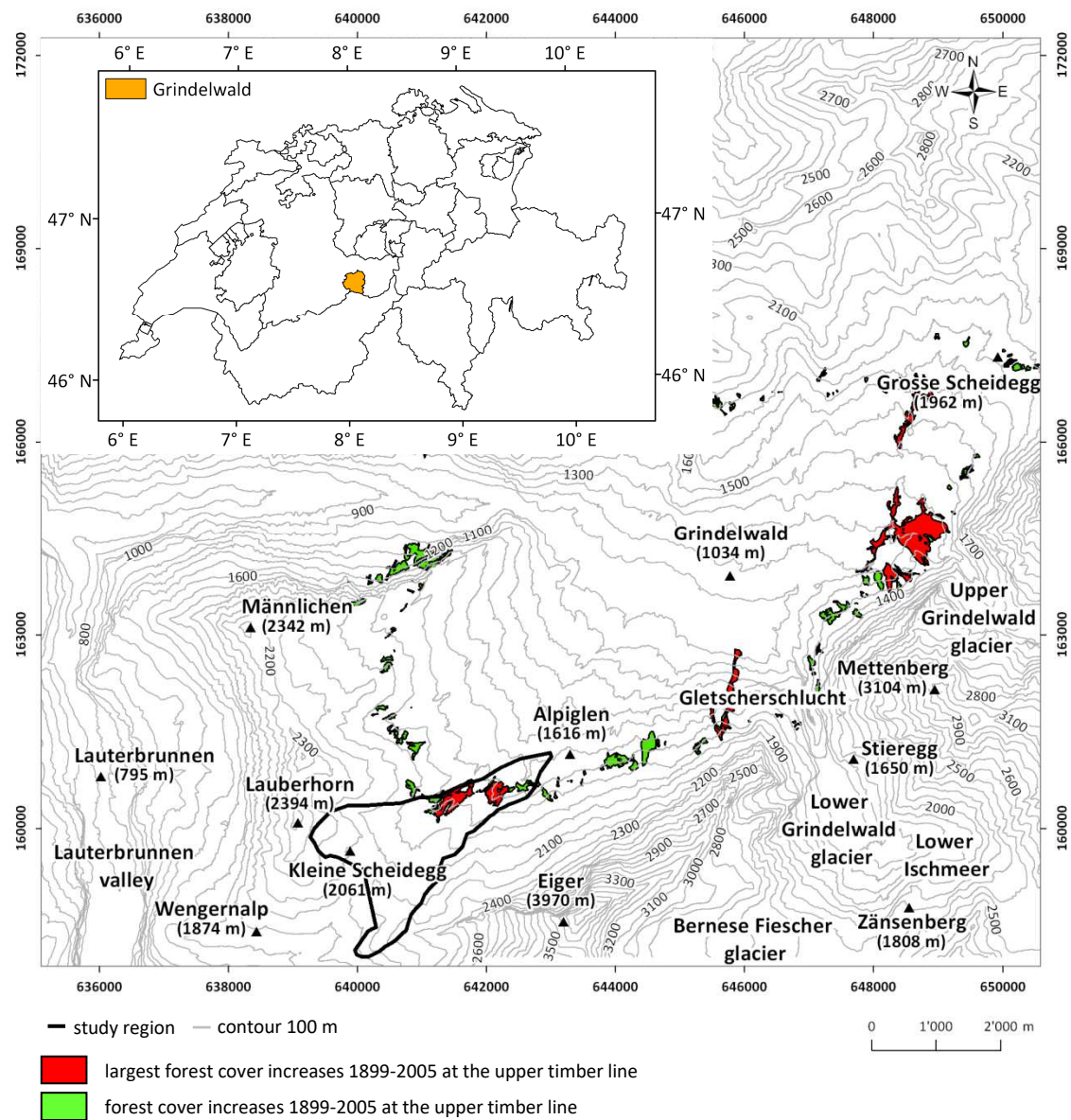
Figure 1 Index map of the study region
Source: Contours: Digitales Geländemodell 2m © swisstopo; site Grindelwald: © GADM database; largest forest cover increases and forest cover increases at the upper timber line: Providoli & Kuhn 2012

Climate: Like several regions in the Northern Alps, Grindelwald is characterized by a subalpine-alpine humid climate, and different wind systems are of great importance for the region's microclimate. Mean annual temperature is 6.1 °C in Grindelwald (1158 m a.s.l.) and -7.6 °C at the Jungfraujoch (3580 m a.s.l.). Mean annual precipitation ranges between 1575 mm at Grindelwald (1158 m) and 1800-2000 mm at Kleine Scheidegg (2061 m). The Federal Office for Meteorology offers air temperature data for Grindelwald only between 1966 and 1989. The weather stations at Jungfraujoch and Meiringen (595 m a.s.l.), both located near Grindelwald, have made long term measurements of air temperature that show an increase in the decadal mean air temperature of 0.9 °C since the beginning of the 19th century, in accordance with the warming observed in other high mountain regions (Meteo Swiss 2010, 2014; Providoli & Kuhn 2012).

Geology and Geomorphology: The landscape features in the study region are a result of complex ancient geological and tectonic structures. According to the geological atlas of Switzerland (1938), the following tectonic units are dominant: (1) the Autochthonous Aar massif (crystalline bedrock): summits of Jungfraujoch and Mönch, deep carvings of Lower and Upper Grindelwald glacier, SW flank of Mettenberg and east slope of Eiger; (2) the Parautochthonous imbrication (massive limestone rocks of Tertiary): steep north-falling base of Eiger, Mettenberg, Wetterhorn, Wellhorn and Engelhörner; and (3) the Mesozoic limestone sediments of: (a) the Helvetic nappes (Wildhorn-nappe): mountain chains of Faulhorn, Lauberhorn, Männlichen, Wetterhorn and some parts of Schilthorn, as well as (b) the Ultrahelvetic nappes (Doldenhorn-nappe), subsidence zone between Kleine Scheidegg, Grindelwald and Grosse Scheidegg (Collet et al. 1938; Labhart 2001; Figure 2; Table A 40).
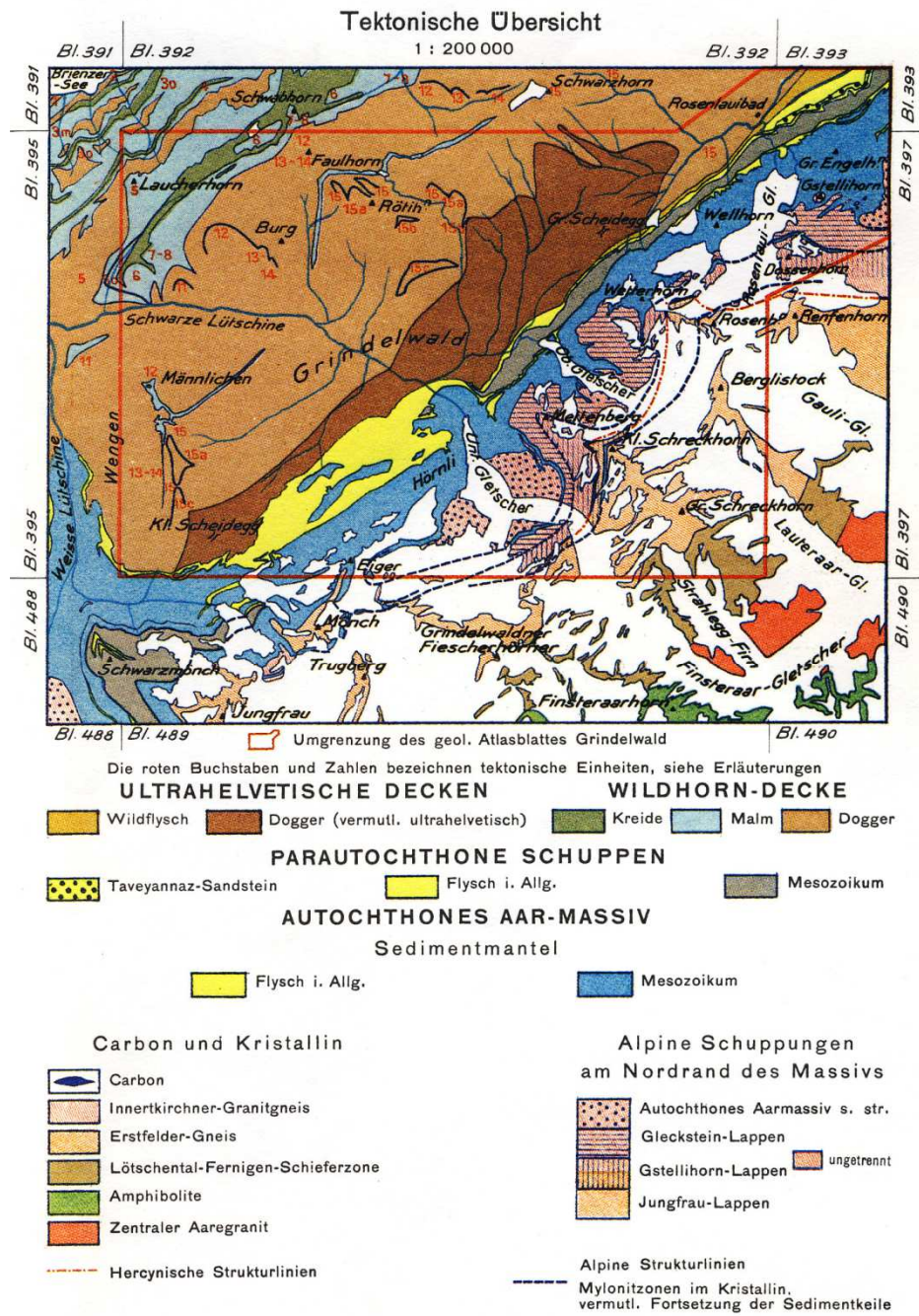
Figure 2 Tectonic overview of the Grindelwald region 1:200'000
Source: Collet et al. 1938, unchanged reprint in 1985

The geomorphology of the region shows strong contrasts caused by: (1) the geology of the underlying bedrock, (2) fluvial processes (Lütschine river), and (3) glacial processes (Lower and Upper Grindelwald Glacier), but also (4) recent processes of landscape evolution (rock-fall and landslide activity). Therefore, wide and smooth slopes, which are predominated by schists of the Wildhorn- or Doldenhorn-nappe (between Kleine Scheidegg, Grindelwald and Grosse Scheidegg), alternate with steep, partly glaciated walls of the high-elevation mountain chains of the Eiger, Mönch, Jungfrau, Mettenberg and Wetterhorn, which are predominated by tough material, such as igneous rocks and limestone breccias. The wide basin of the Grindelwald valley was formed firstly during the Quaternary period by glacial activity of the Lower and Upper Grindelwald glaciers and in more recent times by the Lütschine River (Table A 41). The Lower and Upper Grindelwald glaciers are among the most famous glaciers in the Bernese Oberland and along with the Great Aletsch and Gorner glaciers have been the subject of scientific as well as artistic interest for many centuries (Holzhauser et al. 2005). Especially the Lower Grindelwald glacier (length: 8.85 km, area: 20.6 km^2, see Holzhauser & Zumbühl 2003; Figure A 3) is one of the best-documented glaciers in the Swiss Alps, indeed the world, because of the easy access accorded by its extraordinary low position at 1297 m a.s.l., below the timber line (Zumbühl 1980; Zumbühl et al. 2008). Continuous glacier and permafrost ice melting have enhanced rock-fall and landslide activity within the study region in the recent years (Keusen 2006; Oppikofer et al. 2008; Wagner & Saurer 2008; Huggel et al. 2010, 2011; Werder et al. 2010). The current landscape-forming processes are determined by the composition of bedrock, and thus the smooth slope between Kleine Scheidegg and Grindelwald shows a tendency for landslide activity, because schists show a low permeability and are therefore very moist. In contrast, the coarser grained fraction of the tough rock walls rather shows a tendency for rock fall activity (Collet et al. 1938; Kienholz 1977; Tables A 41-42).

Soils and vegetation: Soil type is determined by the bedrock material, vegetation type and microclimate, as well as the climate conditions that change with elevation. The complex geology gives rise to a wide distribution of soil types. The solid and steep rock walls show a high content of soil skeleton with a large fraction of coarse grained components (blocks and stones: 2-6.3 dm grain diameter; see Table A 42) that weather only slowly, whereas, in contrast, the smoother material formed by schists show a low content of soil skeleton with a large fraction of finer grained components, which are highly erodible and weather more easily. Since limestones are dominant, cambisols with high chalk content are widespread. Vegetation type and microclimate are determinants that can cause soils of forests to differ from those of grassland areas. Soils of forests and subalpine dwarf shrub heath are composed of acid podsols, whereas grasslands and the calcareous debris slopes are dominated by several types of cambisols with varying acidity (Käsermann 2007; Table A 41).

The region of Grindelwald shows a very diverse vegetation pattern with broadleaved and coniferous forests (21%), shrubs and dwarf shrub heath (7%), peat bogs and swamps (2%), cultivated fields (24%), pastures, meadows and grassland (20%). The remaining herbaceous vegetation of 7% comprises richly manured alpine pastures and snow pocket vegetation. 16% is allotted to rock and debris vegetation and in 3% of the region vegetation units have not been defined. Those areas mostly belong to settlement areas (Hegg & Schneiter 1988; Figure A 1; Table A 38). The vegetation of the region is similar to that of other regions in the Northern Swiss Alps, being characterized by: (1) a mountain belt (600-1500 m) with limestone fir-beech forests (Piceo-Abietion); (2) a subalpine belt (1500-1850 m resp. 2000 m) with Norway spruce forests (Vaccinio-Piceion); (3) a timber-line ecotone (1800-2200 m) with ericaceous dwarf shrubs (Rhododendro-Vaccinion, Rhododendro-Vaccinietum); (4) a subalpine and lower alpine belt (2200-2850 m) with *Nardus*-grassland (Nardion, Geo montani-Nardetum) and (5) a snow or nival belt (> 2850 m) with cushion plants, mosses and lichens (see Figure A 2; Lüdi 1948; Braun-Blanquet 1948/1949; Schweingruber 1972; Keller et al. 1998; Delarze & Gonseth 2008).

Land-use practices: Grindelwald has been affected by anthropo-zoogenic impacts, and the Alpine timber line has been strongly modified by human land use, for several hundred years (Naegeli-Oertle 1986; Hegg & Schneiter 1988; Liechti et al., in prep.). According to the latest measurements given by the statistical assessments of 2004/2009, the majority of the area is unproductive (53%) and comprizes glaciers and rocks (SFSO 2014). The agricultural land is mainly used for dairy husbandry and comprises intensively-used agricultural land (i.e., all rich meadows, rich pastures and nutrient rich moist grass), covering around 24% of the community area and extensively-used subalpine, alpine meadows and grassland that are occasionally grazed by goats and cattle, covering around 14% of the community area. The rough climate conditions mean that arable land is presently unimportant (Hegg & Schneiter 1988; Käsermann 2007; Table A 39). The commune of Grindelwald shows a well-organized human-environment system that regulates land-use intensity and therefore pastures have for centuries been protected from being overused. The whole area of the commune is divided into seven Alpine corporations that are involved in organizing and structuring all collective work related to livestock herding and the use of common-property summer pastures. As in many Swiss mountainous regions, land-use practices are focused on the high production potential that is guaranteed in easily accessible areas, so formerly-held extensive pastures along isolated, inaccessible and steep slopes have been completely abandoned and are prone to shrub encroachment (Liechti et al., in prep.).

1.2.2 Main objective

Worldwide treelines follow a common isotherm that was approximated by several older studies (e.g., Imhof 1900; Brockmann-Jerosch 1919; Däniker 1923; Hermes 1955; Troll 1973a, b; Tranquillini 1979). The most quantitative analysis of the altitudinal position of climatic treelines, carried out by Hermes (1955), also includes snow-line elevations, which are relevant to showing the correlation of treeline elevation with temperature.
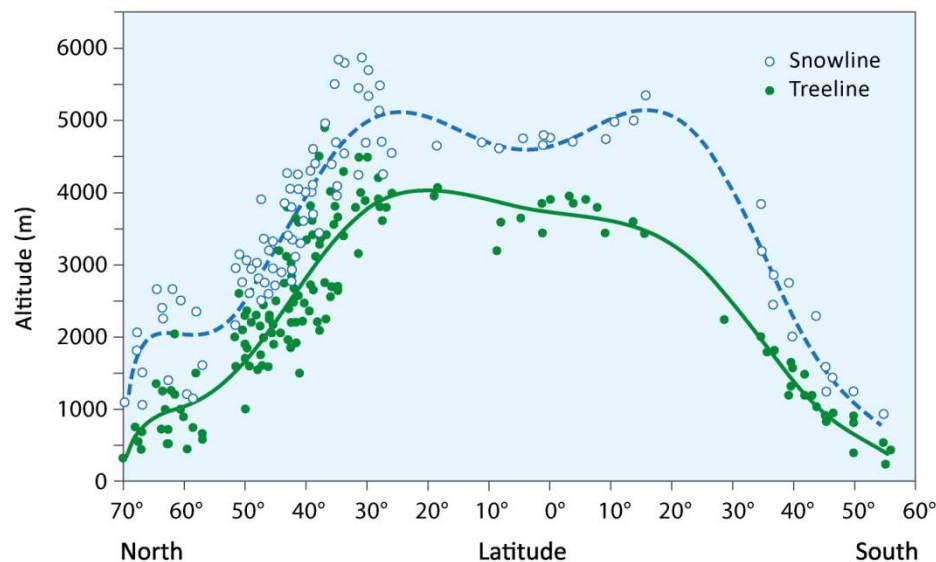
Figure 3 The latitudinal position of treeline and snow-line taken from a worldwide survey by Hermes (1955), supplemented by data from various other sources. Green dots mark points of measured treeline elevations while the white dots indicate points of measured snow-line elevations
Source: Modified from Körner (1998).

The studies by Körner (1998, 2003 and 2007b) and co-authors are particularly important, because they illustrate the effect of heat deficiency on tree physiology and morphology and demonstrate that treelines follow a global thermal boundary. Evidence for treelines following a worldwide position was presented by Körner (1998), who took the worldwide positions of treelines and snow-lines recorded by Hermes (1955) and conducted a polynomial regression analysis with a total of 150 treeline entries to confirm that treeline and snow-line elevations correlate with one another as a function of latitude across the globe (Figure 3). In addition, root-zone temperature measurements with data loggers that were taken at 46 treeline sites between 68 °N and 42 °S evidenced the importance of heat deficiency controlling the growth of trees (Körner & Paulsen 2004). Heat deficiency results by the limited investment of carbon used for structural plant growth, i.e., a carbon sink (Körner 2003) rather than a limited production of assimilates, i.e., a carbon source (Tranquillini 1979).

In reality, high mountain ecosystems usually react to climate and environmental changes in a more complex way and the average values provided by the global-scale latitudinally averaged measurements of treeline position are unlikely to be accurate enough to quantify changes at the local-scale where trees develop (Burga et al. 2003; Beniston et al. 2011). On the one hand, these conditions are triggered by the unpredictable interactions between surface cover and topography that cause non-linear and unknown responses to climate change (Haeberli & Burn 2002; Alftine & Malanson 2004; Kuhn & Yair 2004; Beniston 2005; Gruber & Haeberli 2007; Haeberli 2007; Kullmann 2007b; Zeng et al. 2007; Kuhn et al. 2011). On the other hand, most plant temperature responses (physiological and biological processes) are non-linear and therefore difficult to compare with temperature and precipitation means (Körner 1998, 2003).

The Braun-Blanquet (1964) vegetation mapping method coupled with long-term observation of permanent plots of plant communities has been shown to be effective for measuring changes in environmental conditions (biotic and abiotic) at the scale where trees and other plant species develop. Previous studies have monitored the mountain flora at several mountain peaks by comparing old and new vegetation records, and showed this method to be important for determining the impact of global warming at the scale of plant species development (e.g., Lüdi 1945, 1955; Braun-Blanquet 1957; Perret 2005; Burga & Frey 2007; Burga et al. 2010). In addition, other studies have shown that the timber-line ecotone is well-suited to exploring the response of trees to changes in environmental conditions at the scale of plant species development (i.e., plant structure and phyto-diversity), because it characterizes an ecologically sensitive area (Burga & Perret 2001a, b; Walther et al. 2001). Trees growing at the timber-line ecotone respond to environmental change in different ways (e.g., growth, growth forms, production of viable seeds and distribution pattern of plant communities), because several factors, such as global warming, precipitation distribution, slope erosion, snow avalanches, grazing, and wood clearing, may interact (Holtmeier & Broll 2005).

An important pioneer in vegetation science was W. Lüdi, who introduced plant succession as a genetic-dynamic principal to illustrate changes taking place in the ecosystem over a certain time period and was one of the first scientists who published vegetation maps for the Lauterbrunnen valley in 1921 on the basis of vegetation mappings (Lüdi 1921). This detailed vegetation study of the 1920s (Lüdi 1921), makes it possible not only to study the dynamics of vegetation boundaries over the last 100 years, a period when climate warming has taken effect, but also to distinguish changes attributable to land use from those attributable to climate warming (Strähl & Burga, in prep.). However, these possibilities have not yet been exploited.

My Ph. D. project investigates the effectiveness of vegetation mappings proposed by Braun-Blanquet (1964), in identifying differences in dynamics of vegetation succession at the Alpine timber line and determining their probable driving process, whether land-use changes or climate warming, and will give answers to the following questions:

(1) Does the vegetation mapping method according to Braun-Blanquet (1964) distinguish the impacts of global warming and changes in land-use activity in relevés taken at the timber-line ecotone?

(2) Which mapping variable (plant structure or phyto-diversity) is best suited to inferring an initial sign of warming impact in a newly forested area at the Alpine timber line?

(3) Are the results given by the relevés significant enough to assess what percentage of the Alpine timber line that has locally advanced to higher elevations has advanced in response to global warming and what percentage has advanced in response to land-use changes?

(4) Where do we expect changes in the timber line to be driven by global warming and where not?

(5) Where do we expect an upward shift in the timber line and where not?

To perform this study, we implemented the vegetation mapping method of Braun-Blanquet (1964) in 32 selected sites within the newly forested area at the timber-line ecotone, in which differences between signs of a possible warming impact and signs of reduction in pasture activity can be most reliably detected; and where other impacts (e.g., topography, substrate, surface processes etc.) are as much as possible excluded or kept constant. Vegetation mappings were conducted in areas where subalpine dwarf shrub heath, subalpine and alpine grassland communities interact. Because the habitat-forming capacity is lower in these communities than in forest communities, subalpine dwarf shrub and grassland communities are well-suited to studying the cause of changes in dynamics of vegetation succession over time and therefore often show a relationship to each other (Braun-Blanquet 1964; Glavac 1996; Begon et al. 1999).

Statistical tests were implemented to assess the effectiveness of vegetation mappings proposed by Braun-Blanquet (1964) in identifying differences in the dynamics of vegetation succession in different places at the Alpine timber line and determining whether the probable driving process was land-use changes or climate warming. Statistical tests were also used to judge which vegetation mapping variable, plant structure or phyto-diversity, is more effective at marking initial signs of warming impact in the distribution pattern of plant species at the timber-line ecotone.

2 Forest and plant succession in the timber-line ecotone

The timber line is the most conspicuous vegetation limit in high-mountain areas and has long attracted research for both scientific and practical reasons (Holtmeier 2009).

Timber lines and treelines are natural boundaries that are defined by convention because their borderline strongly depends on the spatial resolution at which they are considered (Armand 1992; Camareo et al. 2000; Körner 2012). In contrast to the snow line, they do not follow a horizontal or vertical distribution along a specific isotherm and are therefore well suited to studying the effects of evolutionary climate change over short spatial distances (Troll 1961; Körner 2007a, b).

2.1 Definition and terminology

The timber line is termed an ecological boundary and shows the upper limit of continuous closed forest (Table 1). In the present study the terms timber line, treeline, krummholz line and timber-line ecotone are applied according to the definitions given by Holtmeier (2009) and Körner (2012) (see Figure 4; Table 2). The rough climate conditions cause a clearly altitudinal zoning of vegetation, because heat deficiency restricts plants from investing enough carbon for their structural growth (Körner 1998). As a result, trees become marginal when low temperatures, below 5 °C during the growing season, limit the investment of carbon required for structural plant growth. Furthermore, increasingly harsh climate conditions cause a reduction in nutrient supply, hence trees are required to spread over a wider area in order to compensate for the loss in nutrient supply and therefore grow less densely (Körner 2003).

Vegetation displays a pattern that changes with increasing elevation, forming several distinct belts that surround the mountains in a roughly circular fashion (Landolt 2003; Figure 10). In the Swiss Alps, altitudinal belts are represented by the **mountainous belt**, **subalpine belt**, **alpine belt** and **nival belt** (Table 1).

Table 1 Characteristics of each altitudinal belt in the Northern Swiss Alps

vegetation belt	elevation [m a.s.l.]	climate	soil	vegetation	utilization	forest and non-forest surface
nival belt	> approx. 3000 m	permanent snow cover, locally melting in summer	immature soils	locally distributed pioneer vegetation, e.g. cushion plants	no land-use	**rock and debris**
alpine belt	2000-approx. 3000 m	vegetation period approx. 60-80 days	rendzina, regosol, cambisol	scree vegetation, perennial herbs, cushion plant, lichen, moss, dwarf shrub heath and krummholz-forms	dairy husbandry during summer, pastures	**grassland**
timber line						
subalpine belt (*Picea abies* boundary)	1400-approx. 1850 m, occasionally -2000 m	mean annual temperature 0-5 °C, vegetation period > 100 days	cambisol, podsol	coniferous forests *Picea-Abies*, *Acer pseudoplatanus*, *Pinus, Picea, Larix*	dairy husbandry during summer	**forest surface**
mountainous belt (*Picea-Fagus* boundary)	800-1400 m (N-exposition), -1500 m (S-exposition)	mean annual temperature 5-8 °C	cambisol, podsol	beech-fir-mixed forests *Abies alba*, *Picea-Abies*-beech forest and *Picea-Abies*-fir forest	agriculture livestock management	

Source: Modified from Ellenberg (1996), Veit (2002) and Landolt (2003)

The timber line forms the boundary between the subalpine and alpine belts (Table 1). Determined according to the definition of Körner (1998) and Körner and Paulsen (2004), i.e., by low temperatures that restrict tree growth, the timber line occurs over a worldwide range, where the seasonal mean air temperature is between 5.5 and 7.5 °C and the mean soil temperature is 6.7 °C ± 0.8 °C at a 10 cm depth.

Table 2 Definition of terms (timber line, treeline, krummholz line, timber-line ecotone). Values expressing elevation refer to the potential natural/non-disturbed limit for the Northern Alps.

	elevation [m a.s.l.]	description
Forest limit / Timber line	1800-2000	– upper limit of continuous closed forest – boundary with gradual decline in tree size and opening of the canopy – tall growing trees with a minimum tree height of 2 m – minimum tree stand cover 30-40 % – minimum distance between the trees ≤ 30 m
Tree limit / Tree line	2200-2300	– highest elevation of upright growing trees – trees with a minimum height of 2 m – minimum distance between the trees > 30 m
Krummholz line	2000-2400	– upper limit of tree existence – dwarfed trees with a height below 2 m
Timber-line ecotone	1800-2200 (2300)	– ecologically sensitive area – transitional zone describing the direction of forest progress

Source: Definition of terms is according to Holtmeier 2009 and Körner 2012. Values expressing elevation are according to Imhof 1900, Brockmann-Jerosch 1919, Däniker 1923 and Landolt 2003. Forest definition is according to the LFI (Brändli 2010), see Figure A 5.
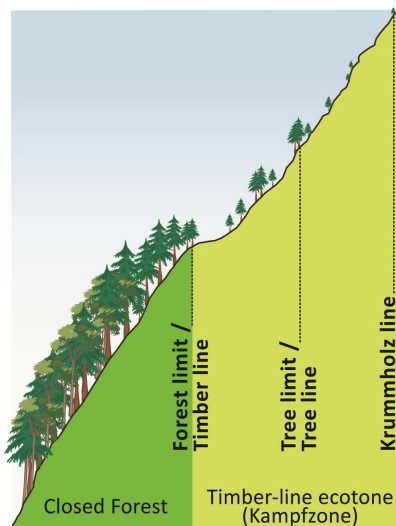
Figure 4 Definition of terms (forest limit / timber line, tree limit / treeline, krummholz line, timber-line ecotone)
Source: Modified from Tranquillini (1979)

Trees are identified as woody, upright-growing plants with a dominant above-ground stem. They form the most obvious vegetation boundary that can be observed by a change in the size and structure of trees (Figure 4; Körner 2012). The critical minimum height for defining a tree ranges from 2 to 8 m and is dependent on the type of tree because each species adapts differently to the harsh climatic conditions at high elevations. On temperate mountains, 2 m is usually used to define the altitudinal limit of tree species, since in that climate and ecological situation taller trees are more exposed to the harsh climate influences above the winter snow cover, whereas smaller individuals are better protected (Holtmeier 2009).

Krummholz species may be either genetically determined or a response to locally deteriorated environmental influences (natural or anthropo-zoogenic). Genetically-determined Krummholz species include all taxa with bush-like growth-forms (e.g., mat growth), such as *Pinus mugo* s. str. or *Alnus viridis*, and are genetically different to tree species. Other Krummholz species, or crippled trees, have forms determined by locally deteriorated environmental influences, displaying the tree-like features (e.g., having a crown, being single- or multi-stemmed) seen in those species that occur in the upper montane forest, but being shorter than the minimum height required to be identified as a tree (Holtmeier 1981).

The timber-line ecotone is designated as the "battle zone" of the forest (Figures 4 and 5; Table 2). Trees are either reinvading their former terrain after forest clearance, as soon as pasture activity reduces (anthropo-zoogenically/disturbed conditions), or invading a new terrain beyond their potential limit (natural/non-disturbed conditions), as global warming allows dispersed diaspores of trees to germinate at a higher elevation beyond the potential current timber line (Holtmeier 2009; Figure 5).
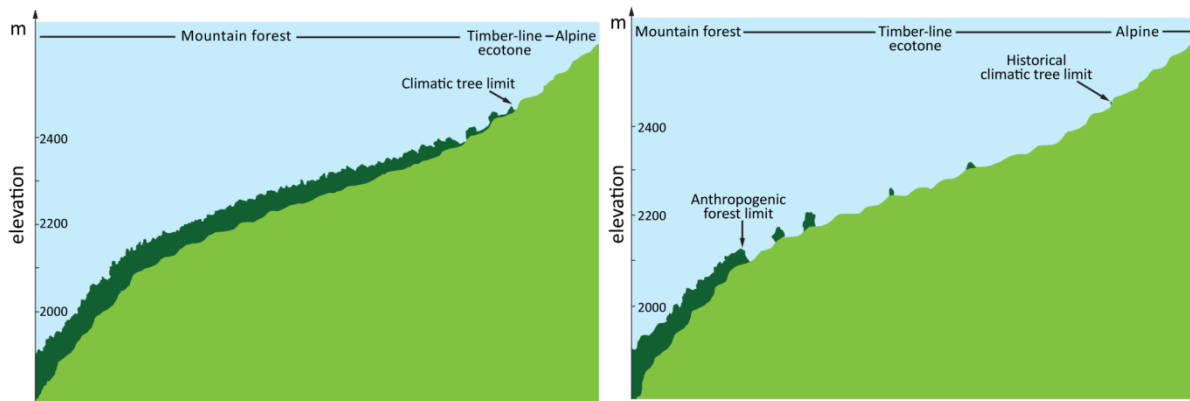
Figure 5 Upper limit of forests under natural/non-disturbed conditions (left picture) and anthropo-zoogenic/ disturbed conditions (right picture).
Source: Modified from Holtmeier (2009)

Hence, there are a large number of environmental factors (e.g., climate, relief, soil, human and cattle) at play here, which drive intense competition between species and result in high dynamics of vegetation succession (Burga & Perret 2001b). Vegetation in the ecotone is fragmented, because individual trees compete with groups of trees as well as dwarf shrubs and herb species. Diversity is therefore high, comprising approximately 100 different plant species (Burga & Perret 1998). The shape and maximum altitudinal width of the timber-line ecotone (i.e., from tree to shrub-like growth forms) is determined by the shape of landscape. In steep terrain the ecotone is narrow, compressed into as little as a few hundred meters or less in the temperate high mountains, whereas in flat terrain it may stretch as wide as 10-100 km in subarctic lowlands (Holtmeier & Broll 2010). The ecotone is narrower where plant species react more sensitively to the environmental gradient, whereupon the boundary approaches a line. Steep mountain slopes, for example, compress climatic gradients and therefore produce a narrow transition zone of tree decline near the distribution limit (Körner 2012).

In contrast to the irregular natural boundaries formed by the timber line and treeline, as a thermal boundary, the snow line appears as an abrupt line, because it connects points above which the ground remains snow-covered for most of the year and precipitation falls as snow. The climatically-driven snow line is dependent on the mean summer temperature and the amount of precipitation. It corresponds to the elevation at which the mean air temperature of the warmest month of the year is 0 °C (Troll 1961; Körner 1998).

In Grindelwald the altitudinal variation of timber line, treeline, krummholz line and timber-line ecotone behaves in the same manner as in other northern Alpine regions (Figure 7; Table 2). The current timber line shows a non-continuous shape in the study region and is partly interrupted. The upper limit of continuous closed forest is characterized by ribbons of forest trees forming groups or troops (Figure 6).
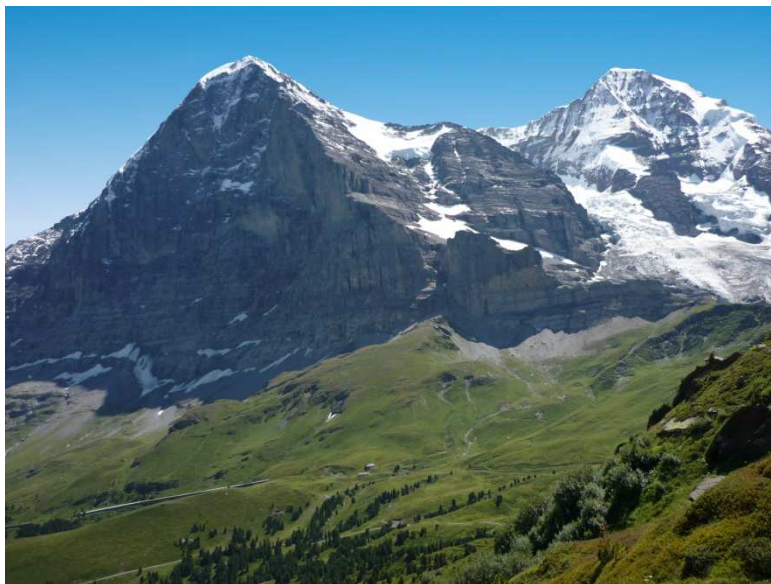
Figure 6 The current timber line in the study region is characterized by ribbons of forest trees forming groups or troops. This photo was taken from a site near the Kleine Scheidegg with view to the summits of Eiger and Mönch as well as the Eiger north wall. Photo: S.C. Strähl, August 2009

Dominant timber line-forming tree species are *Picea abies* and *Pinus mugo* ssp. *uncinata*, whereas *Larix decidua* is less frequent. As in other northern Alpine regions, *Pinus cembra* shows a fragmented distribution (Hegg & Schneiter 1988; Käsermann 2007). The main distributional range of Swiss stone pine forests are usually in areas with a climate of extremely continental character, such as the Central Swiss Alps. Swiss stone pine forests may exceptionally also occur in northern alpine regions, especially in rear valley sections, i.e., isolated high-lying valleys, where soil conditions favour its development. Because of its valuable wood, Swiss stone pine forests were cleared in several areas of the Northern Swiss Alps, and tall examples found nowadays are relicts of these former forests (Imhof 1900; Rikli 1909; Schweingruber 1972; Keller 1998; Steiger & Carraro 2010). A large population of *Pinus cembra* is located on the eastern flank of the Kleine Scheidegg. This area includes forests of the

upper Wärgistal, e.g., Itramenwald, that form loose stocks extending between 1650 and 2000 m a.s.l. (Rikli 1909). Like in several northern alpine regions, areas of former *Pinus cembra* forests are currently being invaded by *Picea abies*, which has similar ecological preferences, but is more competitive than *Pinus cembra*, because of its ability to reproduce by layering (Käsermann 2007; Holtmeier 2009). *Picea abies* forms denser stands and more abrupt timber lines than *Pinus cembra*, which influences both changes in the pattern shape at the timber-line ecotone (distribution of dwarf shrub and grassland vegetation) and ecological behaviour of the habitat (Ellenberg 1996; Holtmeier 2009).

The elevation of the potential timber line is between 1800 and 2000 m a.s.l. (Figure 7) and has increased by approximately 30 m over the past 100 years. Major changes have been largely attributed to reduction in land-use activity and effects of surface morphology, with only minor changes related to global warming (Providoli & Kuhn 2012). The current timber line is anthropo-zoogenically determined to a large extent and is therefore situated far below the potential timber line of Northern Swiss Alps, at an elevation of approximately 1643 m a.s.l. (Bundesamt für Landestopographie 1861, 1899; Office of Geoinformation 2007; Providoli & Kuhn 2012).

Figure 7 Extent of timber line, tree and krummholz line and timber-line ecotone for Grindelwald (Northern Swiss Alps). Photo: S.C. Strähl, October 2011

2.2   Crucial factors controlling tree growth dynamics at the timber line
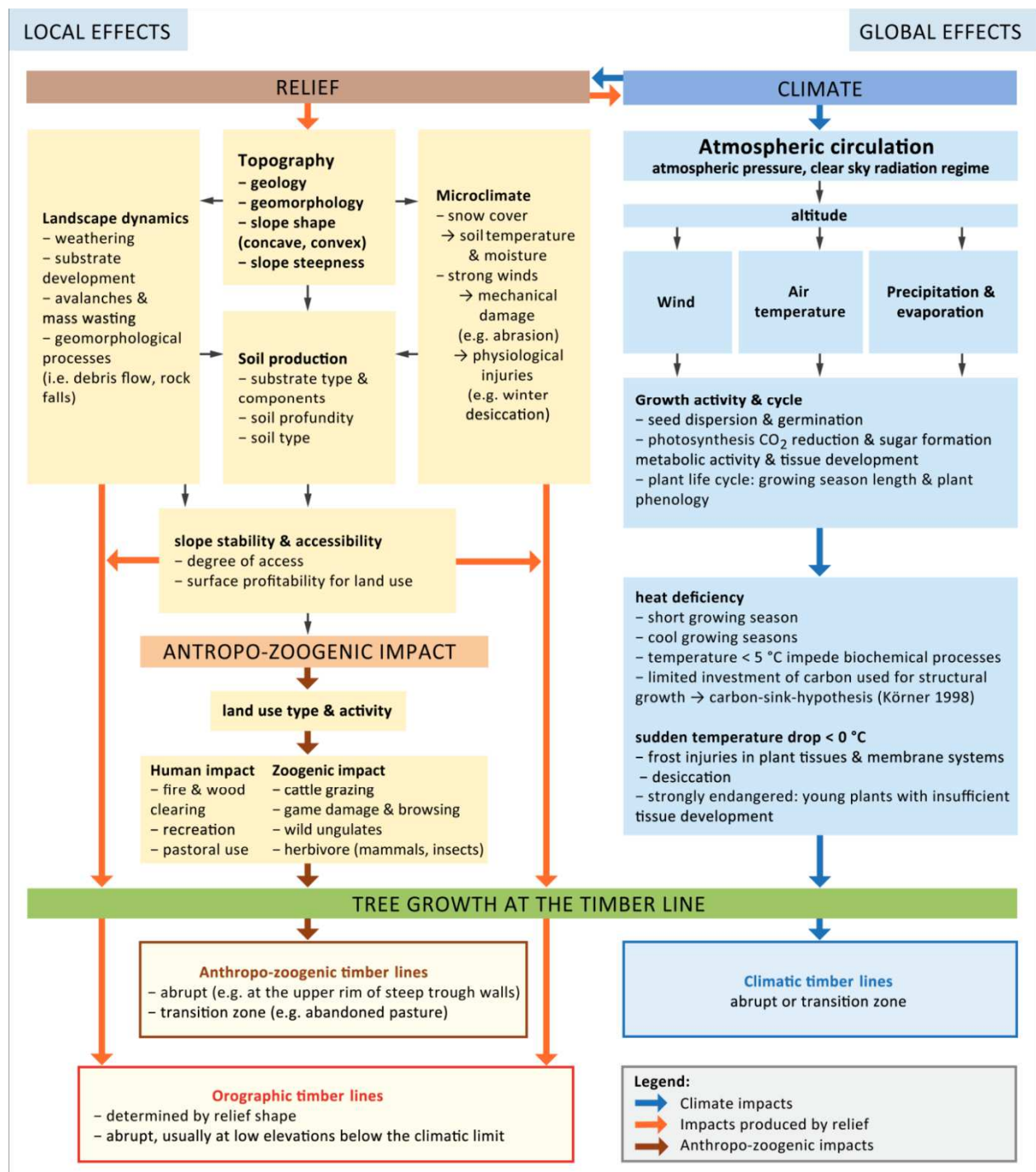
Figure 8 Flowchart expressing the factors crucial for tree growth at the timber line
Source: Modified from Holtmeier & Broll 2010

Tree growth at the timber line varies drastically. This is due to a wide range in microhabitats over short distances that interact with each other and together at several scales (global and local) (Figure 8; Landolt 1977, 2003; Ellenberg 1996; Burga & Perret 2001a,b; Holtmeier & Broll 2005, 2010; Malanson et al. 2009).

2.2.1 Climatic factors

In high mountain ecosystems, the weather and climate are complex and often show extremes. This is due to interactions between mountains (topography) and the general circulation of the atmosphere (changes in air pressure and solar radiation) (Figure 8; Beniston 2005, 2006). Mountain climates are characterized by important parameters such as air temperature, precipitation and wind, and these in turn strongly depend on elevation. As a consequence, climatic conditions increasingly deteriorate as elevation increases: temperature drops of 0.55 °C per 100 m, precipitation increases of 100 mm per 100 m and growing season length reductions of 9 days per 100 m (Theurillat et al. 1998; Menzel & Estrella 2001; Landolt 2003). Changes occur rapidly and systematically over very short distances. At higher elevations, tall-growing plant species like trees are more exposed to the prevailing atmospheric conditions than short-growing plant species. Therefore, the potential of trees to invest assimilates for growth is strongly reduced when temperatures decline (Hoch & Körner 2003, 2009, 2012; Körner & Hoch 2006). In addition, trees growing near treelines must be highly adapted in order to persist against the harsher climatic conditions at higher elevations. They are forced to develop special growth forms with reduced height, such as mat growth, where trees resemble stunted shrubs just a few cm tall and less than 1 m long that help them to profit from the more favorable climatic conditions that exist near the ground. Furthermore, they must show a high degree of frost resistance in their plant cells in order to tolerate low temperatures. For example, *Picea abies* and *Pinus sylvestris* survive temperatures of down to -40 °C when needles are fully developed. *Pinus cembra* is known to be the most frost-resistant tree species in the European Alps. It can tolerate temperatures as low as -70 °C (Tranquillini 1979). In contrast to upright trees, prostrate shrubs and herbs are, owing to their short growth, especially when they are covered by snow in winter, less exposed to the prevailing atmospheric conditions. They therefore reach higher elevations. Moreover, some of them may be also more adapted in their physiology to survive the rougher climate conditions at high elevations (Figure 9). Apart from temperature reduction with elevation, changes in precipitation intensity also strongly affect vegetation succession dynamics at the timber line. The amount of precipitation is responsible for the availability of moisture, which is as important as heat deficiency for survival, especially when considering the local-scale of plant species development. Snow cover protects plants from freezing damages and is important for the plant-available soil moisture. At the same time, snow pack increases soil temperatures in winter, which increases nutrient availability and has a positive feedback on plant growth. Therefore, a lack of plant-available soil moisture may impede germination, seedling establishment and survival at the timber line (Holtmeier 2009; Hagedorn et al. 2014).
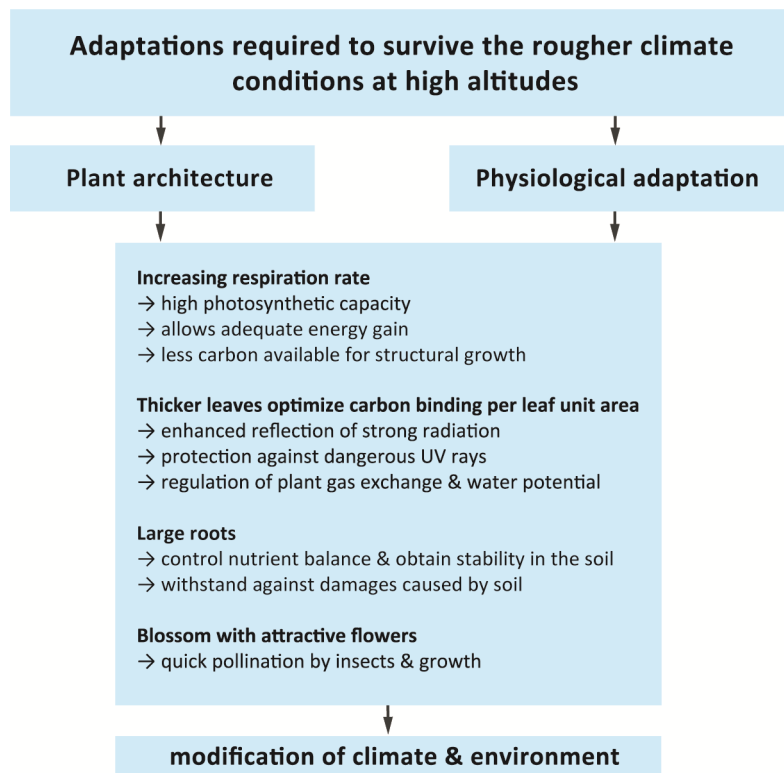
Figure 9 Flowchart showing crucial adaptation mechanisms of alpine plants to high mountain climate
Source: Modified from Körner 2003

2.2.2   Relief and soil

Relief is an influential factor in high mountain ecosystems that creates distinct local environments that interact with other factors, such as temperature, moisture and nutrient availability, wind exposure, seasonal snow cover, geological substrata and soil forming processes (Figure 8). Relief may modify and locally overrule climate factors, for instance, by affecting the amount of rainfall, the proportion of rain to snow, persistence of snow, temperature, exposure to sunshine, also insolation intensity and growing season length (Beniston et al. 1997; Grabherr et al. 2003). The duration and depth of snow varies between convex- and concave-shaped sites: Concave-shaped sites may be covered by snow until the beginning or middle of July, occasionally even until early August. In contrast, convex topography is mostly devoid of snow in the winter and also becomes snow-free earlier in spring. A deep and long-lasting snow cover negatively affects and pressurizes trees in mountain forests, especially during restocking. Snow fungus is mainly harmful for young growth of coniferous trees, such as *Picea abies*, *Pinus cembra* and *Pinus mugo* ssp. *uncinata*, as long as their crowns remain covered by snow until spring. Damage from snow fungus is mainly observed in areas with high humidity and late snow melt, such as in topographical depressions, e.g., dells and gullies, where young dwarfed trees restricted to heights below 1 m are unable to break out of the maximal snow cover (Ott et al. 1997).

In areas protected by a favorable topography, the growing season length may be prolonged. Habitats shaped by rocks may be free of snow almost two months earlier, which allows plants to flower earlier in a warmer climate (Keller et al. 2005). Spring-flowering vascular plants (flowering individuals of *Gentiana verna* as well as *Viola calcarata* and *Anthyllis alpestris*) have been observed in blossom as early as November in wind-sheltered areas at 2000 m a.s.l. in the Avers valley in the Eastern Swiss Alps (Burga 2014, oral communication).

Relief controls insolation intensity and surface heating, so creating climate differences between central and outer mountain ranges. Therefore, the elevation of vegetation boundaries varies considerably between the Northern, Central and Southern Alps (Figure 10). This effect of mass elevation was already applied by Brockmann-Jerosch in 1919 to explain that the worldwide elevation of timber lines strongly correlates with mass elevation, the highest timber line elevations corresponding to areas with the highest mass elevation. Mass elevation is defined as the mean elevation of a mountain massif and can be calculated by transforming the mountain massif into a plateau without changing the mountain's basal area and volume. Large mountain massifs serve as a heating surface, which causes day-time summer temperatures to be higher in the central than in the outer mountain ranges. In response, vegetation boundaries (e.g., mountainous boundary, subalpine boundary) are higher in the inner ranges than in the outer ranges and the vegetation shows a different character (Figure 10). Similarly, the elevation of the timber line is higher in the Central Alps (2200-2400 m) than in the Northern Alps (around 2000 m). Moreover, mass elevation determines the energy used for snowmelt and evaporation, which is less in the central than in the outer mountain ranges. Snow cover duration is therefore shorter in the Central Alps (200 days) than in the Northern Alps (280 days), and the growing season is subsequently longer. Furthermore, the elevation of the snow line can be assumed to be dependent on mass elevation (Brockmann-Jerosch 1919), because the snow line in the Northern Alps (2400 and 2700 m a.s.l.) is at a lower elevation than in the Central Alps (2700-3200 m a.s.l.) (Landolt 2003). Mass elevation is also responsible for the climate to be more continental in the Central Alps, because sunshine hours are higher and precipitation is lower (Burga and Perret 2001b; Holtmeier 2009).
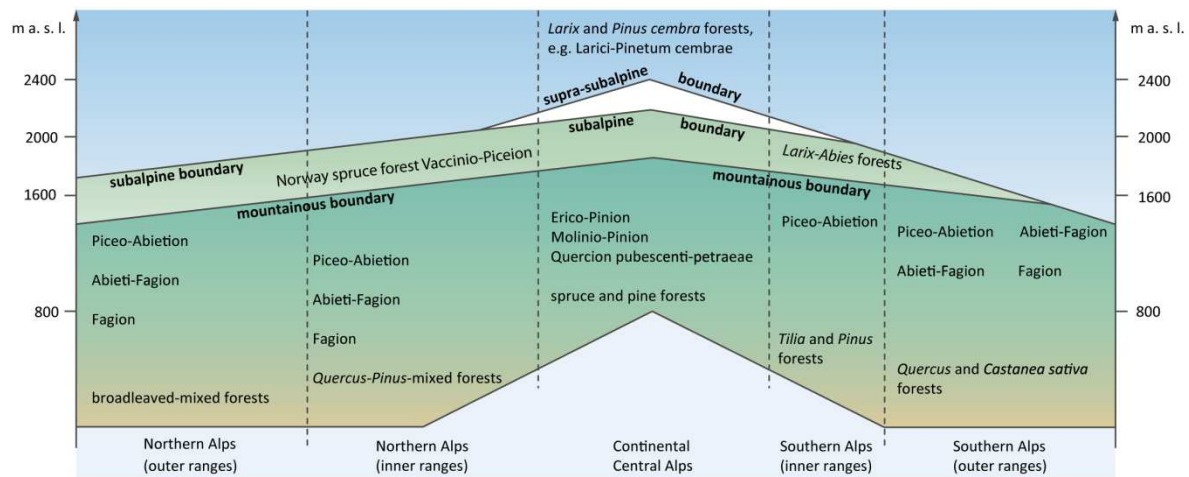
Figure 10 The effect of relief on the elevation of boundaries between the Northern, Central and Southern Swiss Alps. Source: Modified from Ott et al. 1997

Tree development also depends on relief (Nagy et al. 2003; Batlori et al. 2009). Trees can establish and grow better in areas showing a stable substrate (i.e., where grain size is optimal for soil and vegetation to develop), or between blocks where organic matter and fine mineral matter accumulate and provide more moisture and nutrient supply (Holtmeier et al. 2003; Burga et al. 2010; Vitasse et al. 2012). Rugged topography and areas with a protective snow cover, such as concave or wind-sheltered slopes with locally optimized microclimates or edaphic conditions, also favor tree growth and govern the structure of treeline vegetation (Kullmann 2001, 2002, 2007b; Kullmann & Öberg 2009). Relief, however, also prevents trees from developing and reaching their potential climatic altitudinal limit (orographic timber lines, see Figure 8). Most notably, this occurs in areas dominated by bedrock geomorphic units, steep rock walls, slopes with mass wasting or covered by debris, talus cones and avalanche tracks, but convex topography allowing strong winds and wind-exposed slopes, also restricts the development of trees or causes injuries in existing trees (Holtmeier et al. 2003; Kullmann 2005; Holtmeier & Broll 2010; Marcias-Fauria & Johnson 2013).

Soil, which serves as an important water and nutrient reservoir for plant growth, is on the one hand dependent on the form and texture of relief and on the other hand by climate. Climate controls the soil forming processes performed by decomposers (microbial activity). The time during which soil genesis is optimal, i.e., soil temperature ≥ 5°C, is limited to about 45 to 110 days, and thus plant and animal life cycles, which have the most obvious effects on soil decomposition and genesis, are reduced or even prohibited. Soils accumulate a large amount of organic matter at the surface horizons, develop only very slowly in the upper 20-25 cm and, as presented in studies that were carried out in the Rocky Mountains, alpine soils need about 10,000 years to reach a thickness of 30 cm. In contrast, most leaf litter at low elevations is recycled within a year. As a consequence, soils at the tree limit (Ah- and Bv-horizon between 10-20 cm) and forest limit (Ah- and Bv-horizon

between 30-40 cm) are shallower than in lowland areas (Ah- and Bv-horizon approx. 1 m) (Retzer 1974; Larcher 1977; Körner et al. 1996; Ott et al. 1997; Körner 2003; Kammer 2006). In treeline soils the Bv-horizon is usually not completely developed or even missing. Soils above the timber line are shallow, show a high amount of coarser grained components (e.g., blocks with grain diameter of 2-6.3 dm), vary over very short distances and display the form of the relief. The uptake of water and nutrients required for plant growth is better provided in deeper soils (90-120 cm depth) than in shallow soils (15-30 cm depth) because deeper soils are better decomposed, but also the intensity of root penetration is optimized in deeper soils (Ott et al. 1997). Soils therefore influence the type of vegetation, whereas missing soil cover or shallow soils restrict tree growth (edaphic timber lines) and prevent trees from reaching their possible climatic altitudinal limit. However, also areas with waterlogged soils, such as hollows, gullies or other depressions collect a large amount of moisture due to longer lasting or deeper snow cover and may remain treeless as well.

2.2.3 Impacts of land-use changes

The anthropo-zoogenic impact is a further important factor for the timber line, because population growth and changes in life style have been the main drivers of the activities of humans and animals in several high mountain regions of the world, like the European Alps, for thousands of years. Until the mid-19th century or even earlier, settlements took place in several easily accessible areas near the timber line and forests were cleared, because the production of cheese and charcoal required a large amount of wood and thus, forested areas were converted to settlement areas, pastures and meadows. In contrast, inaccessible steep and shaded slopes remained free from settlers or were little used (e.g., for hay cropping), and in these places the potential timber line was preserved (Burga & Perret 1998).

During the mid-twentieth century, modernisation of agriculture has led to a fundamental change in agricultural land in mountainous regions (Rey Benayas et al. 2007). The intensity of land-use activity, which is dependent on both physiogeographic or abiotic drivers (e.g., topography, elevation, geological substrate, slope, aspect, fertility, soil depth, soil erosion, climate and climate change) and socio-economic drivers (e.g., degree of access and stability of slope) (Figure 8), has caused and continues to cause, on the one hand, an intensification of agricultural land-use along easy accessible slopes with high profitability. On the other hand, poorly accessible slopes, far from cattle sheds, which are not profitable for agricultural land-use, have been less intensively used and have been completely abandoned (Tasser & Tappeiner 2002; Tasser et al. 2007). Since abandoned areas are most prone to shrub invasion or reforestation, the dramatic decrease in the areas of montane and alpine pastures in the Swiss Alps during the past 150 years has resulted in an increase in the forest area of about 40% (Peter et al. 2006; Gellrich et al. 2007, 2008; Brändli 2010).

The current Alpine timber line is almost entirely anthropo-zoogenically determined (Figure 8) and is sometimes located far below the elevation to which forest would advance in the given climatic conditions. Therefore, the observed forest surface often shows the marks of previous anthropo-zoogenic activities, such as forest clearings and fire disturbances, overgrazing and trampling by cattle grazers, but also the effects of wild ungulates (e.g. *Cervus elaphus*) as well as winter and summer tourism (Nagy et al. 2003; Pauli et al. 2003a; Rixen et al. 2003). As a result, anthropo-zoogenic timber lines may be abrupt (e.g., due to man-induced forest fires), but can also show a wide transition zone (e.g., abandoned pasture surfaces), and thus there is no general characteristic shape common to all anthropo-zoogenic timber lines (Holtmeier 2009).

2.3 Plant succession processes at the timber line

In response to climate, relief, soil and anthropo-zoogenic impacts, the position and spatial pattern of timber lines characterizes a dynamic phenomenon that can be described by plant succession processes (Figures 8 and 11). In the Alps several scientists have shown that plant succession processes are important for studying initial changes in the biotic/abiotic conditions of a habitat by analyzing the behavior of plant communities at the level of association (Dierschke 1994). This is because when plant species move from a certain location, as occurs when the timber line advances or recedes, the ecology of the invaded habitat is transformed. High mountain regions like the Alps also provide a rich source of micro habitats within short distances, in which initial changes in the dynamics of vegetation succession can be well analyzed (Ellenberg 1996).

Lüdi (1921) applied plant succession to study the dynamics of vegetation boundaries in the Lauterbrunnen valley and introduced plant succession as a genetic-dynamic principal to illustrate changes taking place in the ecosystem over a certain time period. He was one of the first scientists to describe an Alpine valley according to the genetic-dynamic principal and the genetic-dynamic vegetation map of plant communities for the Lauterbrunnen valley (northern Swiss Alps) that was published in 1921 is an early study of plant sociology in the Alps (Lüdi 1921). Lüdi (1921) analyzed initial changes in the elevation of the Alpine timber line by studying the effect of invasive plant species in several plant communities using vegetation mapping (e.g., invasion by plant species of ericaceous dwarf shrub communities of the Rhododendro-Vaccinion into grassland communities of the Geo montani-Nardetum). In addition, he investigated the vegetation development of several Swiss glacier forelands (e.g., Lüdi 1945, 1955). Lüdi based his work on previous studies by American scientists, who had already asserted the genetic-dynamic principle to be an important discipline in geobotany. Lüdi established the genetic-dynamic principle by comparing the importance of soil and climate for plant succession processes, as suggested by Ramann (1918), and applied the model of plant succession processes that was developed by Cowles (1911).

Plant succession follows a cycle of four important stages (Figure 11), during which vegetation changes in structure (i.e., the vertical and horizontal layer of a population) and diversity (i.e., number of different plant species) (Dierschke 1994; Ellenberg 1996).
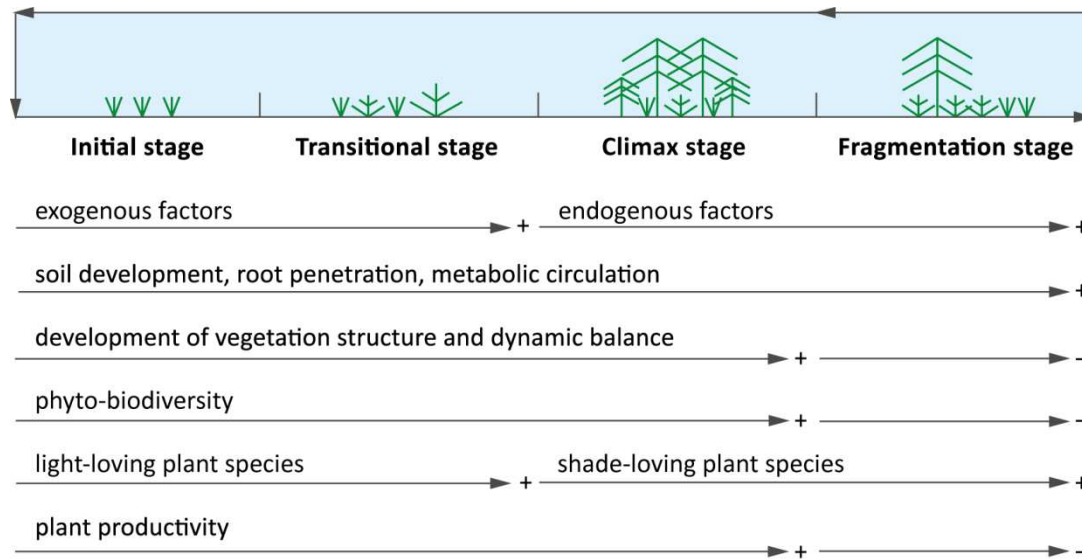
Figure 11 The cycle of plant succession at the timber line. For details see Table 3 on page 32.
Source: Modified from Dierschke (1994)

Plant succession processes are initiated as soon as diaspores of trees are dispersed to a certain habitat and are able to germinate. Diaspores get dispersed either by wind (anemochorous) or by animals (zoochorous). Tree diaspores may be dispersed into a newly exposed land surface without developed soil and initiate the process of **primary plant succession**. Elsewhere, tree diaspores may get dispersed into an already vegetated land surface with a more- or less-developed soil containing diaspores from the preexisting vegetation and initiate the process of **secondary plant succession** (Dierschke 1994). Primary plant succession processes are only observable along areas covered by rocks or scree, or on the moraines of shrinking glaciers. However, in most cases where the shifting timber line is observable, plant succession processes are a result of secondary processes. In this case, an already vegetated area at the opening of forests (i.e., transition from forest to subalpine dwarf shrub heath, subalpine and alpine grassland) gets transformed in its structure and diversity in a way that depends on whether conditions are non-disturbed/naturally determined (e.g., climate warming) or disturbed/anthropo-zoogenically determined (e.g., changes in land-use practices). The cycle through which plant succession proceeds is strongly dependent on the germination capacity, as well as the amount and quality of dispersed diaspores (Frey & Lösch 2010).

2.3.1 Natural/non-disturbed versus anthropo-zoogenically/disturbed plant succession processes

Plant succession under natural/non-disturbed conditions:

At the subalpine boundary excessively low temperatures reduce, on the one hand, the number of seed-producing years, and most seeds produced at the timber line are either empty or do not fully mature. On the other hand, excessively low temperatures restrict plant tissue development and maturation and so reduce the rate of growth; indeed, growth can only proceed at all when the root system is sufficiently developed and forms robust shoots that enable an upright growth (Körner 1998, 2003; Holtmeier 2009).

The upper limit of produced viable seeds is usually located below the physiological limit of tree growth, and unfavorable climatic and environmental conditions are the main reason why tree seedling establishment takes place only episodically and trees cannot mature fully when approaching the upper limit of viable seeds. Trees can only develop if viable seeds are produced at sufficiently short intervals. At the timber line, good seed production can only be expected every 9-11 years, and most tree species growing at the timber line reproduce at a relatively old age. For example, *Pinus cembra* reproduces only slowly, since it depends on spotted nutcrackers (*Nucifraga caryocatactes*) for seed dispersal and therefore reaches its reproductive age at 70 or 80 years. While seeds are not always dispersed to suitable seedbeds and microsites (i.e., optimal microclimate, sufficient illumination, soil moisture, soil acidity and other), germination and seed survival may not always be guaranteed for plant succession to follow a continuous process. Similarly, the slow growth rates of trees at the subalpine belt delay the process of plant succession and hinder it from following a continuous process. While the optimal root growth in *Picea abies* trees occurs at a temperature of around 14 °C, whereas in the subalpine belt the above-ground temperature in the shade generally remains between 8 and 12 °C, trees found at the elevation of the timber line may take 50 years (e.g., *Picea abies*) or even longer to reach a height of about 100 cm. In this context, the development sequence of a settlement of initial tree seedlings into the climax forest stage may be either impeded or only completed after several centuries. Many areas at the timber line therefore bear plant communities whose form has adapted to the deteriorated climate and environmental conditions of the habitat and that are likely to remain in this adapted form (Table 3; Leibundgut 1986; Dierschke 1994; Ott et al. 1997; Holtmeier 2009; Burga et al. 2010).

Table 3 Natural/non-disturbed plant succession processes at the timber line in the European Mountains (Swiss Alps)

	Initial stage (approx. 30 years)	Transitional stage (approx. 200 years)	Climax stage (150-450 years)	Fragmentation stage (400-600 years)
vegetation structure	– low cover (mosses, herbs & dwarf shrubs) – dispersion of diaspores of trees → **short growth (Ø 10 cm)**	– increasing cover (shrubs & trees) – germination & tree growth → **plant growth (Ø 100 cm)**	– dense cover (trees) – tall-growing trees building forests → **plant growth (Ø 20 m)**	– exhausted habitat resources – fragmented vegetation – opening cover → **reduced plant growth (Ø 10 m)**
phyto-biodiversity	– low number of plant species – short living – light loving – highly reproductive – flexible → **vegetation cover changes**	– increasing number of plant species – adjusting to environment & ressources of habitat → **vegetation cover changes**	– highest number of plant species – well adapted to the habitat – highest reproduction & development – steady state of exogenous & endogenous factors → **vegetation cover remains steady**	– destructive processes – reducing number of plant species – increase of decomposing plant species, e.g., young trees within shrub layers → **vegetation cover changes**
soil	– immature soils – gravel or scree substratum → **initial soil development**	– altered depth – e.g. Ranker or Rendzina → **development adjusted to habitat**	– well developed & deep – e.g., Cambisols or Podsols → **soil formation processes remain steady**	– open soils – exposed to increased soil erosion → **soil degradation**

Source: Characteristics of vegetation structure, phyto-diversity and soil forming processes during each successional stage under natural undisturbed conditions are according to Dierschke (1994); Ott et al. (1997) and Holtmeier (2009)

Under natural/non-disturbed conditions, the process of shifting timber line can be described by the following: As soon as trees reach their thermal threshold, the pattern of vegetation shows a gradual opening up of forests towards their upper limit. The opening of the tree canopy provides opportunity for plant species typical of forests, shrubs and ericaceous dwarf shrub heath to invade the surface of grassland. At the timber-line ecotone, interactions between plant species originating from forest, shrub, ericaceous dwarf shrubs and grassland communities take place (Ellenberg 1996).

The initial tree and shrub invaders are of great importance for the onset of a forest's progression into a new habitat, because on the one hand they are adapted to wind dispersion, and on the other hand they produce a humus layer by shedding their leaves and needles, which serves as an important nutrient supply basis for plant species with higher environmental requirements. In addition, their adjustment to vegetative reproduction by layering builds surface stability, which is important for tree species that are more sensitive to environmental conditions, such as *Abies alba*, *Picea abies* or *Pinus cembra* (Leibundgut 1986; Ott et al. 1997; Steiger & Carraro 2010). *Calluna vulgaris*, *Empetrum hermaphroditum*, *Erica carnea*, *Rhododendron ferrugineum*, *R. hirsutum*, *Vaccinium myrtillus* and *V. vitis-idaea* are among the most important initial shrub invaders, while *Betula pendula*, *Larix decidua*, *Pinus mugo* ssp. *uncinata* and *Sorbus aucuparia* are among the most important initial tree invaders. The dwarf shrub species *Empetrum hermaphroditum* is known to be highly competitive in shallow areas where soil is at its initial stage of development, because the rapid

shoot growth of this non-rooting espalier favors the development of soil (Schweingruber 1972). The tree species *Pinus mugo* ssp. *uncinata* is most adaptable to climate and environmental changes and is best-adapted to thrive in unfavorable habitats with extreme environmental conditions (steep and windy slopes, shallow, moist and nutrient poor areas) (Schweingruber 1972). This is due to its high root depth value (WT 5), which makes *Pinus mugo* ssp. *uncinata* resistant to uprooting in areas with harsh climate and unfavorable environmental conditions (e.g., strong winds, landscape instability) (Landolt et al. 2010). Similarly, *Betula pendula*, *Larix decidua*, *Sorbus aucuparia*, but also the shrub species *Alnus viridis*, are able to create surface stability, because their highly flexible stems and roots produce a compact and well connected structure (Steiger & Carraro 2010). *Larix decidua*, in particular, is equipped for surviving in unfavorable areas where seed production and dispersion are limited, by too low temperatures or high risk potential, due to its ability to vegetative reproduction by layering (Frey & Lösch 2010). Vegetative reproduction is effected by the formation of adventitious roots that usually develop in the organic soil layer where highest soil moisture occurs. Under vegetative production, trees form a compact and well connected structure of clonal groups, troops or tussocks that help them survive in areas subjected to frequent disturbances and unfavorable climate conditions, e.g., at locations that are exposed to permanent winds. *Picea abies* similarly switches to vegetative reproduction by layering as soon as environmental conditions become unfavorable for successful seed dispersion (Holtmeier 2009).

Trees that establish themselves and adapt to the given abiotic/biotic conditions of a habitat can reach remarkably old age. *Picea abies* may reach an age of more than 400 years and *Pinus cembra* even more than 1000 years at the climatic treeline. *Pinus cembra*, which is highly frost resistant and usually found in areas with the highest climatic timber line line in the Swiss Alps, e.g., Saas valley, Central Swiss Alps (2370 m a.s.l.), may therefore be a relic of a former climatic optimum (Figure 12; Leibundgut 1986; Steiger & Carraro 2010).
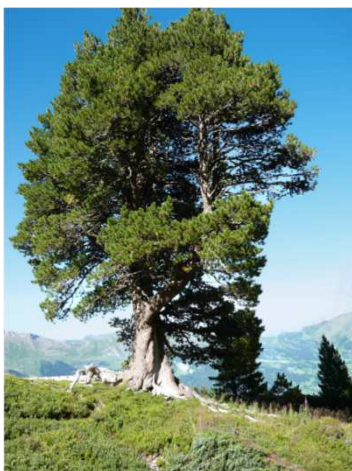
Figure 12 *Pinus cembra* solitary tree at timber-line ecotone near Kleine Scheidegg. Photo: S.C. Strähl, August 2009

Plant succession under disturbed conditions (anthropo-zoogenical practices):

At the timber line, anthropo-zoogenically driven plant succession processes have diverse causes, such as: (a) forest clearings and fire disturbances, (b) overgrazing and trampling by cattle or other domesticated grazers, (c) overfertilization; e.g., herbal layer of Alnetum viridis, (d) grazing and trampling by wild ungulates; e.g., *Cervus elaphus*, (e) winter and summer tourism, as well as (f) abandoned pastures. As a result, several surfaces have become impoverished due to soil exhaustion (Table 4; Lüdi 1948; Hegg 1984a, b; Hegg et al. 1992; Spielberger et al. 2006).

Table 4 Anthropo-zoogenic dynamics of vegetation succession at the timber line (Northern Swiss Alps)

impacts	anthropo-zoogenic vegetation dynamics
(a) forest clearings & fire disturbances	climax forest communities → replaced by secondary communities: – meadows, hay meadows – hedges – marshes – pasture – hay crop
(b) overgrazing and trampling by cattle grazers	impoverishment of grassland communities, e.g., of Geo montani-Nardetum: – dissapearance of low competitive plant species, e.g., orchids: *Gymnadenia conopsea, Nigritella rhellicani & Pseudorchis albida* – replacement by trivial plant species of rich meadow communities (*Poa alpina, Deschampsia cespitosa* or *Leontodon helveticus*) – selective feeding & increasing density of pasture weeds (e.g., *Nardus stricta*) – reduction of plant species diversity
(c) overfertilization, e.g., herbal layer of Alnetum viridis	development of richly manured alpine pasture (Rumicetum alpini) dominated by: – *Rumex alpestris* – *Senecio alpinus*
(d) wild ungulates such as red deer (*Cervus elaphus*)	inhibiting rejuvenation by: – browsing fresh annual shoots – bark stripping – trampling of tree seedlings
(e) winter and summer tourism	winter tourism: – injuries & death of ericaceous dwarf shrubs (*Rhododendron ferrugineum, Vaccinium gaultherioides* or *Loiseleuria procumbens*) – artificial snow production by snow cannons → soil degradation & impoverishment summer tourism: – mountain hikers → plant species distribution & diversity
(f) pasture reduction & abandonment	– increasing density of ericaceous dwarf shrub heath (e.g., *Calluna vulgaris, Rhododendron ferrugineum, Vaccinium myrtillus* and *V. uliginosum* aggr.) – spruce young growth & shrub species (*Pinus mugo & Alnus viridis*) – transformation & degradation of surface → reduction of plant species diversity

Source: Anthropo-zoogenic dynamics of vegetation succession are described according to Lüdi (1921, 1948), Braun-Blanquet (1964), Hegg (1984a, b), Hegg et al. (1992, 1993), Runge (1994), Ellenberg (1996) and Burga & Perret (2001b)

In areas of artificial lowering of the timber line (i.e., either produced by forest clearance or fire disturbances), there is a wide presence of plant communities which are undemanding, such as grassland communities of the alpine belt that invade areas of former forests. As soon as the grassland community has adapted to the degraded conditions of the invaded habitat, the vegetation that becomes established lacks character species and species richness (Hegg et al. 1993).

Geo montani-Nardetum is a dominant grassland community of the subalpine and alpine boundary on acid soil and is therefore widespread in areas of alpine grassland as well as in Vaccinio-Piceion spruce forests. Geo montani-Nardetum communities are mainly anthropo-zoogenically shaped and seldom naturally determined. However, its natural diversity can be inferred from the intensity of land-use in the places where it is found (Hegg et al. 1993). In areas of extensive and moderate traditional grazing with cattle and sheep, Geo montani-Nardetum is able to maintain its potential natural vegetation pattern and therefore shows, like other alpine grassland communities, a high presence of orchids and character species, such as *Pseudorchis albida*, *Geum montanum*, *Gentiana acaulis*, *Ajuga pyramidalis*, *Campanula barbata*, *Arnica montana*, which are accompanied by other important accessory plant species. In such areas spurs of ericaceous dwarf shrubs (e.g., *Calluna vulgaris*, *Rhododendron ferrugineum* or *Vaccinium myrtillus*) are also found. In overgrazed areas, some species, mainly orchids (e.g., *Pseudorchis albida*) are missing. Overgrazing has a destructive impact on vegetation, and orchids, in particular, react sensitively to the effects of overgrazing, because they are less competitive than undemanding trivial plant species of rich meadow communities, like *Leontodon helveticus*, *Poa alpina*, *Rumex alpestris* or *Deschampsia cespitosa*, which become dominant (Figure 14). Overgrazing causes on the one hand mechanical damage, such as trampling of the plants themselves, but also soil compaction that increases runoff and may massively reduce highland productivity. On the other hand, overgrazing also changes plant communities through preference-driven biomass consumption, where selective feeding encourages the growth of avoided pasture weeds, such as *Nardus stricta*, which has low nutrient values. Moreover, cattle manure promotes *Nardus stricta* (Braun-Blanquet 1948/1949; Edwards et al. 2004; Delarze & Gonseth 2008; Aguilar 2011).

In areas of overfertilization, such as herbal layers of Alnetum viridis, richly manured alpine pastures (Rumicetum alpini) develop that are dominated by *Rumex alpinus* or *Senecio alpinus* (Hegg et al. 1993).

Wild ungulates, such as red deer (*Cervus elaphus*), contribute to a similar destructive effect on the vegetation pattern of a surface as cattle or other domesticated grazers. Notably, browsing of fresh annual shoots and bark stripping are dangerous for tree seedlings and small trees and may impede rejuvenation of forests (Ellenberg 1996).

Similarly, the impacts produced by winter and summer tourism are as noticeable in the vegetation pattern at the timber-line ecotone as for agricultural land use. Winter tourism endangers the existence of several dwarf shrub species, such as *Rhododendron ferrugineum*, *Vaccinium gaultherioides* or *Loiseleuria procumbens*, since ski edges cause injuries that can kill dwarf shrub species. Furthermore, the fertilization effect of artificial snow is likely to account for soil degradation and impoverishment, because more water and harmful additives are input (Rixen et al. 2003). Summer tourism may be responsible for changes in the range and diversity of certain plant species, notably at several mountain peaks, but also at the timber-line ecotone. Mountaineers may contribute to the colonization process through aiding species dispersal, since seed and nutrients are occasionally accidentally redistributed. But at the same time, mountaineers cause disturbance and damage by trampling (Pauli et al. 2003a; Wipf et al. 2013).

Pasture reduction and abandonment cause the penetration of competitive invasive plant species, such as herbaceous (e.g., *Calamagrostis villosa*) and shrubby vegetation (e.g. *Calluna vulgaris*, *Rhododendron ferrugineum*, *Vaccinium myrtillus*, *V. uliginosum* aggr. and *V. vitis-idaea*), which profit first from the enhanced light levels in the forest openings, into areas of grassland vegetation. One result is an increase of unaltered litter on the ground, which leads to worsening of the pasturing qualities (Rey Benayas et al. 2007). At the same time, the grazing cattle promote the growth of dwarf shrubs is by avoiding them as pasture weeds and by fertilizing them with their manure. Hence, many of the formerly forested areas show extended patches of ericaceous dwarf shrub heath that transform the grassland surface into heathland. Geo montani-Nardetum invaded by dense patterns of ericaceous dwarf shrubs is frequent in disturbed areas of the timber-line ecotone that show reduction in pasture activity and represents a transition form to a potential coniferous forest. The higher the density of Geo montani-Nardetum that has been transformed into heathland, the longer the time that has passed since abandonment (Braun-Blanquet 1948/1949; Hegg et al. 1993; Tasser & Tappeiner 2002; Peter et al. 2006; Delarze & Gonseth 2008). The same applies to Rhododendro-Vaccinion, where dense patterns at the timber-line ecotone, correspond to degraded areas of former forests. Rhododendro-Vaccinion is a sub-cohort of Vaccinio-Piceion, because it has a similar potential natural vegetation pattern, but lower plant species richness (Schweingruber 1972; Ellenberg 1982, 1996; Delarze & Gonseth 2008). Hence, the upper occurrence of *Rhododendron ferrugineum* has been used to indicate the potential limit of former forests (Hager 1916; Landolt 2003; Holtmeier 2009). Former forests, having been cleared for pastures that have now been abandoned, are not only being invaded by dense patterns of dwarf shrub heath but also being recaptured by single trees or tree hordes, such as Norway spruce (*Picea abies*), larch (*Larix decidua*) or pine tree (*Pinus mugo*, particularly at sun-exposed and dry sides). Therefore, the number of invasive tree species increases in areas where pasture activity reduces (Bischof 1984).

Furthermore, shrub species (*Alnus viridis*, particularly at shaded and moist slopes) are also invading large areas in the Alps that were formerly pastured. *Alnus viridis* is able to symbiotically fix nitrogen, and hence grows more rapidly than most other woody plant species, spreading at a rate two to three times faster than the current forest expansion in Switzerland (Brändli 2010; Bühlmann et al. 2014). The invasion of *Alnus viridis* into areas of former pasture causes a loss in phyto-diversity, which is enhanced by the excessive nitrogen input of the *Alnus-Frankia* symbiosis. Increased nitrogen availability leads to a decline in plant species richness, because nitrophilic, fast-growing plant species suppress slow-growing plant species and only a few plant species can cope with the shady, cool and moist conditions beneath the *Alnus* canopy. Nitrogen enrichment and dense canopy reduce phyto-diversity and hamper vegetation succession towards coniferous forest (Bühlmann et al. 2014).

Forests are usually unsuccessful when regenerating on an abandoned surface. This is due to the dense growth pattern and foliage of competitive shrub and dwarf shrub species, which smother less competitive plant species, prevent other plants from germinating, and increasingly acidify the soil. Especially light wind-dispersed seeds of the initial tree species invaders suffer from this situation, because those seeds may either get caught in the dense shrub layer, suffer from lack of light or be pressed and buried in the ground by snow or the foliage of shrubs. Hence, the presence of dense shrub and dwarf shrub patterns delays the establishment of tree seeds and may impede rejuvenation of forests (Ott et al. 1997; Holtmeier & Broll 2007).

2.3.2 Plant succession processes in the study region

In the study region, like in most northern Alpine regions, the Alpine timber line has been strongly affected by human and cattle activities. Anthropo-zoogenic dynamics of vegetation succession are for the most part a response to former forest clearings (Figure 13; Table 4). Several climax forest communities were cleared to provide areas for settlement and agricultural land, and formerly forested areas were subsequently replaced by modified secondary communities such as meadows, hedges or marshes (Hegg & Schneiter 1988). Similarly important are anthropo-zoogenic dynamics of vegetation succession in response to overgrazing, which have affected the composition of plant species of the dominant grassland community of the study region (Geo montani-Nardetum). In addition, a wide part of anthropo-zoogenic dynamics of vegetation succession at the Alpine timber line of Grindelwald have been produced by pasture reduction, especially along isolated slopes, which are prone to the effects of increasing landscape instability (Huggel et al. 2010, 2011; Werder et al. 2010). As a result, the total area of abandoned pastures has increased (Hegg & Schneiter 1988; Käsermann 2007; Liechti et al., in prep.). Last, but not least, the impacts of winter and summer tourism, have left noticeable traces in the vegetation pattern at the Alpine timber line of Grindelwald. Most evident are the injuries and deaths of several ericaceous dwarf shrubs, as has been observed in other alpine regions (Rixen et al. 2003).

Figure 13 Forest patches and single spruces invading the surface of former pastures near Kleine Scheidegg (left picture). Abandoned pastures near Kleine Scheidegg being invaded by dense patches of ericaceous dwarf shrubs and single spruces (right picture). Photos: S.C. Strähl, August 2009

Plant succession at the current timber line is therefore driven more by anthropo-zoogenically disturbed processes than by naturally/non-disturbed processes, the latter expected to occur only in a few local areas with poor accessibility. In the study region, the progressing forest can be described as follows: several plant species belonging to the dominant plant communities of Vaccinio-Piceion forests, Rhododendro-Vaccinion ericaceous dwarf shrub heath and Geo montani-Nardetum grassland interact at the timber-line ecotone (Figure 14).

Vaccinio-Piceion forests

Potential natural vegetation pattern

→ trees (**Picea abies,** *Larix decidua* and *Sorbus aucuparia*)
→ shrubs (*Lonicera caerulea, Rhododendron ferrugineum,* **Vaccinium myrtillus** and *Vaccinium vitis-idaea*)
→ herbs (*Lycopodium annotinum, Athyrium distentifolium, Blechnum spicant, Oreopteris limbosperma, Avenella flexuosa,* **Calamagrostis villosa,** *Melica nutans, Luzula luzulina, Luzula nivea, Luzula sieberi, Corallorrhiza trifida, Listera cordata, Saxifraga cuneifolia, Oxalis acetosella, Orthilia secunda, Pyrola rotundifolia, Veronica urticifolia, Melampyrum sylvaticum,* Galium triflorum, *Linnaea borealis, Adenostyles alliariae, Cicerbita alpina* and *Homogyne alpina*)

Natural progression	**Anthropo-zoogenic regression**

Rhododendro-Vaccinion dwarf shrub heath

Potential natural vegetation pattern

→ krummholz-trees
(*Pinus mugo* ssp. *mugo*)
→ shrubs (*Lonicera caerulea,* **Rhododendron ferrugineum, Vaccinium myrtillus**)
→ herbs (*Diphasiastrum alpinum, Huperzia selago, Avenella flexuosa, Astrantia minor* and *Pyrola minor*)

Rhododendro-Vaccinion dwarf shrub heath

Deteriorated vegetation pattern

→ fragmented and disturbed pattern of dwarf shrub heath
→ vegetation pattern predominated by *Rhododendron ferrugineum* and *Vaccinium myrtillus*

Geo montani-Nardetum grassland

Potential natural vegetation pattern

→ shrubs (spurs of *Calluna vulgaris, Rhododendron ferrugineum* and *Vaccinium myrtillus*)
→ herbs (*Botrychium lunaria, Anthoxanthum alpinum, Avenella flexuosa, Festuca rubra* s.str., **Nardus stricta**, Luzula alpina, *Luzula multiflora, Nigritella rhellicani,* Pseudorchis albida, *Polygonum viviparum, Pulsatilla alpina* ssp. *apiifolia, Alchemilla alpina, Potentilla aurea, P. erecta,* **Geum montanum**, *Trifolium alpinum,* Meum athamanticum, *Gentiana acaulis, Gentiana punctata, G. purpurea,* Ajuga pyramidalis, *Pedicularis tuberosa, Plantago alpina,* Campanula barbata, **Antennaria dioica**, Arnica montana, *Homogyne alpina,* Hypochaeris uniflora and **Leontodon helveticus**)

Geo montani-Nardetum grassland

Deteriorated vegetation pattern

→ shrubs (expanded patches of *Calluna vulgaris, Rhododendron ferrugineum* and *Vaccinium myrtillus*)
→ herbs (*Deschampsia cespitosa,* **Nardus stricta**, *Poa alpina, Rumex alpestris, Alchemilla alpina, Ligusticum mutellina* and *Leontodon helveticus*)

Figure 14 Identification key for natural/non-disturbed progression and anthropo-zoogenic/disturbed regression of Vaccinio-Piceion forests at the timber-line ecotone of the study region. Plant species marked in bold refer to dominant plant species of the vegetation layer. Plant species marked in red refer to characteristic species of the plant community. Source: Classification of plant species for Vaccinio-Piceion and Rhododendro-Vaccinion: Delarze & Gonseth 2008; classification of plant species for Geo montani-Nardetum grassland: Braun-Blanquet 1948/1949, Delarze & Gonseth 2008.

3   Methods

Non-disturbed (naturally determined) and disturbed (anthropo-zoogenically determined) dynamics of vegetation succession differ in their vegetation structure and phyto-diversity, as is well known from previous studies (Lüdi 1921, 1948; Braun-Blanquet 1964; Hegg 1984 a, b; Hegg et al. 1992, 1993, Burga & Perret 2001b; Perret 2005; Strähl & Burga in prep.). We therefore applied those differences to identify areas of the timber-line ecotone where climate warming is the driving factor and areas where land-use change is the driving factor. We chose a site at the timber line where the proportion of forest cover has shown one of the largest increases since 1899 and have selected our relevés (a total of 32) in the field to observe most clearly the distinction between timber lines responding to climate warming and those responding to land-use change. To test the differences in vegetation records between locations where climate warming is the driving factor and locations where land-use change is the driving factor, 16 relevés were chosen above the 1899 timber line, i.e., in areas likely to be responding to the impact of climate warming, and 16 relevés were chosen below the 1899 timber line, i.e., likely to be responding to the impact of land-use practices.

In a first step, we recorded the current vegetation pattern in the timber-line ecotone at the selected test sites in the field, using vegetation mappings as prescribed by Braun-Blanquet (1964); and in a second step the recorded patterns of vegetation were analyzed and statistically tested. Vegetation mappings and vegetation pattern analysis were used to show: (a) the differences in the current vegetation structure and phyto-diversity between relevés located below and above the 1899 timber line, (b) how significant the results recorded by means of vegetation mappings are, in order to determine the differences in vegetation structure and phyto-diversity and (c) which vegetation mapping variable (plant structure or phyto-diversity) is best suited to inferring an initial sign of warming impact in a newly forested area at the timber-line ecotone, at the local scale where plant species develop. In a final step we used these results to estimate: (a) the proportion of current timber line that we expect to exhibit signs of a warming impact and (b) the proportion of current timber line that we expect to exhibit an upward shift using the results obtained in the study region.

3.1   Vegetation mappings according to Braun-Blanquet (1964)

In reality, any natural boundary is impossible to locate precisely, since vegetation cover in any landscape exhibits heterogeneous dynamics as a result of different plant layers and plant communities. Hence, the dynamics of vegetation succession are difficult to define for research purposes, because there are no standard guidelines for analyzing the complex behavior of vegetation. Dissection of vegetation layers is difficult, and therefore even accurate measurements and counting of certain single vegetation forms may not give an exact representation of the dynamics of vegetation succession. More reliable results are provided by assessments made in selected relevés, like vegetation mappings, where a large reduction of attributes takes place and reduce the complexity of vegetation cover by averaging over large areas (Glavac 1996).

The Braun-Blanquet (1964) vegetation mapping method is a well-known method that is applied to understand dynamics of vegetation succession on a local level, where trees and other plant species develop. This is due to the fact that plant species are strongly bound to their abiotic and biotic environments and therefore not randomly distributed within a certain habitat. Each plant species shows values for climate (L: light, T: temperature and K: continentality) and soil (F: moisture, R: soil reaction, N: nutrients, H: humus and D: aeration), and thus, every habitat expresses the relationship between the physical and living environments (Ellenberg 1996; Landolt et al. 2010). In this context, the study of dynamics of vegetation succession requires a combined approach including both habitat factors (i.e., climate, geology, relief, soil, and anthropo-zoogenic influences) and plant sociological aspects.

Plant communities are an important subject of terrestrial ecosystem research because they display the current living conditions of a habitat, which is a result of the interactions of plant species with their physical environment (Braun-Blanquet 1964; Theurillat 1995; Glavac 1996; Begon et al. 1999). Braun-Blanquet (1921) developed a syntaxonomic classification system that shows a hierarchic classification for plant communities. The *association* is defined as the basic unit of a plant community, which consists of particular species with a characteristic structure in a typical habitat. According to Braun-Blanquet (1964) a plant *association* is determined by a set of **character species**, in addition to **differentiating species** and other **accessory plant species**. A change in habitat factors affects the plant communities at the level of an *association*. Anthropo-zoogenic impacts, for instance caused by grazing activity, may produce noticeable changes in the distribution pattern of plant species within plant communities, where character species tend to disappear first, since they react most sensitively to environmental changes (Lüdi 1948; Hegg et al. 1992, 1993; Dierschke 1994).

3.2 Selection of study region
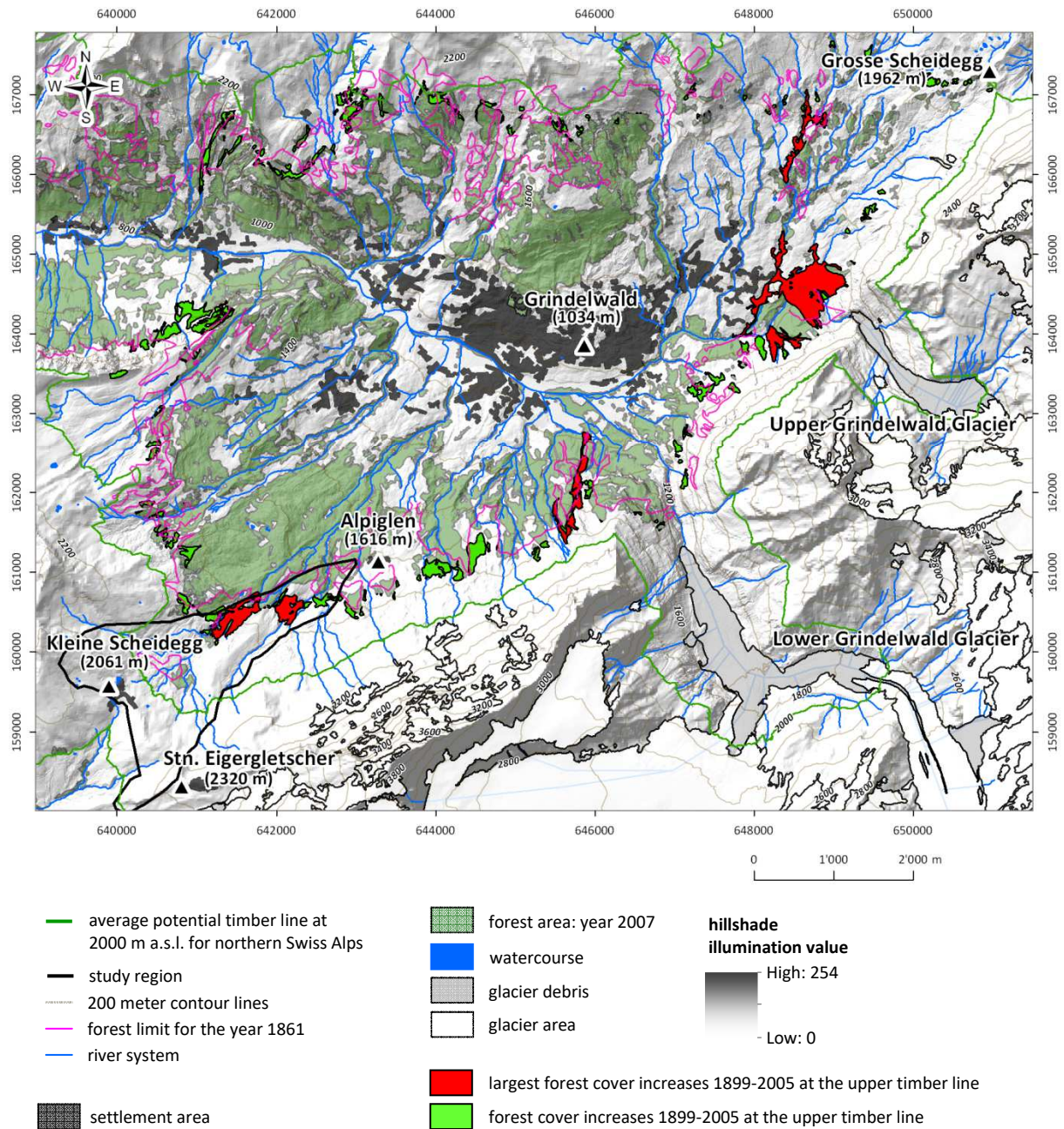
Figure 15 The study region selected is situated between Alpiglen and Kleine Scheidegg. The study region has been selected on the basis of the GIS-forest-cover analysis by Providoli & Kuhn (2012), which have shown areas of forest cover increase at the timber line between 1899 and 2005 and could indicate the areas with the largest forest cover increases. The map has been generated with ArcGIS.
Source: Hillshade and contours: Digitales Geländemodell 2m © swisstopo; watercourse, river system, settlement area, forest area of the year 2007, glacier debris and glacier area: VECTOR25 © swisstopo; forest limit for the year 1861: DUFOUR © swisstopo; average potential timber line elevation: Landolt 2003, Holtmeier 2009; largest forest cover increases and forest cover increases at the upper timber line: Providoli & Kuhn 2012

We fixed our study region to one of the areas in the region of Grindelwald, between Alpiglen and Kleine Scheidegg, where the GIS-forest-cover-analysis by Providoli & Kuhn (2012) identified the largest proportion of forest cover increases between the years 1899 and 2005 (Figure 15). For our analysis we selected sites that satisfied the following two criteria: (1) the locations must show the best possible contrast in the dynamics of vegetation succession between non-disturbed areas, most probably responding to climate warming, and disturbed areas, likely responding to changes in land-use activity and (2) the locations must have smooth topography, where impacts such as surface processes and landscape instability have least influence on the current dynamics of vegetation succession. These criteria were fulfilled at 32 sites, at which we arranged our relevés in the field.

We used the altitudinal limit of the timber line for the year 1899, at 2021 m a.s.l., as a reference value to identify areas of the current timber line that are most likely responding to changes in land use (below the 1899 timber line) from areas that are possibly responding to climate warming (above the 1899 timber line) (Figures 16 and 17; Table A 11). This altitude of 2021 m a.s.l. is an interpolated value, namely the average elevation given by all highest located closed forest covers calculated for the year 1899 (Providoli & Kuhn 2012).

We mapped equal numbers of relevés above (i.e., 16 relevés: 4-6, 8-9, 11, 19-20, 23, 25 and 27-32, with probable response to global warming) and below 2021 m a.s.l. (i.e., 16 relevés: 1-3, 7, 10, 12-18, 21-22, 24 and 26, most responsive to land-use activity) and calculated the appropriate size of each relevé according to the concept of minimum area (Braun-Blanquet 1921). Transitional areas, such as timber-line ecotones comprising forest, dwarf shrub heath and grassland communities, require a relevé size of approximately 100 m^2, whereas pure grassland communities require a much smaller relevé size of about 1-4 m^2. Our vegetation relevés were selected in areas where subalpine dwarf shrub heath (mainly Rhododendro-Vaccinion) and subalpine meadows (mainly Geo montani-Nardetum) interact (Figure 18). Hence, we used an area of 100 m^2 for all vegetation relevés, in order to gather sufficient data to analyze current vegetation succession at the timber-line ecotone and to allow statistical comparisons. The division of vegetation relevés into sets below and above the 1899 timber line was applied not only to analyze differences in vegetation succession between disturbed and undisturbed areas, but also to identify which vegetation mapping variable (plant structure or phyto-diversity) is best suited to inferring initial signs of a warming impact in a newly forested area at the timber-line ecotone.
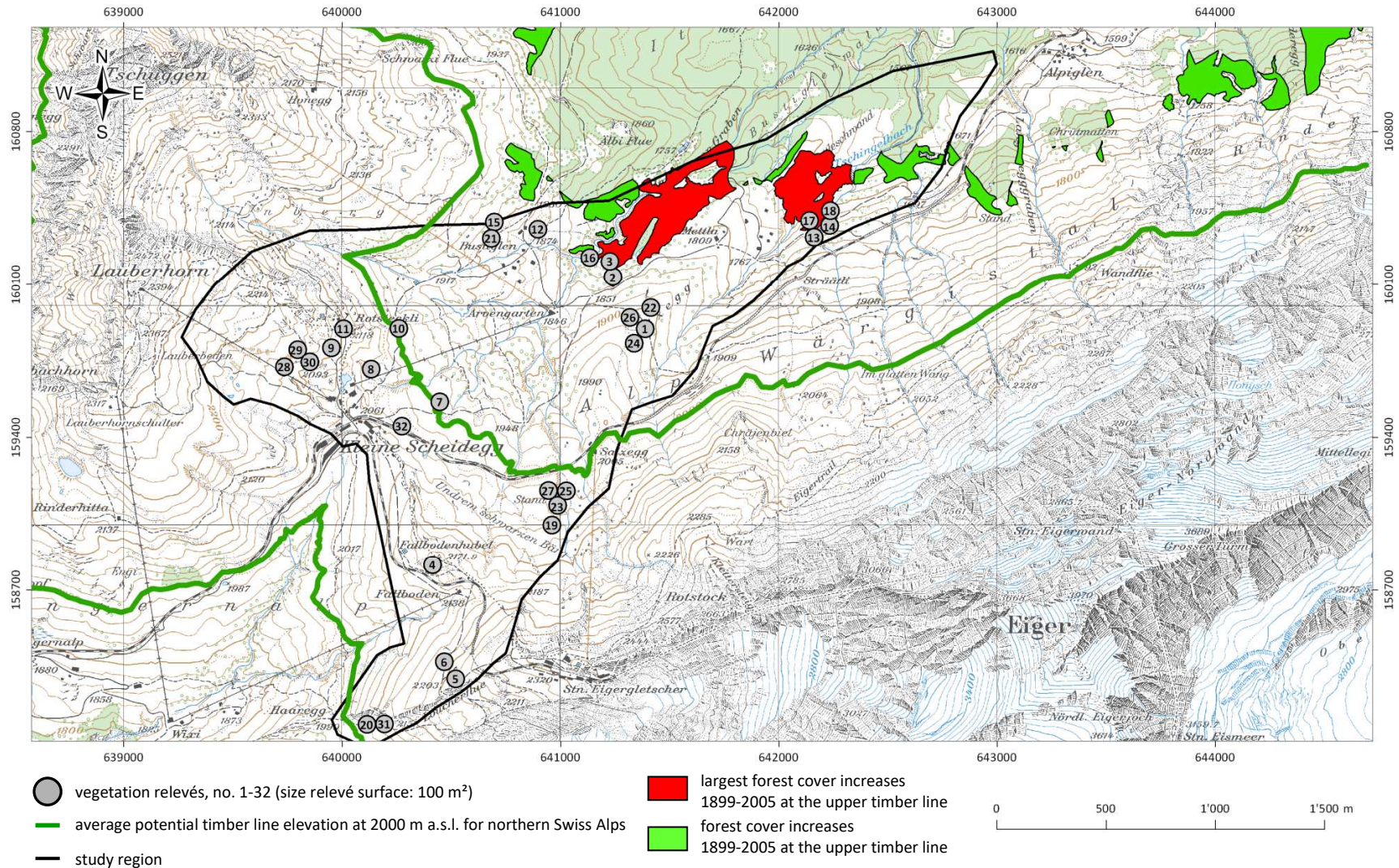
Figure 16 Study region located near Kleine Scheidegg (Grindelwald, Switzerland). Vegetation relevés (nos. 1 to 32) are situated in areas of the timber-line ecotone where forest cover increased between the years 1899 and 2005. The potential timber line shows the limit of expansion of forest trees for the northern Swiss Alps, located at 2000 m a.s.l. The map has been generated with ArcGIS.

Source: Topographical map: PK25 © 2006 swisstopo; average potential timber line elevation: Landolt 2003, Holtmeier 2009; largest forest cover increases and forest cover increases at the upper timber line: Providoli & Kuhn 2012

Prior to the fieldwork, the study region was thoroughly reconnoitred, in order to gather as accurate results as possible regarding the habitat properties. In this preparation work, mapping the geology and substrate, as well as the plant communities, served as an important basis for the plot selection, fieldwork and subsequent data analysis.
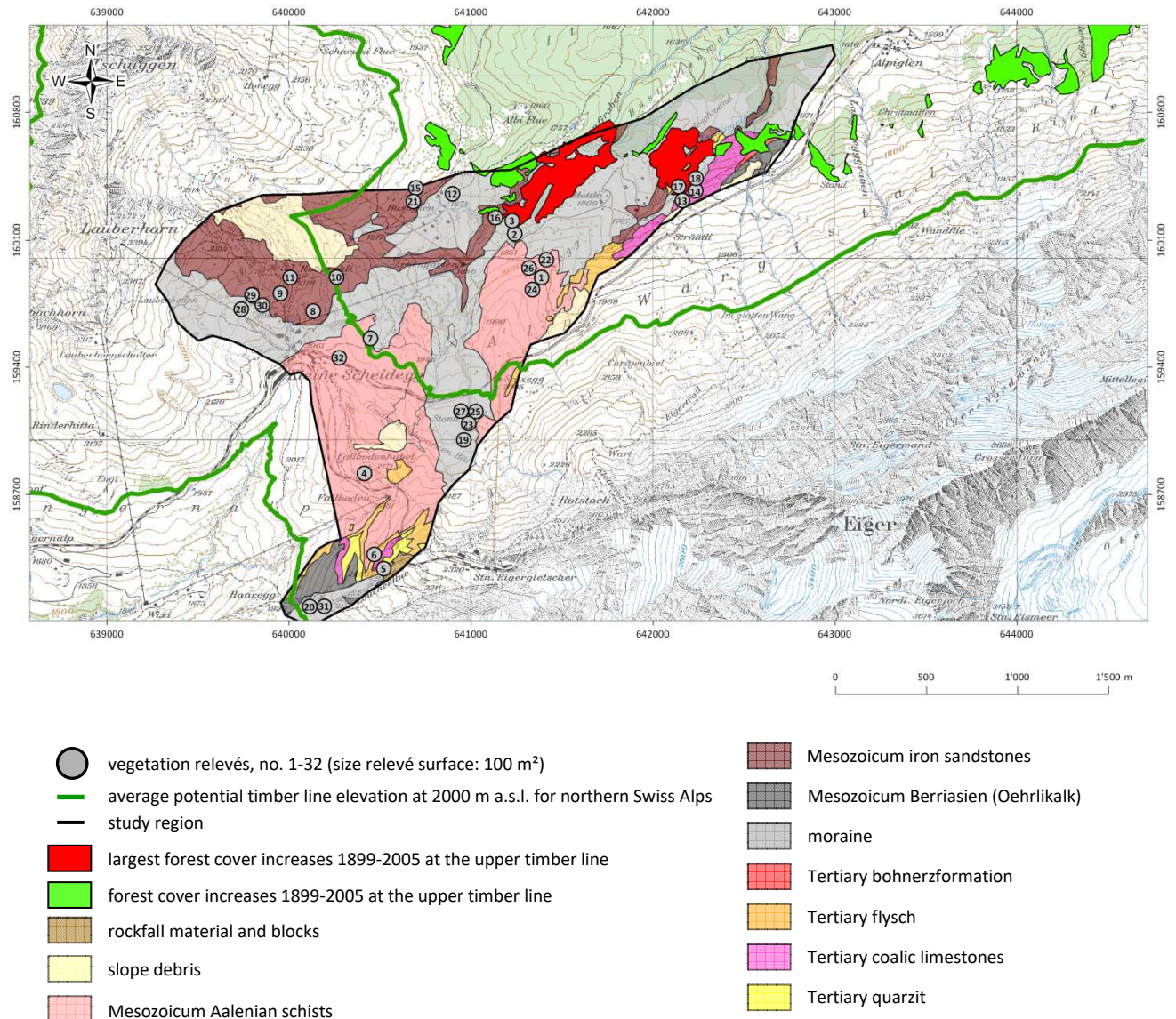
Figure 17 Substrate type in the study region corresponding to the geological bedrock components. The map has been generated with ArcGIS.
Source: Topographical map: PK25 © 2006 swisstopo; average potential timber line elevation: Landolt 2003, Holtmeier 2009; substrate type: Collet et al. 1938; largest forest cover increases and forest cover increases at the upper timber line: Providoli & Kuhn 2012

In the selected study region, the predominant substrate types allow the formation of deep soils. Moraines (44%) cover the largest part, followed by Mesozoic Aalenian schists (25%) and Mesozoic iron sandstones (16%). Less frequent are substrate types with coarser-grained components (blocks and stones: 2-6.3 dm grain diameter; see Table A 42) of the Tertiary (6%) that do not allow deep soils to develop. Some parts of the area are covered by slope debris (6%) (Figure 17).
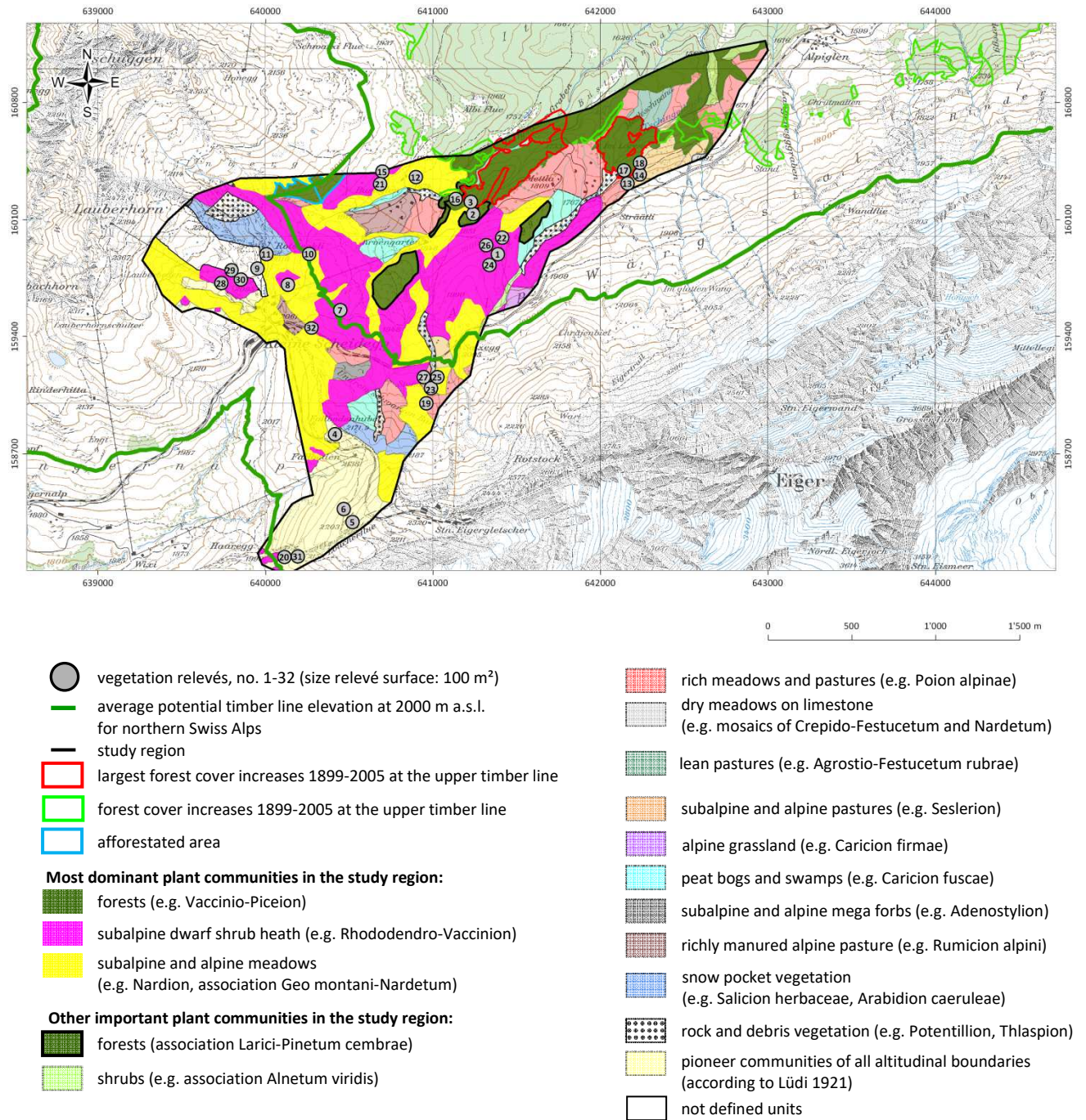
Figure 18 Plant communities in the study region corresponding to the type of substrate. The map has been generated with ArcGIS.

Source: Topographical map: PK25 © 2006 swisstopo; average potential timber line elevation: Landolt 2003, Holtmeier 2009; extend of each plant community: Hegg & Schneiter 1988; nomenclature of plant communities: Braun-Blanquet 1948/1949, Hegg & Schneiter 1988, Delarze & Gonseth 2008; pioneer communities of all altitudinal boundaries: Lüdi 1921; largest forest cover increases and forest cover increases at the upper timber line: Providoli & Kuhn 2012

In correspondence to the locally changing type of substrate, plant communities in the study region display a heterogeneous pattern. Most dominant are forests (Vaccinio-Piceion) and subalpine dwarf shrub heath (Rhododendro-Vaccinion) that together cover 43% of the study region (Figure 18). Most of the forested area is covered by the association Homogyno-Piceetum, although Larici-Pinetum cembrae, which generally dominates in central alpine regions, cover around 10%. Among the subalpine dwarf shrub heath, the major part is allotted to the association Rhododendro-Vaccinietum. Subalpine and alpine meadows (Nardion, association Geo montani-Nardetum) account for much of the remaining area (22% of the total). Geo montani-Nardetum, which is an association of the cohort Nardion, is the most frequent subalpine and alpine meadow in the study region (Figure 18). In some parts rich meadows (Poion alpinae) (10%) are widely spread (Figure 18; Hegg & Schneiter 1988; Delarze & Gonseth 2008).

3.3   Field work and data acquisition

Fieldwork started by selecting the area of each relevé in such a way that the current dynamics of vegetation succession could be assessed as accurately as possible. Therefore, each relevé was chosen to an area where plant species associated to Rhododendro-Vaccinion and Geo montani-Nardetum are dominant (Figure 18). Each relevé was a square of 10 m x 10 m (100 m^2) (Figure 19). Subsequently, each relevé was located and identified with GPS in x- and y-coordinates given by the Geographic Coordinate System GCS_CH1903 in Swiss Grid.

Figure 19 Example of vegetation relevé that was mapped near Kleine Scheidegg (Grindelwald, Bernese Oberland). Photos: S.C. Strähl, June 2009

In addition, assessments of vegetation cover, phyto-diversity, tree height and tree distribution were carried out in the field, in order to determine the current dynamics of vegetation succession at the timber-line ecotone, and to relate them to the climate and environmental conditions. The vegetation pattern in each relevé was surveyed according to:

(a) Vegetation cover and phyto-diversity

(b) Tree height and distribution

For each vegetation relevé, all flowering plant species, ferns, mosses and lichens were recorded. Accurate results can only be achieved when all plant species in the field are recorded, and thus vegetation mappings must either be repeated several times or carried out during the season in which plant growth is optimal, i.e., when most angiosperms are in blossom. For plant communities at the Alpine timber line, most seed-plant species flower during the summer months, between June and September, which is the reason why field work took place during several field campaigns between June and September in the years 2008, 2009 and 2010.

(a) Vegetation cover and phyto-diversity

Plant species were first recorded according to the identification key of Binz & Heitz (1990) and Landolt (2003); the present plant species nomenclature follows that of Lauber et al. (2012). Small trees and tree seedlings were included within the tree layer, dwarf shrubs and shrublets within the shrub layer, pteridophytes within the herb layer and lichens within the moss layer. In the present study, we modified the combined cover-abundance index according to Braun-Blanquet, in order to estimate the cover of a plant species.

The combined cover-abundance index according to Braun-Blanquet (see Table 5) has been criticized in plant sociology by several scientists (see Dierschke 1994). One criticism is that each cover-abundance index covers a wide range of densities (e.g., index 2: a density of 5-25%) and is therefore not suitable for giving an accurate estimate of the density of a plant species, especially one with low abundance, e.g., index 1 or 2 (Table 5). Therefore, the Braun-Blanquet cover-abundance index 2 (5-25%) has often been split up into several sub-cover-abundance index steps (Dierschke 1994). For example, Strähl & Burga (in prep.) have split the Braun-Blanquet cover-abundance index 2 (5-25%) into four sub-cover-abundance index steps, each of 5% (i.e., 20: >5-<10%; 21: >10-<15%; 22: >15-<20% and 23: >20-<25%). In this present study, we applied individual percent scale factors (e.g., 1%, 2% etc.) to estimate the cover of each plant species and to allow statistical comparisons of the data (Tables A 1-10 and A 13-17).

Table 5 Combined cover-abundance index according to Braun-Blanquet (1964). Abundance refers to the number of species individuals per area. Dominance refers to the horizontal cover of all species individuals per area. Sociability expresses the way plant species are distributed within an area. The mean cover value (m) shows the mean value of the amplitude of variation for the column of species abundance and dominance and cannot be calculated for plant species with a mass scale "r"

mass scale	species abundance and dominance combined density value [%]		mean cover value (m)	sociability
r	rare, 1 individual per surface area	< 1		1 = growing one in a place, singly
+	sparsely or very sparsely present; cover very small	≤ 1	0.1%	2 = grouped or tufted
1	plentiful but of small cover value	1 - < 5	2.5%	3 = in troops, small patches, or cushions
2	very numerous, or covering at least $\frac{1}{20}$ of the area	5 - 25	15.0%	4 = in small colonies, in extensive patches, or forming carpets
3	any number of individuals covering $\frac{1}{4}$-$\frac{1}{2}$ of the area	25 - 50	37.5%	5 = growing in great crowds (pure populations)
4	any number of individuals covering $\frac{1}{2}$-$\frac{3}{4}$ of the area	50 - 75	62.5%	
5	covering > $\frac{3}{4}$ of the area	75 - 100	87.5%	

Source: Mass scales, the species abundance and dominance combined density values, and the sociability index are according to Braun-Blanquet (1964). The mean cover value is according to Dierschke (1994).

(b) Tree height and distribution

Subsequent to the mapping of vegetation cover and phyto-diversity, an inventory of tree height and tree distribution was essential for analyzing the type of forest opening towards the timber line. The upper occurrence of single trees or tree hordes have been used as an approximation for showing a sign of timber line shift possibly responding to the impact of global warming (Hager 1916; Hess 1923; Braun-Blanquet 1964; Delarze 1994; Ellenberg 1996; Landolt 2003; Holtmeier 2009). Because of low average annual temperatures, trees are not able to invest in their radial growth, and therefore grow shorter and less densely together, whereas forest cover gradually lightens towards the timber line (Körner 2003). However, the feature of forest opening can often be misinterpreted when human activity and cattle grazing modify the structure and form of forest openings (Brockmann-Jerosch 1919). For example, single trees of Norway spruce are usually connected to pasture activity and their number increases mainly in areas where pasture activity has reduced (Bischof 1984).

The inventory of tree height and tree distribution considers the following important steps:

- All trees (including small trees and tree seedlings) within a relevé were localized as x- and y-coordinates by means of GPS.

- Height values were estimated for each tree, small tree and tree seedling separately. Additionally, the average height was calculated for each relevé.

- The number of tall growing trees (height ≥ 2m) was separated from the number of krummholz (including all small trees and tree seedings with a height of < 2 m).

- Distribution was measured by the number of trees, small trees and tree seedlings per relevé and the shortest distances between all neighboring trees, small trees and tree seedlings. Distance values were calculated with the application of ESRI ArcGIS algorithms.

Subsequent to the fieldwork, each relevé was characterized by its: (a) elevation, slope and aspect, and (b) surface character (soil and micro relief), type of land use and accessibility. This information was important for completing the field work data (Table A 11).

Elevation, aspect and slope were extracted from the 2 m-DEM (Office of Geoinformation 2000) based on standard ESRI ArcGIS algorithms. Surface character (soil data and micro relief) was interpolated from data collected in a parallel Ph. D. project (by Ulrike Hoffmann) and gathered in several transect mappings (Hoffmann et al. 2014). Soil depth is the thickness of the complete soil profile that could be mapped down to the bedrock material. In general, soils are required to show at least a moderate depth ($\geq$ 30 cm), in order to assure root penetration for trees (Lutz & Chandler 1955; Ott et al. 1997). Type of land use was also studied in the transects of soil mappings (Hoffmann et al. 2014) and completed with data provided by the Office of Geoinformation (1992/1997), which indicates the dominant land cover type for 100 x 100 m grid cells. Accessibility, which was measured by a value that considers walking time to closest barns, slope, paths (enabling factor) and brooks (hindering factor), was derived from data of the GIS-Cost-Distance-Model provided by K. Liechti (Centre for Development and Environment, University of Bern) (see Liechti et al., in prep.). Values between 0 and 0.5 show areas with walking time from 0-30 min, 0.5-0.75 indicates areas with 30-45 min walking time and 0.75-1 indicates a walking time from 45 min-1 h. Therefore, low values represent highly accessible areas.

3.4 Data analysis

3.4.1 Analysis of vegetation pattern

Subsequent to the data acquisition, the pattern of vegetation was analyzed, in order to determine the character of current dynamics of vegetation succession. As in the study of my master thesis (Strähl 2006), we analyzed each mapped relevé by its type of impact, by differentiating between: (1) non-disturbed, naturally determined vegetation patterns and (2) disturbed vegetation patterns caused by anthropo-zoogenic practices (e.g., forest clearance and overgrazing).

In a **first step** the structure of the vegetation was assessed: (a) by the cover distribution of shrubs and herbs and (b) by the growth and distribution of trees. Cover values were determined for each relevé and the mean for all relevés located above and for all relevés below the altitude of the 1899 timber line. Values for the growth and distribution of trees are given on the one hand by the mean height of trees in each relevé and on the other hand by the density of trees in each relevé, i.e., the total number of krummholz (< 2 m height) and tall growing trees (≥ 2m height) and the shortest distance between all neighboring trees, small trees and tree seedlings. Like cover values, growth values are not only determined for each relevee separately, but also as mean values, for all relevés located above and for all relevés below the altitude of the 1899 timber line.

In a **second step** phyto-diversity was determined, as for vegetation structure, for each relevé separately and as a mean value for all relevés located above and for all relevés located below the altitude of the timber line in 1899. The surface of each mapped relevé was determined by its non-disturbed and degraded vegetation pattern, which we have identified by the effect of shrubby and arboreal plant species immigration into Geo montani-Nardetum grassland (Figure 14). This is due to the wide occurrence of Geo montani-Nardetum grassland in the study region, as well as the frequently observed invasion by ericaceous dwarf shrubs (e.g. *Calluna vulgaris*, *Rhododendron ferrugineum* and *Vaccinium myrtillus*) into areas of the timber-line ecotone that show reduction in pasture activity and a transition form to the potential coniferous forest (Hegg & Schneiter 1988; Hegg et al. 1993). The character of non-disturbed vegetation was derived by the abundance of Geo montani-Nardetum character species per relevé, which was determined by the total number and density of Geo montani-Nardetum character species. The character of degraded vegetation was identified by the intensity of deteriorated Geo montani-Nardetum to heathland per relevé, which was determined by the density of all plant species associated with Geo montani-Nardetum grassland that are frequent on a deteriorated surface (Figure 14).

The classification system of Delarze & Gonseth (2008) was applied, because it allows the determination of a plant community at the cohort level and considers plant communities at the scale of landscape structures, by showing: (a) the abundance of character species and (b) the abundance of other important accessory plant species characterizing the plant community.

3.4.2 Statistical analysis

The statistical analysis was performed in the IBM SPSS-Statistics program. For the purpose of this study we have used a statistical test with a pairwise comparison (Paired Samples *t*-test and Wilcoxon-signed-rank test) because our aim was to find out whether the same test variables differ between a climate or land use surface. The dependent *t*-test (Paired Samples *t*-test) is a parametric test, therefore, is valid as an important condition that the random check distribution is normal and the variances are continuously homogeneous in the data. If these conditions are not fulfilled, a non-parametric test is used. In non-parametric tests the assumptions are not dependent directly on the type of the data because non-parametric tests work after the principle of the rank order of data. The raw data are divided in ranks and the analyses are carried out on the base by rank orders and not on the basis of the raw data directly. The Wilcoxon-signed-rank test is the non-parametric recompense to the dependent t-*t*est. In comparison to the raw data the differences are compared between the ranks (Field 2009).

In order to check the appropriateness of assumptions of parametric and non-parametric data, the scores in the gathered data were tested for normality and homogeneity of variances. All scores in the recorded data were tested for normality using a Kolmogorov-Smirnov and Shapiro-Wilk test, and for differences in variance using Levene's test (Table A 31).

For the set of vegetation relevés above 2021 m a.s.l. and the set of relevés below 2021 m a.s.l. we calculated the mean value of each test variable for cover distribution of shrubs and herbs (i.e., pairs of shrub and herb cover), growth and distribution of trees (i.e., pairs of tree height, amount of trees ≥ 2 m and < 2 m and shortest tree distance) and phyto-diversity (i.e., pairs of total number of Geo montani-Nardetum character species, density of Geo montani-Nardetum character species and density of deteriorated Geo montani-Nardetum to heathland) and compared each pair of mean values to seek significant differences between the higher and lower relevés. A **dependent-*t*-test** (Paired Samples *t*-test) was implemented for parametric data and a **Wilcoxon-signed-rank test** for non-parametric data. Since the number of compared differences was 16, i.e., less than 30, the Wilcoxon-signed-rank test for non-parametric data was performed for all recorded data. In addition, we made simple bar diagrams to visualize means and standard errors.

The statistical analysis allowed us to assess the significance of our vegetation mapping results in differentiating between a non-disturbed/naturally controlled and a disturbed/anthropo-zoogenically modified vegetation pattern at the timber-line ecotone, and secondly, to assess which variable, plant structure or phyto-diversity, is best suited to inferring an initial sign of a possible warming impact in a newly forested area at the timber-line ecotone.

3.5 Areas attributed to an upward shift of the Alpine timber line in probable response to global warming

In this last step, we analyzed our results to identify areas where the possible impact of global climate warming is likely to cause an upward shift of the Alpine timber line in our studied region.

We therefore applied the abundance of Geo montani-Nardetum character species, whose degree of non-disturbed/naturally determined vegetation pattern is a good indicator for the process that is driving plant succession in probable response to global warming.

- For each relevé, this degree was classified according to: (a) the total number of Geo montani-Nardetum character species and (b) the density of Geo montani-Nardetum character species. ESRI ArcGIS was used for defining 3 categories: **1=** highest degree: most probably related to climate warming, **2=** intermediate degree: possible reduction in pasture activity and other reasons (e.g., site conditions) and **3=** lowest degree: clearest signs of pasture reduction.

- Relevés with the highest number and density of Geo montani-Nardetum character species were allocated to 1; those with intermediate values were allocated to 2 and those with lowest values to 3. Subsequently, the degree of abundance in each relevé was determined as the average of the two classifications (total number of Geo montani-Nardetum character species and density of Geo montani-Nardetum character species) to show which relevés are most and least responsive to global warming (Table A 34).

In addition, the proportion of areas that show signs of an upward shift of the Alpine timber line was determined by the intensity of spruce forests (Vaccinio-Piceion) invading the Geo montani-Nardetum grassland at the timber-line ecotone. The invasion density of spruce forests into non-forested areas was indicated by the appearance of plant species that are allocated to Vaccinio-Piceion (Table A 24).

Following the same procedure, which was applied to determine the degree of non-disturbed and degraded vegetation pattern at the timber-line ecotone, each relevé was classified with ESRI ArcGIS into 3 categories according to its stage of spruce forest plant succession, which was given by the invasion density of Vaccinio-Piceion spruce forest vegetation: **1=** highest degree: transitional to climax stage, **2=** intermediate degree: transitional stage and **3=** lowest degree: initial to transitional stage (Table A 35).

This work was concluded by the study of an additional area adjacent to the study region where the GIS-forest-cover-analysis by Providoli & Kuhn (2012) has also shown an increase in forest cover since 1899 (Figures 20 and 21). This additional area was studied to assess the effect of site conditions (edaphic & topographic factors and surface processes) on the dynamics of the currently advancing timber line and to determine areas where we propose that the timber line is likely to fringe and remain at a lower elevation in future, below the potential limit of 2000 m a.s.l. with ongoing environmental change.

Like the study region, the selected area at Rinderalp, near Alpiglen, has also been influenced by former pasture activity, because it is easily accessible from the nearest barn and its topography has a profile that is smooth and not too steep. In contrast to the study site, however, limestones with coarse-grained components of the Tertiary (blocks and stones: 2-6.3 dm grain diameter; see Table A 42) have formed the substrate (Tables A 11 and 30). Cattle were pastured here until the year 1970, whereupon environmental risks, such as the high frequency of avalanche activity as well as the unstable steep limestone rock wall of the Eiger, provoking a high risk potential for rock-fall activity and debris flow, caused cattle pasturing to be given up and replaced only by extensive pasturing of goat and sheep (Naegeli-Oertle 1986). A further key driver of the reduced pasture activity is the massive wall of the Eiger, which enhances shading effects and leads to a longer lasting snow cover that reduces the length of growing season (Hegg & Schneiter 1988).

In this selected site, 8 relevés each with an area of 100 m^2, were chosen within the nearest surroundings of increased forested cover (i.e., from the area of increased forest cover up to the highest-altitude tree species found), mapped and analyzed, as for the relevés elevated in the study region. Moreover, the proportion of areas at the timber-line ecotone that show signs of an upward shift in timber line was derived according to the same GIS-classification procedure, as applied for the study region (Table A 37).

Figure 20 Additionally surveyed area at the Rinderalp, near Alpiglen. Photo: S.C. Strähl, July 2009
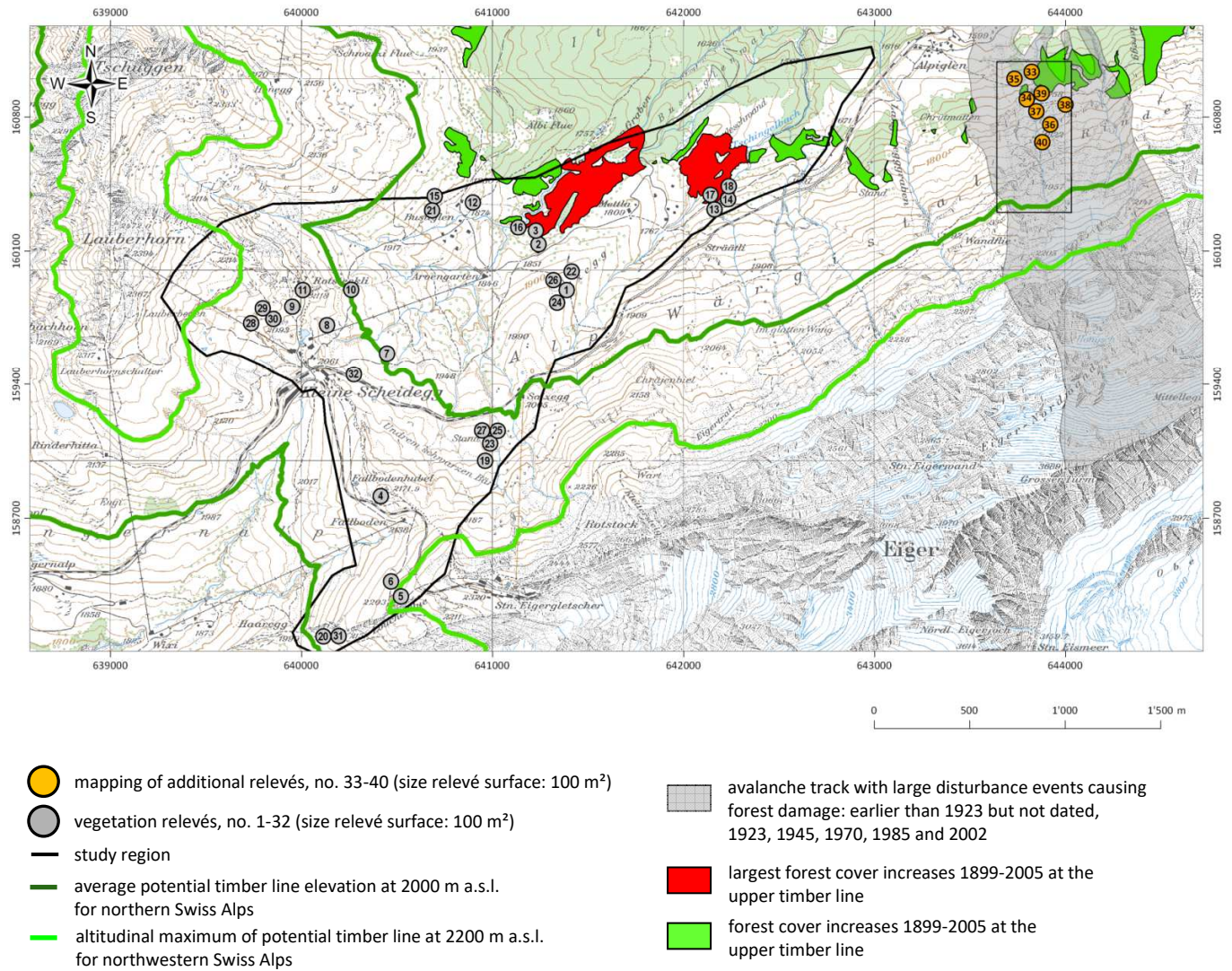
Figure 21 Mapping of additional relevés near the study region at Rinderalp (Alpiglen). The mapping area of Rinderalp is marked by a black rectangle and the mapping relevés are marked in orange. The map has been generated with ArcGIS. Source: Topographical map: PK25 © 2006 swisstopo; avalanches: Lawinenkataster des Kantons Bern © Abteilung Naturgefahren des Kantons Bern; ski piste: Bauverwaltung Einwohnergemeinde Grindelwald (2001); average potential timber line elevation and altitudinal maximum of potential timber line: Landolt 2003, Holmeier 2009; largest forest cover increases and forest cover increases at the upper timber line: Providoli & Kuhn 2012

4   Results

4.1   Vegetation structure and phyto-diversity

4.1.1   Vegetation structure

Our results recorded for vegetation structure showed for both krummholz-forms and trees a significantly higher ratio ($p < 0.05$) in vegetation relevés below the 1899 timber line than in vegetation relevés above. In addition, there was a significantly higher amount of krummholz than trees in relevés both below and above the 1899 timber line (Figure 22). In relevés above the 1899 timber line, 80% of all recorded tree species were shorter than 2 m, whereas below the 1899 timber line, 61% of all recorded tree species appeared as krummholz with a height of less than 2 m (Table A 20). However, tree height and the shortest distance to the neighboring trees displayed no significant difference ($p \geq 0.05$) (Figure 22). Nevertheless, the growth of trees was less dense for relevés above the 1899 timber line, ranging from a minimum average distance measured for a relevé of 1.24 m, up to a maximum average distance measured for a relevé of 12.6 m. Below the 1899 timber line the average distance between trees in a relevé was much less (0.46 m to 6.58 m) (Figures 23 and 24; Table A 20). Less variability was seen in the cover of shrubs and herbs. On average, the percentages of shrub and herb cover were almost equal for relevés above (mean shrub cover: 44%; mean herb cover: 44%) and below (mean shrub cover: 44%; mean herb cover: 47%) the 1899 timber line, and did not differ significantly between the sites ($p \geq 0.05$) (Figure 22; Table A 19).

shrub cover

m = 44	*m* = 44
se = 3.9	*se* = 4.2

n = 16

non-significant difference
p = 0.988 ≥ 0.05

herb cover

m = 47	*m* = 44
se = 3.4	*se* = 3.8

n = 16

non-significant difference
p = 0.406 ≥ 0.05

tree height

m = 255	*m* = 94
se = 67.02	*se* = 19.03

n = 16

non-significant difference
p = 0.050 ≥ 0.05

shortest tree distance

m = 174	*m* = 413
se = 39.3	*se* = 131.7

n = 16

non-significant difference
p = 0.578 ≥ 0.05

number of krummholz

m = 6	*m* = 2
se = 1.6	*se* = 0.8

n = 16

significant difference
p = 0.026 < 0.05

number of trees

m = 4	*m* = 1
se = 1.2	*se* = 0.7

n = 16

significant difference
p = 0.020 < 0.05

Figure 22 Bar diagram visualizing the change in the vegetation structure for vegetation relevés above (≥ 2021 m a.s.l.) and below (< 2021 m a.s.l.) the 1899 timber line. The height of a bar displays the mean (*m*) of that variable. The T-bars display the standard error (*se*), which shows +/- two-fold standard error (+/- 2*se*) of the mean. The significance of the change in vegetation structure between vegetation relevés above and below 2021 m a.s.l. was calculated using pairwise comparisons: (*t-test* for parametric data and Wilcoxon-Rank-Sign-Test for non-parametric data); the significance value (*p*) and the number of pairs (*n*) are shown for each variable. Calculations have been carried out using SPSS. The graphic has been generated with Adobe Illustrator.
Note: Values for the mean are rounded up to the scale values with no decimal place. Values for the standard error are rounded up to the scale values with one or two decimal places.

59
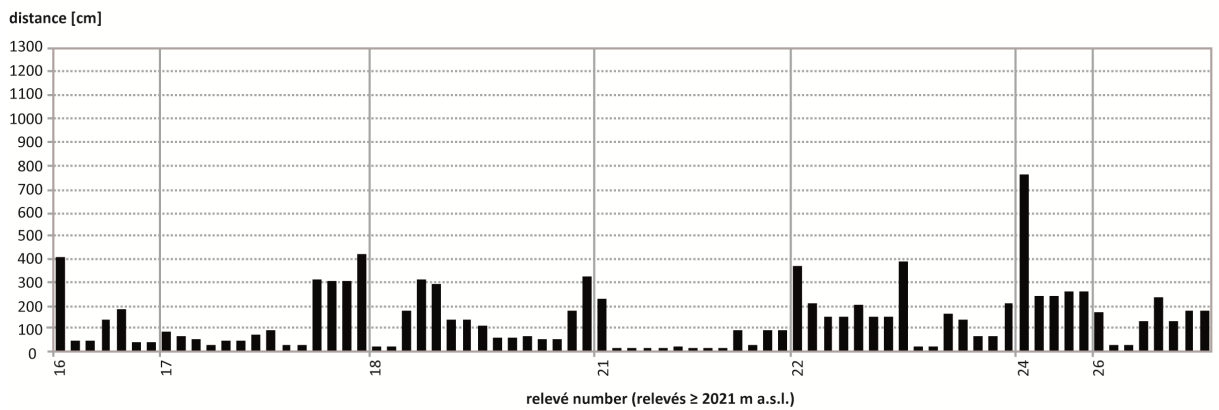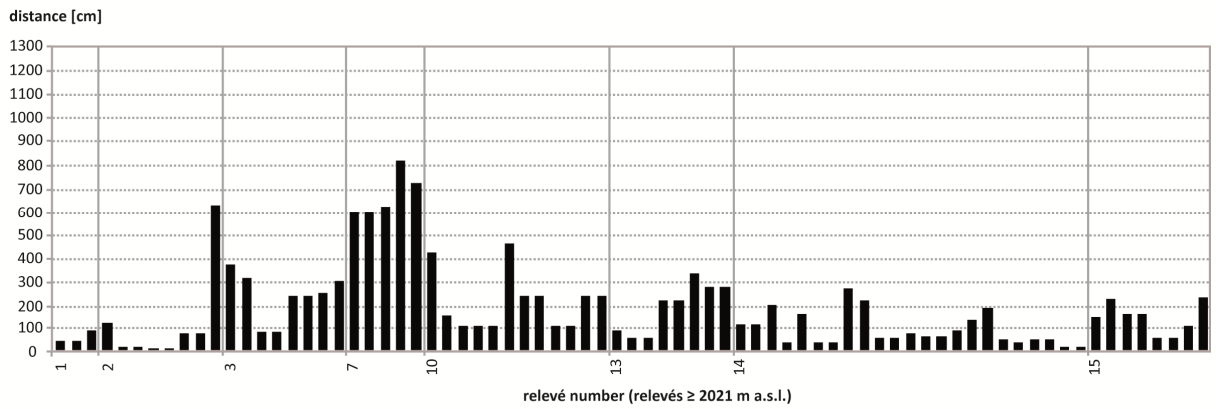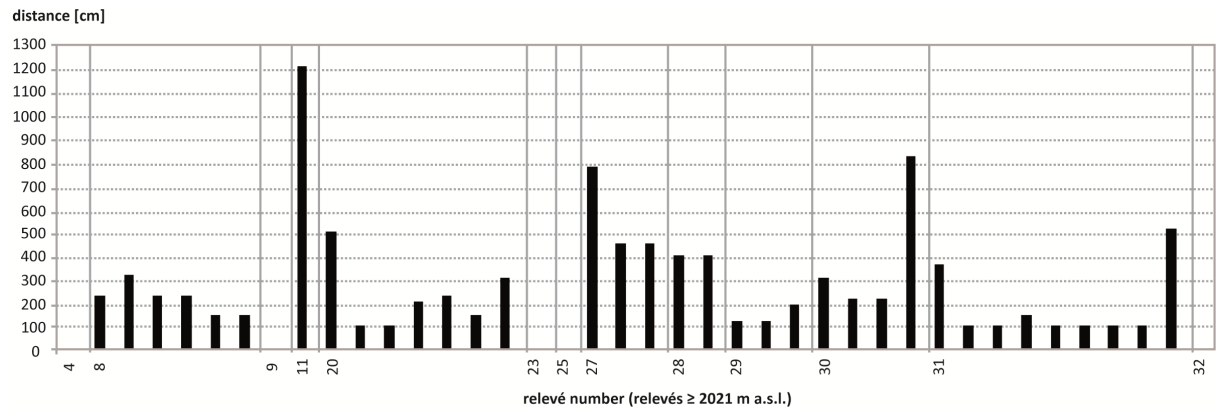
Figure 23 Shortest distances between two neighboring trees, small trees and tree seedlings for each vegetation relevé. The upper most diagram refers to vegetation relevés ≥ 2021 m a.s.l. (no. 4-32), whereas the lower two diagrams refer to vegetation relevés < 2021 m a.s.l. (no. 1-15 and 16-26). Relevés 4, 9, 23, 25 and 32 showed only one tree per relevé and therefore no distance value is recorded for those vegetation relevés. The graphic has been generated with Adobe Illustrator.

Picea abies (52%) showed the largest proportion of area covered among the recorded tree species in the study region. *Pinus cembra* was also represented in several vegetation relevés and occurred with a frequency of 39% (Figures 24-26; Table A 12). The majority of *Picea abies* (75%) were recorded as trees growing 2 m and taller, whereas the majority of elevated *Pinus cembra* (75%) appeared as krummholz (Figures 24-26; Table A 12). In vegetation relevés 8, 9 and 11, *Pinus cembra* was only represented as krummholz, whereas in relevé 23 one tall tree of approximately 5 m was found (Figures 23 and 25). Other tree species such as *Pinus mugo* ssp. *uncinata* (7%) were less frequent in the study region and were growing mostly as krummholz (Figures 24 and 27). *Pinus mugo* ssp. *uncinata* was only found in the vegetation relevés 4 and 11 as krummholz (Figures 24 and 27).

Tree species diversity and frequency differed between vegetation relevés below and above the 1899 timber line. In relevés located below the 1899 timber line, *Pinus cembra* (47%) was slightly more frequent than *Picea abies* (44%) (Figures 24-26; Table A 12). Especially the tall *Pinus cembra* trees appeared in areas of former forests (Figures 24, 26 and 28). *Pinus mugo* ssp. *uncinata* was not represented in any of the vegetation relevés below the 1899 timber line; however other tree species like *Sorbus aucuparia* (6%) and *Betula pendula* (2%) were occasionally found in some relevés, as trees but also as krummholz (Figures 24 and 27). *Larix decidua* (relevé 24) and *Sorbus aria* (relevé 17) were growing in only one relevé each, as krummholz (Figures 24 and 27).
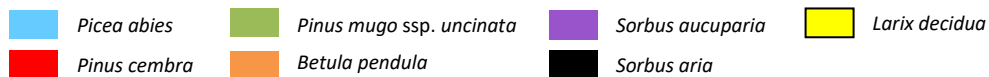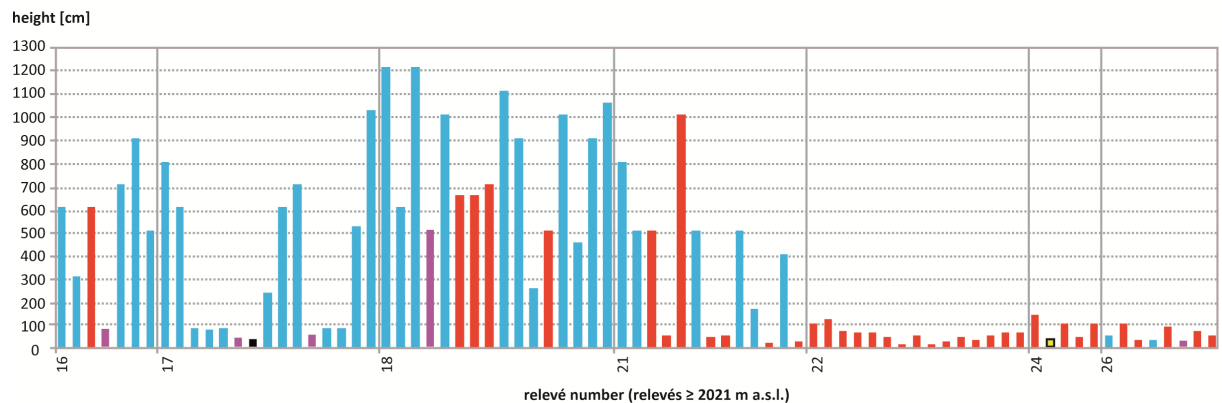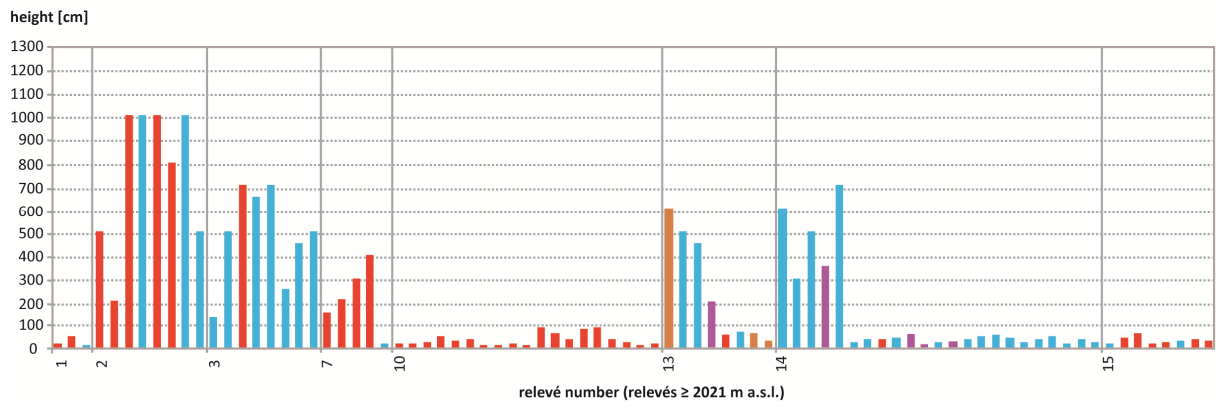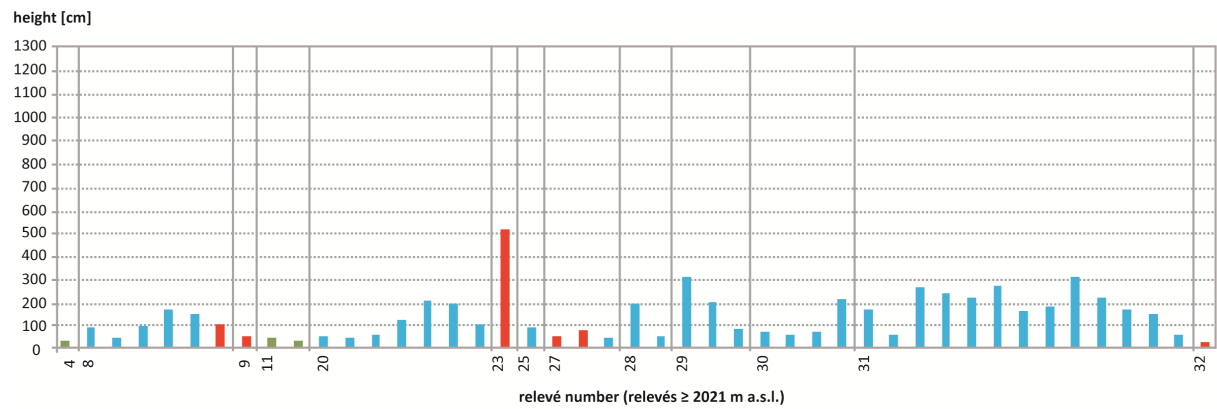
Figure 24 Height and type of tree, small tree and tree seedling species expressed for each vegetation relevé. Height values have been estimated as decribed in Section 3.3. The upper diagram refers to vegetation relevés ≥ 2021 m a.s.l. (no. 4-32), whereas the lower two diagrams refer to vegetation relevés < 2021 m a.s.l. (no. 1-15 and 16-26). The graphic has been generated with Adobe Illustrator.
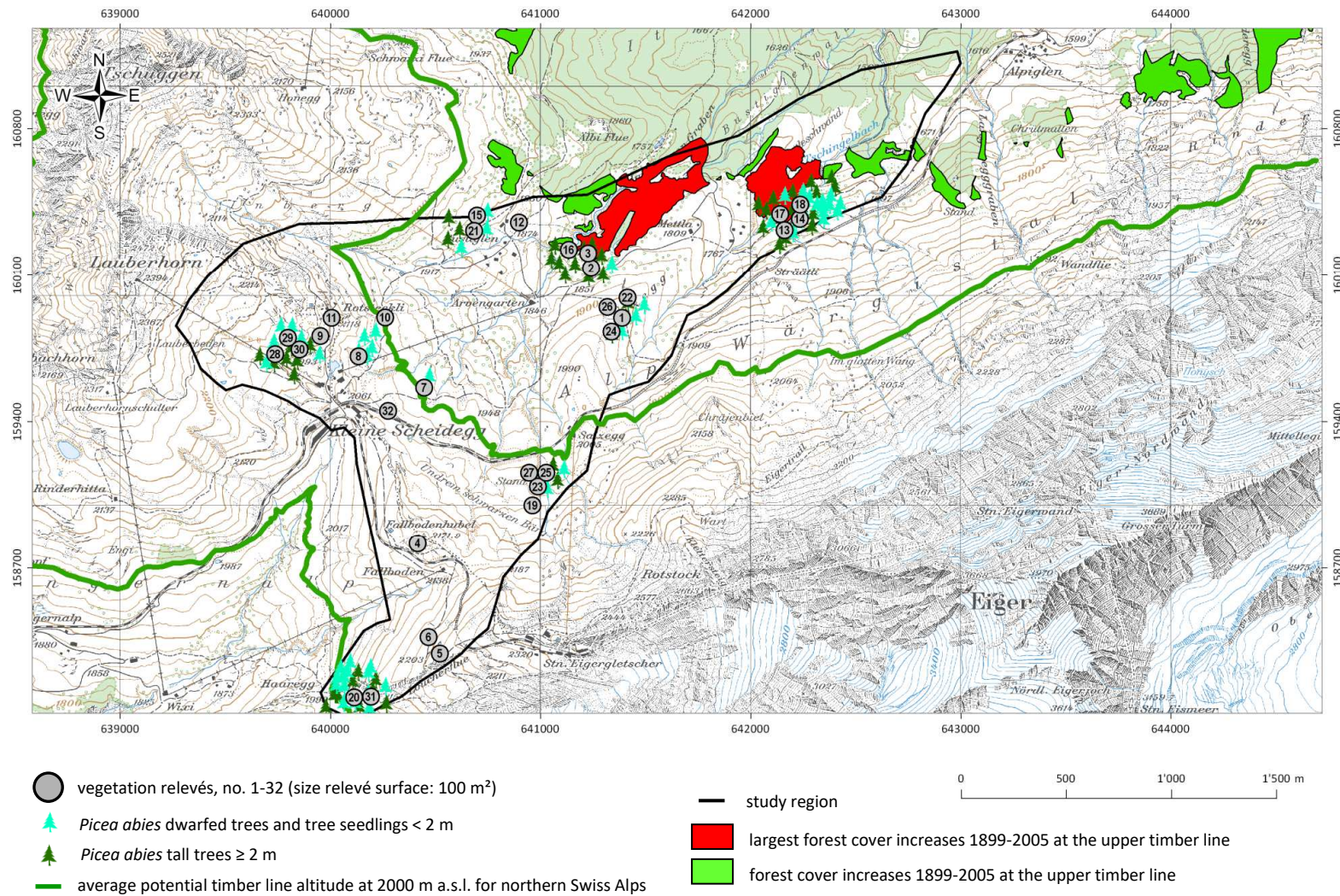
Figure 25 Most frequent tree species in the study region: spruce (*Picea abies*). The map has been generated with ArcGIS.
Source: Topographical map: PK25 © 2006 swisstopo; average potential timber line altitude: Landolt 2003, Holtmeier 2009; largest forest cover increases and forest cover increases at the upper timber line: Providoli & Kuhn 2012; tree species: own observation of vegetation mappings of the period 2008-2010.
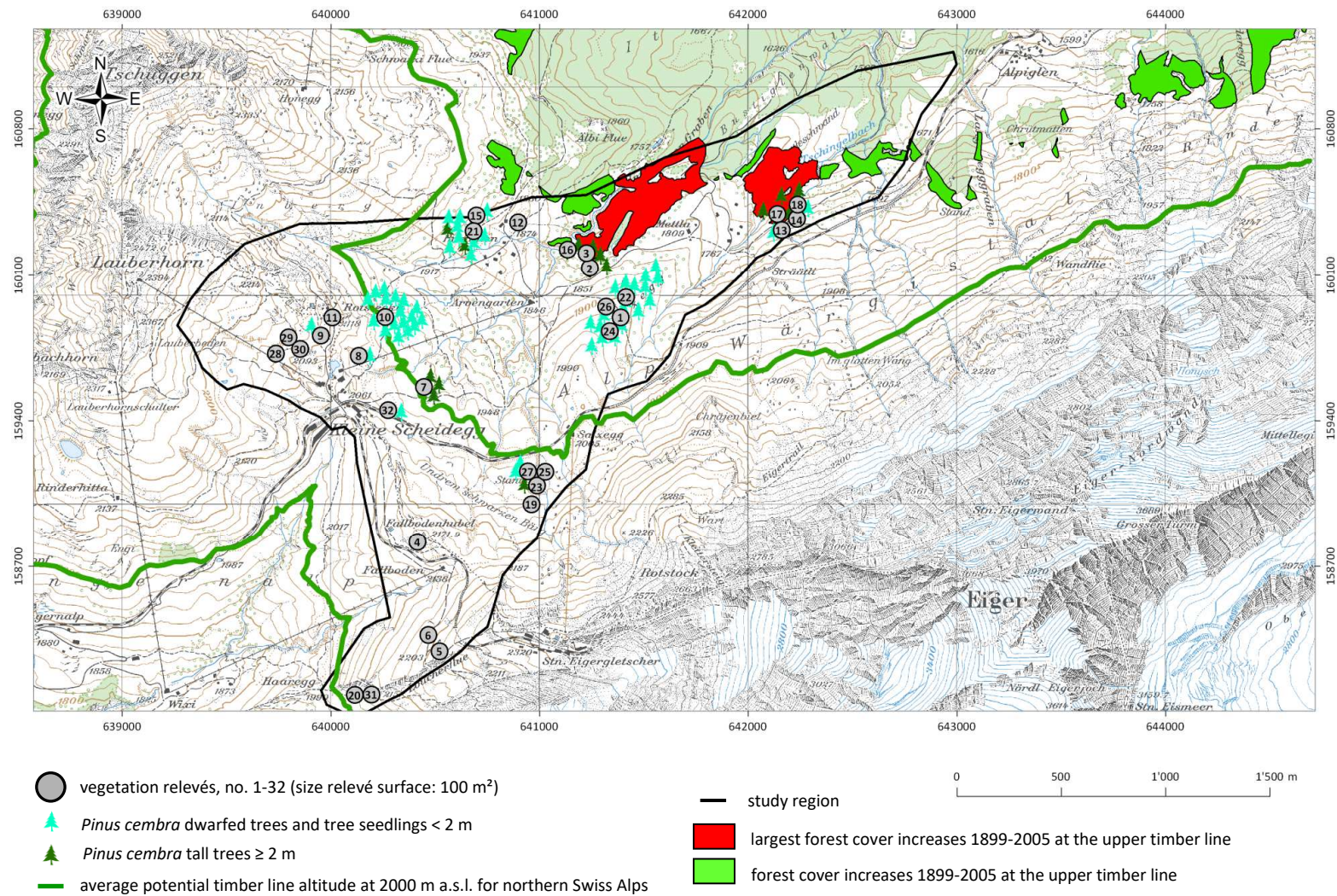
Figure 26 Most frequent tree species in the study region: Swiss stone pine (*Pinus cembra*). The map has been generated with ArcGIS.
Source: Topographical map: PK25 © 2006 swisstopo; average potential timber line altitude: Landolt 2003, Holtmeier 2009; largest forest cover increases and forest cover increases at the upper timber line: Providoli & Kuhn 2012; tree species: own observation of vegetation mappings of the period 2008-2010.
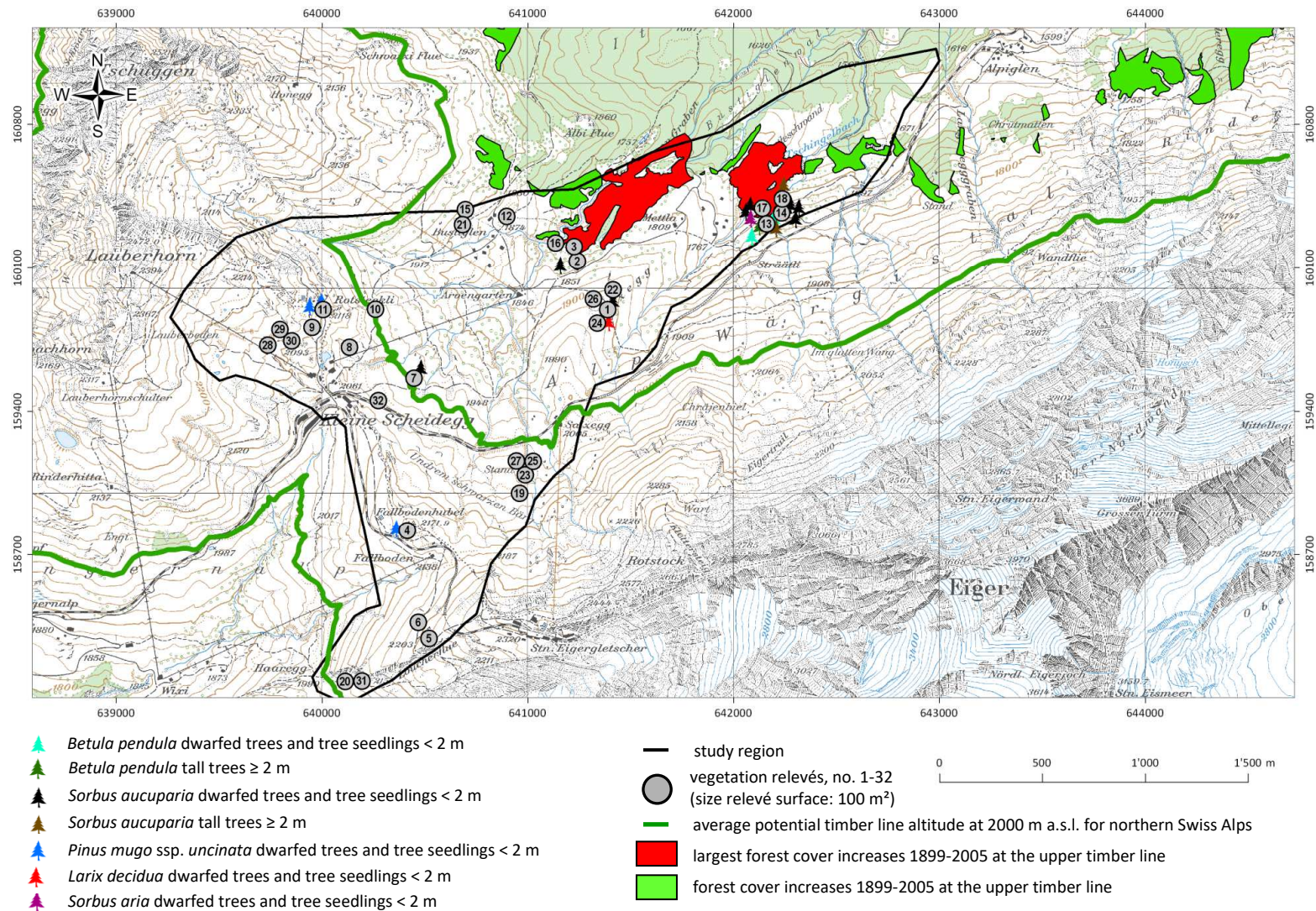
Figure 27 Remaining important tree species of the study region: Birch, European Larch, Pine tree, Rowan tree and Whitebeam (*Betula pendula*, *Larix decidua*, *Pinus mugo* ssp. *uncinata*, *Sorbus aucuparia* and *Sorbus aria*). The map has been generated with ArcGIS.
Source: Topographical map: PK25 © 2006 swisstopo; average potential timber line altitude: Landolt 2003, Holtmeier 2009; largest forest cover increases and forest cover increases at the upper timber line: Providoli & Kuhn 2012; tree species: own observation of vegetation mappings of the period 2008-2010.
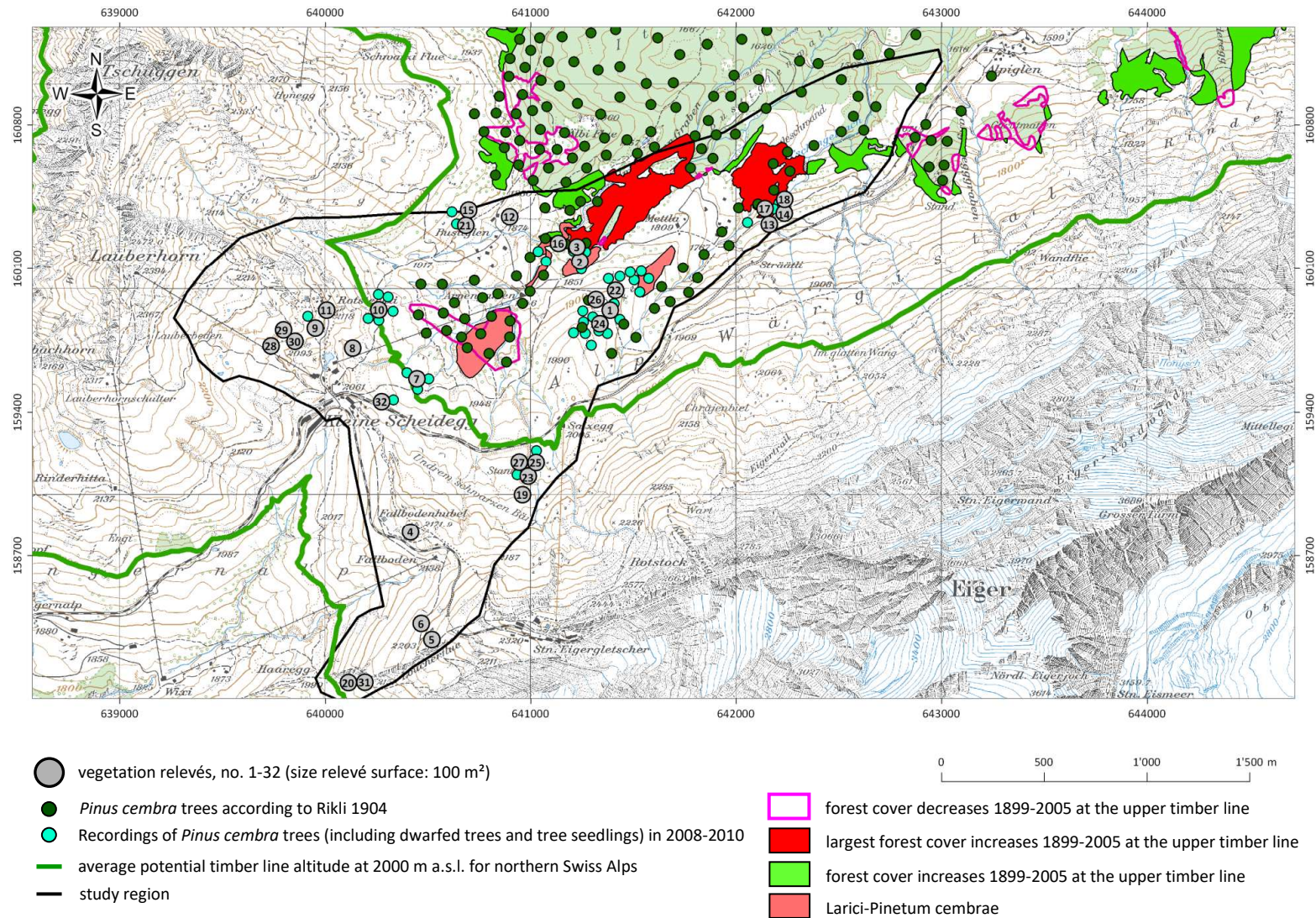
Figure 28 Distribution of *Pinus cembra* trees in 2008-2010 and for the year 1904. The map has been generated with ArcGIS.
Source: Topographical map: PK25 © 2006 swisstopo; average potential timber line altitude: Landolt 2003, Holtmeier 2009; Larici-Pinetum cembrae: Hegg & Schneiter 1988; largest forest cover increases, forest cover increases and decreases at the upper timber line: Providoli & Kuhn 2012; *Pinus cembra* trees 1904: Rikli 1909; recordings of *Pinus cembra* trees in 2008-2010: own observation of vegetation mappings.

4.1.2 Phyto-diversity

Our phyto-diversity results show a significantly higher abundance of Geo montani-Nardetum character species in vegetation relevés above the 1899 timber line; with a large amount of relevés showing 4 or 5 character species and a maximum density of assessed character species of 16% for relevé no. 5 (Figure 29; Tables A 21-23). In contrast, relevés below the 1899 timber line showed a significantly lower abundance of Geo montani-Nardetum character species, with a maximum of only 3 recorded character species and a density ranging up to a maximum of 8% (Figure 29; Tables A 21-23). The majority of our relevés, however, showed only a low abundance of recorded Geo montani-Nardetum character species (Table A 21). Significant differences were only displayed for the test variable "abundance of Geo montani-Nardetum character species", but not for the test variable "density of deteriorated Geo montani-Nardetum to heathland", although the frequency of disturbed Geo montani-Nardetum was higher in relevés below (mean cover density: 42%) than in relevés above (mean cover density: 38%) the 1899 timber line (Figure 29; Table A 21). In relevés showing a disturbed pattern of Geo montani-Nardetum, the vegetation lacked diversity and had a wide occurrence of trivial vegetation, such as rich meadow species (*Poa alpina*, *Rumex alpestris* or *Deschampsia cespitosa*), but also showed a dominance of *Nardus stricta* (Tables A 1-8; 22-23).

Overall, our data returned, on average, highest significance differences (Wilcoxon-Test), with (p < 0.01), for the test variable "total number of Geo montani-Nardetum character species" (p = 0.001; Figure 29; Table A 33).
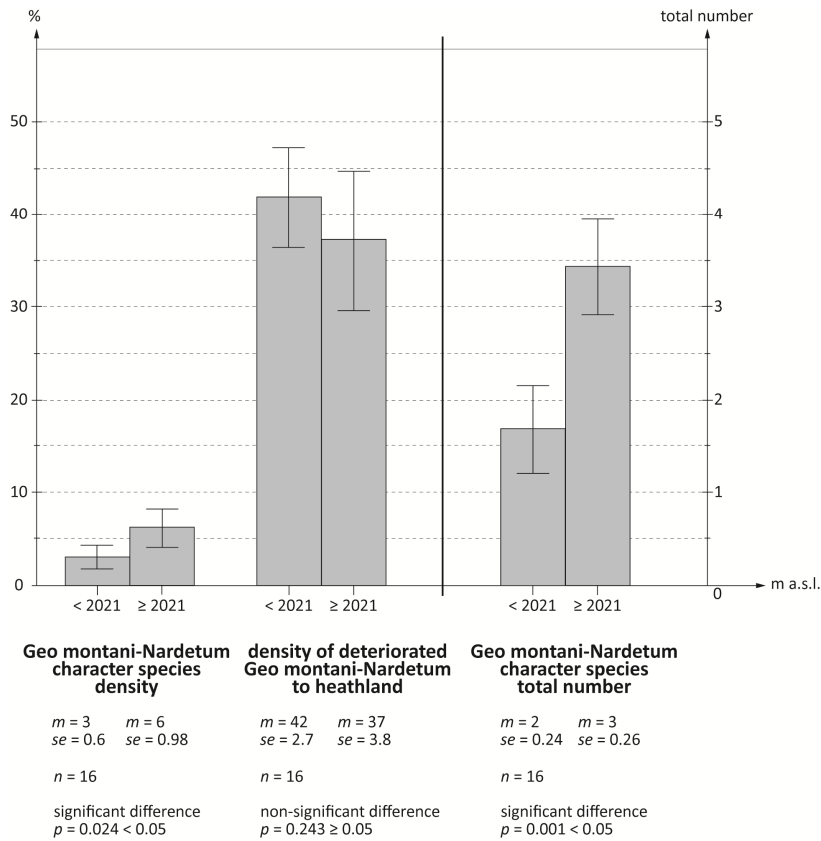
Figure 29 Bar diagram visualizing the change in phyto-diversity by: the abundance of Geo montani-Nardetum character species (including: total number and density) as well as density of deteriorated Geo montani-Nardetum to heathland for vegetation relevés above the 1899 timber line (≥ 2021 m a.s.l.) and below (< 2021 m a.s.l.). The height of a bar displays the mean (*m*) of that variable. The T-bars display the standard error (*se*), which shows +/- two-fold standard error (+/- 2*se*) of the mean. The significance of the change in vegetation structure between vegetation relevés above and below 2021 m a.s.l. was calculated using pairwise comparisons: (*t-test* for parametric data and Wilcoxon-Rank-Sign-Test for non-parametric data): the significance value (*p*) and the number of pairs (*n*) are shown for each variable. Calculations have been carried out by SPSS. The graphic has been generated with Adobe Illustrator.

Note: Values for the mean are rounded up to the scale values with no decimal place. Values for the standard error are rounded up to the scale values with one or two decimal places. The applied classification of plant species for Geo montani-Nardetum grassland corresponds to the publication "Lebensräume der Schweiz" (Delarze & Gonseth 2008) for indicator and important accessory plant species for Nardion, and to the publication "Übersicht über die Pflanzengesellschaften Rätiens" (Braun-Blanquet 1948/1949) for important accessory plant species for Geo montani-Nardetum.

4.2 Areas attributed to an upward shift of the Alpine timber line in probable response to global warming

The proportion of relevés that have been attributed to the lowest influences of land-use practices and a possible sign of warming impact was low (**16%**) in the study region and considerable only in local areas (Figure 30; Tables A 34 and 36).

Our results showed for relevés 5 (2227 m a.s.l.) and 6 (2176 m a.s.l.) the most undisturbed Geo montani-Nardetum, having the highest recorded abundances of character species (Figure 30; Tables A 21-23). These relevés were those with the highest elevations and were among those with the lowest access (Table A 11). The location of relevé 4 (2160 m a.s.l.) was at a similarly high elevation; however, access was better (Table A 11). Our data illustrated a higher degree of disturbed Geo montani-Nardetum pattern in relation to non-disturbed Geo montani-Nardetum pattern (Tables A 21-23). In relevé 4 there was a wide appearance of short-growing vegetation, accompanied by one recorded *Pinus mugo* ssp. *uncinata* krummholz and dense cover of dwarf shrub species *Loiseleuria procumbens* and *Calluna vulgaris* (Tables A 1-8 and A 12). In the GIS-classification, vegetation relevés 19 and 31 were also allocated to the category of highest abundance of Geo montani-Nardetum character species, hence indicating a non-disturbed area (Figure 30; Tables A 21-23), although these were at lower elevations than relevés 4, 5 and 6 (Table A 11).

In the majority of our mapped relevés **(84%)**, the degree of Geo montani-Nardetum character species was either low or intermediate (Figure 30; Tables A 21-23, A 34 and 36). Yet, only 47% of our mapped vegetation relevés have been attributed to areas showing lowest abundance of Geo montani-Nardetum character species, with clearest signs of pasture reduction (Figure 30; Tables A 34 and 36). Those relevés were mostly located below the 1899 timber line, i.e., in relevés 1, 2, 3, 7, 13, 14, 16, 17, 18, 21 and 22 (Table A 11). A quite large proportion of relevés **(38%)** have been attributed to an intermediate abundance of Geo montani-Nardetum character species, where not only pasture reduction, but also other reasons (e.g., site conditions) are likely influencing the current dynamics of vegetation succession at the Alpine timber line ecotone (Figure 30; Tables A 34 and 36).
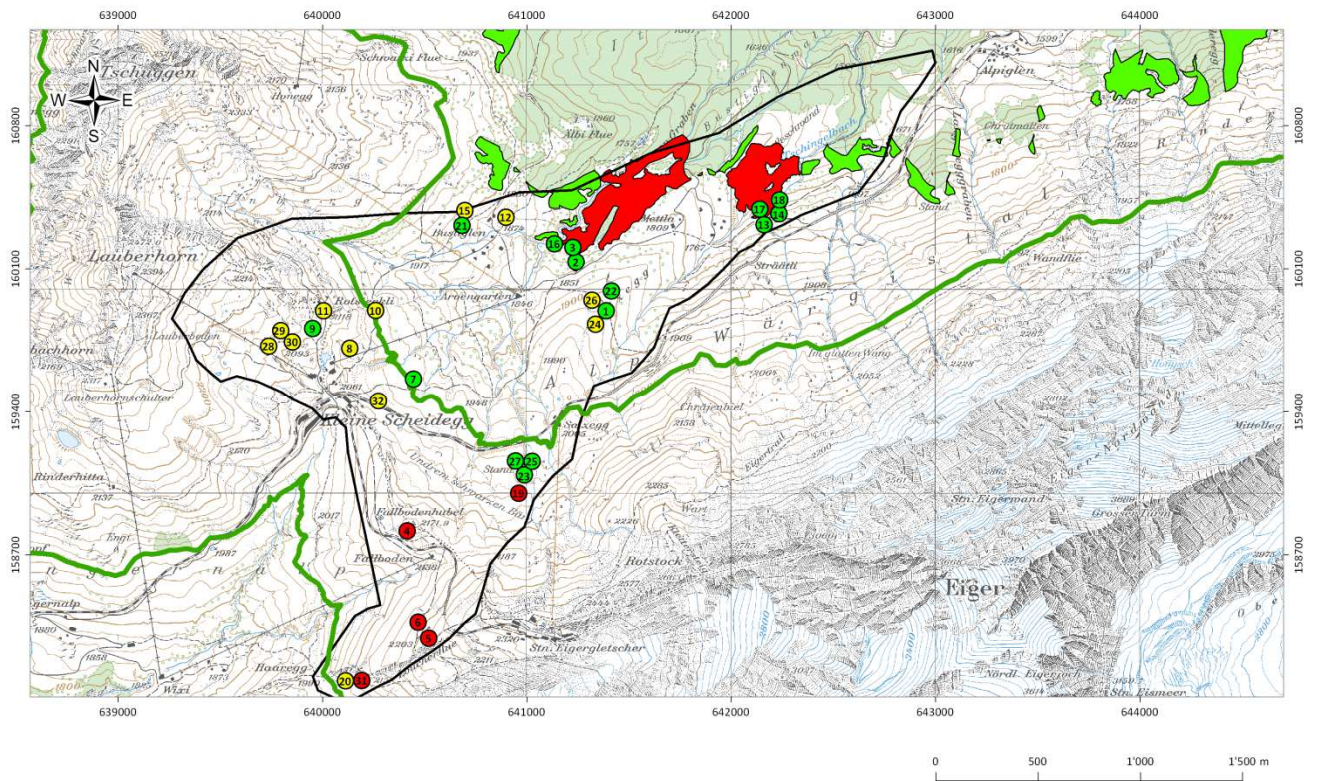
Vegetation relevés attributed to areas with probable response to global warming
rates classified with GIS (class 1: highest degree, class 3: lowest degree)

🔴 **1 =** highest degree:
most probably related to global warming

🟡 **2 =** intermediate degree:
possible reduction in pasture activity and other reasons
(e.g., site conditions)

🟢 **3 =** lowest degree:
clearest signs of pasture reduction

━━ average potential timber line
altitude at 2000 m a.s.l. for northern Swiss Alps
━━ study region

🟥 largest forest cover increases 1899-2005
at the upper timber line

🟩 forest cover increases 1899-2005
at the upper timber line

Figure 30 Vegetation relevés attributed to areas that are most probably responding to global warming. The response of probable warming effect is expressed by the degree of non-disturbed/natural vegetation pattern of Geo montani-Nardetum. Vegetation relevés are ordered according to the rates classified for abundance of Geo montani-Nardetum character species. Rates classified as 1 are allocated to areas with highest abundance degree, rates classified as 2 are allocated to areas with intermediate abundance degree and rates classified as 3 are allocated to areas with lowest abundance degree and clearest signs of pasture reduction. The location and altitude of the 1899 timber line, at 2021 m a.s.l. refers to an interpolated value according to Providoli & Kuhn (2012). The map has been generated with ArcGIS.
Source: Topographical map: PK25 © 2006 swisstopo; average potential timber line altitude: Landolt 2003, Holtmeier 2009; largest forest cover increases and forest cover increases at the upper timber line: Providoli & Kuhn 2012; parameters for vegetation dynamics responding to recessive pasture activity: own observation of vegetation mappings of the period 2008-2010.

Only 25% of our mapped relevés have been attributed to the highest degree of Vaccinio-Piceion spruce forest invasion (Figure 31; Tables A 35 and 36). The proportion of areas attributed to the highest degree of Vaccinio-Piceion spruce forest invasion is most pronounced in relevés below the 1899 timber line. At this point of the current forest limit, almost half our relevés (2, 3, 13, 14, 16, 17 and 18) mapped below the 1899 timber line, were allocated to the highest invasion density of Vaccinio-Piceion (Figure 31). The proportion of areas attributed to the lowest degree of Vaccinio-Piceion spruce forest invasion was most pronounced in relevés located above the 1899 timber line, where almost half our relevés (4, 5, 6, 11, 20 and 31), were allocated to the lowest invasion density of Vaccinio-Piceion (Figure 31). The largest proportion of all our mapped relevés in the study region (i.e., 7, 9, 10, 12, 15, 19, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30 and 32) were attributed to an intermediate degree of Vaccinio-Piceion spruce forest invasion (Figure 31; Table A 36).
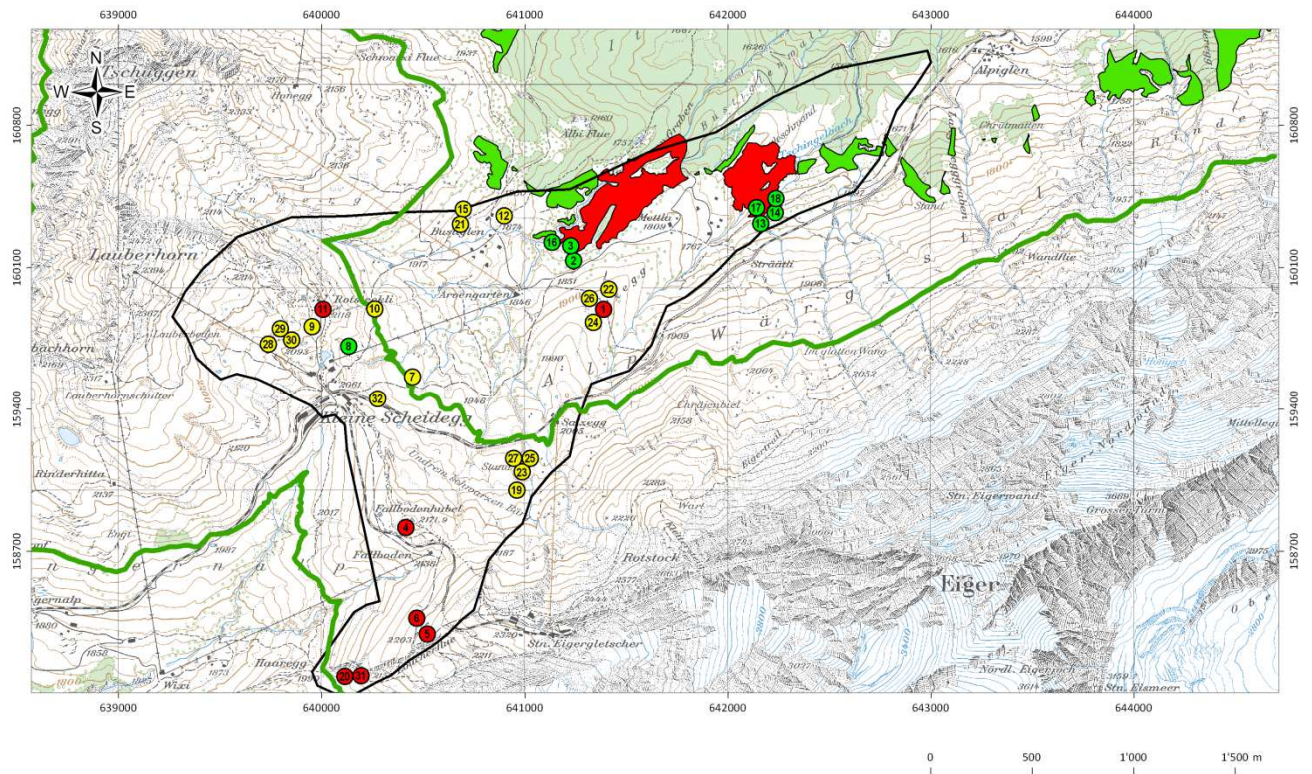
Vegetation relevés attributed to areas showing signs of an upward shift in timber line

rates classified with GIS (class 1: highest degree, class 3: lowest degree)

🟢 **1 =** highest degree of Vaccinio-Piceion spruce forest invasion: transitional to climax stage

🟡 **2 =** intermediate degree of Vaccinio-Piceion spruce forest invasion: transitional stage

🔴 **3 =** lowest degree of Vaccinio-Piceion spruce forest invasion: initial to transitional stage

— average potential timber line altitude at 2000 m a.s.l. for northern Swiss Alps

— study region

🟥 largest forest cover increases 1899-2005 at the upper timber line

🟩 forest cover increases 1899-2005 at the upper timber line

Figure 31 Vegetation relevés attributed to areas showing signs of an upward shift in timber line. The proportion of areas with signs of an upward shift in timber line is shown by the progress of spruce forest vegetation (Vaccinio-Piceion) into non-forested areas. Vegetation relevés are ordered according to the rates classified for invasion density of Vaccinio-Piceion spruce forest vegetation. Rates classified as 1 are allocated to areas with highest invasion density of Vaccinio-Piceion (i.e., most advanced stage of spruce forest plant succession), rates classified as 2 are allocated to areas with intermediate invasion density of Vaccinio-Piceion and rates classified as 3 are allocated to areas with lowest invasion density of Vaccinio-Piceion (i.e., initial to transitional stage of spruce forest plant succession). The location and altitude of the 1899 timber line, at 2021 m a.s.l., refers to an interpolated value according to Providoli & Kuhn (2012). The map has been generated with ArcGIS.
Source: Topographical map: PK25 © 2006 swisstopo; average potential timber line altitude: Landolt 2003, Holtmeier 2009; largest forest cover increases and forest cover increases at the upper timber line: Providoli & Kuhn 2012; parameters for intensity of forest progress: own observation of vegetation mappings of the period 2008-2010.

Relevés 4, 5, 6 and 31, which have been allocated the highest degree of non-disturbed Geo montani-Nardetum and are most probably responding to global warming, have been attributed a low advancing rate of spruce forest. The low advancing rate of spruce forest was also shown by the proportion of recorded plant species associated to Vaccinio-Piceion, which was much smaller in relation to Geo montani-Nardetum (Figures 30-32; Tables A 34-36). Relevé 19, which has also been allocated the category of least disturbed Geo montani-Nardetum surface, has been attributed an intermediate advancing rate of spruce forest (transitional stage) (Figures 30-32; Tables A 34-36). Furthermore, relevé 19 showed a higher invasion density of plant species associated to Vaccinio-Piceion compared to relevés 4, 5, 6 and 31 (Table A 24), although the proportion of plant species that were associated to Geo montani-Nardetum was, as for relevés 4, 5, 6 and 31, much higher in relation to Vaccinio-Piceion, indicating only a weak advancing rate of spruce forest (Figure 32).

Relevé 5 was found to be at the earliest stage of spruce forest progress, since ericaceous dwarf shrubs were very scarce, and vegetation cover was low and showed transitions to snow pocket vegetation (Tables A 1-8 and 24). In addition, the location of relevé 5 had the highest elevation of all mapped vegetation relevés, at 2227 m a.s.l. actually sitting above the altitudinal maximum of potential timber line at 2200 m a.s.l. (Table A 11).

In the 15 relevés (1, 2, 3, 7, 9, 13, 14, 16, 17, 18, 21, 22, 23, 25 and 27) that were attributed the lowest degree of Geo montani-Nardetum character species, and therefore showed the clearest signs of pasture reduction, the advancing rate of spruce forest was high for fewer than half the relevés (2, 3, 13, 14, 16, 17 and 18), all located below the 1899 timber line and near the region of largest forest cover increases since 1899 (Figures 30 and 31; Table A 36). These relevés also showed in their vegetation pattern a higher or almost equal proportion of plant species associated to Vaccinio-Piceion in relation to Geo montani-Nardetum (Figure 32). A quite large fraction of relevés (7, 9, 21, 22, 23, 25 and 27) were allocated as areas with intermediate invasion density of Vaccinio-Piceion and the proportion of plant species associated to Vaccinio-Piceion was smaller in relation to Geo montani-Nardetum (Figure 32). One relevé (no. 1) was allocated as an area with lowest invasion density of Vaccinio-Piceion and also showed a smaller proportion of plant species associated to Vaccinio-Piceion in relation to Geo montani-Nardetum (Figures 31 and 32).
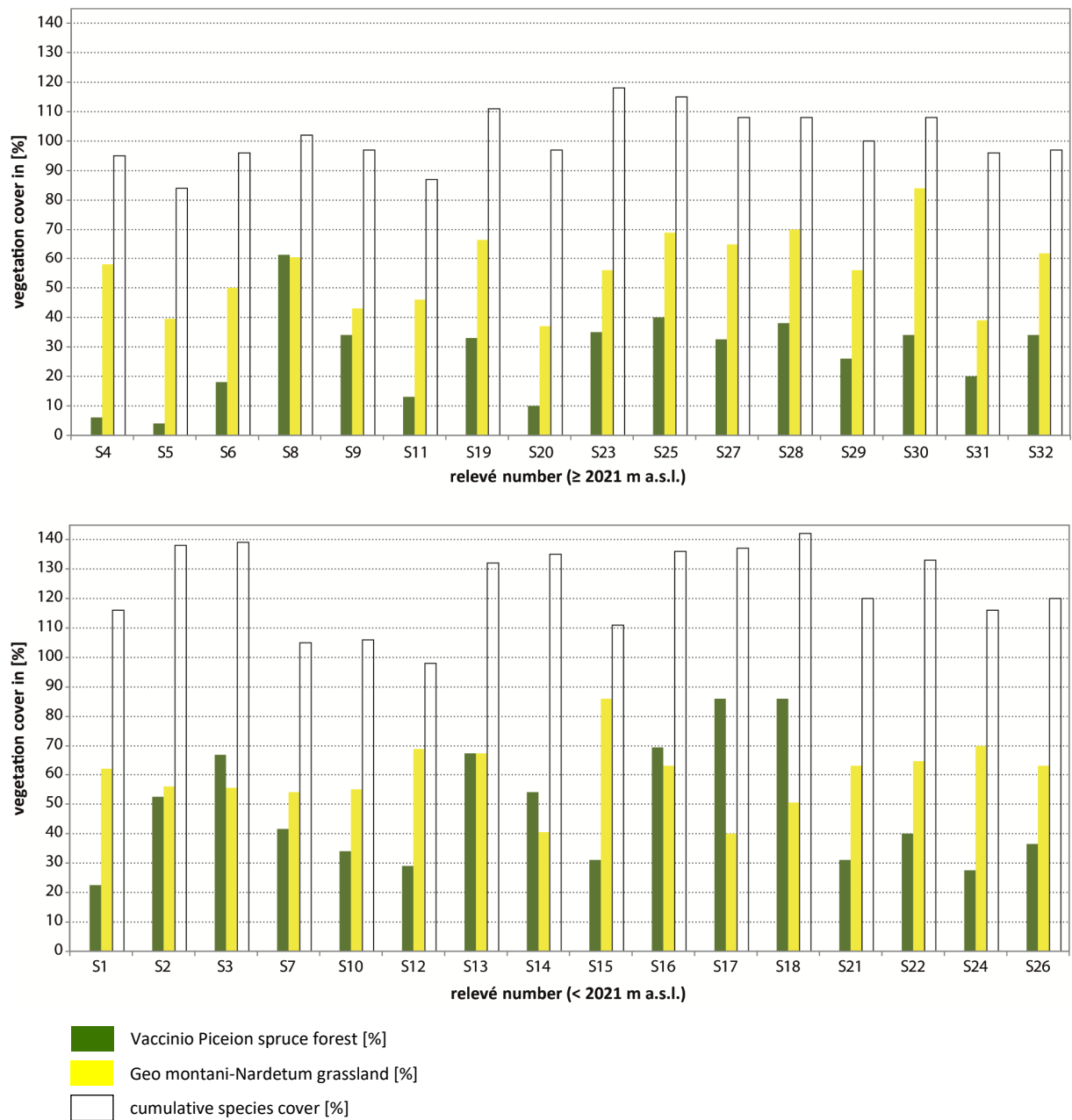
Figure 32 The progress of spruce forest vegetation (Vaccinio-Piceion) into non-forested areas of Geo montani-Nardetum grassland is expressed for each mapped relevé by the fraction of plant species associated to Vaccinio-Piceion spruce forest in relation to plant species associated to Geo montani-Nardetum. The cumulative species cover includes all recorded plant species of each vegetation layer (i.e., tree-, shrub-, herb- and moss layer). A cumulative density value of more than 100% can occur, since the parts of each vegetation layer may overlap. The upper graphic shows vegetation relevés located above 2021 m a.s.l., whereas the lower graphic shows vegetation relevés located below 2021 m a.s.l. The graphic has been generated with Adobe Illustrator.

In the additional studied area at Rinderalp, we also found evidence of former cattle pasturing in the vegetation pattern at the timber-line ecotone, here in the high abundance of plant species associated to the rich meadow community Poion alpinae (Tables A 28-29). Compared to the studied region, vegetation showed a large density of undemanding pioneer plant species (e.g., *Dryas octopetala*, *Saxifraga exarata* ssp. *moschata* and *Salix retusa*), initial tree invaders, such as *Pinus mugo* ssp. *uncinata* and *Sorbus aucuparia* as well as a higher frequency of plant species associated with Erico-Pinetum montanae than with Vaccinio-Piceion (Figures 24 and 34; Tables A 13-16; 28-29). Moreover, tall-growing trees (≥ 2 m) were dominated by *Pinus mugo* ssp. *uncinata* (50%) and less by *Picea abies* (32%) (Figures 24 and 34; Table A18). In addition, the majority of our relevés were either attributed an initial- or transitional stage (63%) of spruce forest succession (Figure 33; Table A 37). Compared to the studied region, there was a large amount of dwarf *Picea abies* (82%) (Figures 24 and 34) and the current limit of tree existence was at a markedly low elevation (Figure 33; Tables A 11 and 30).
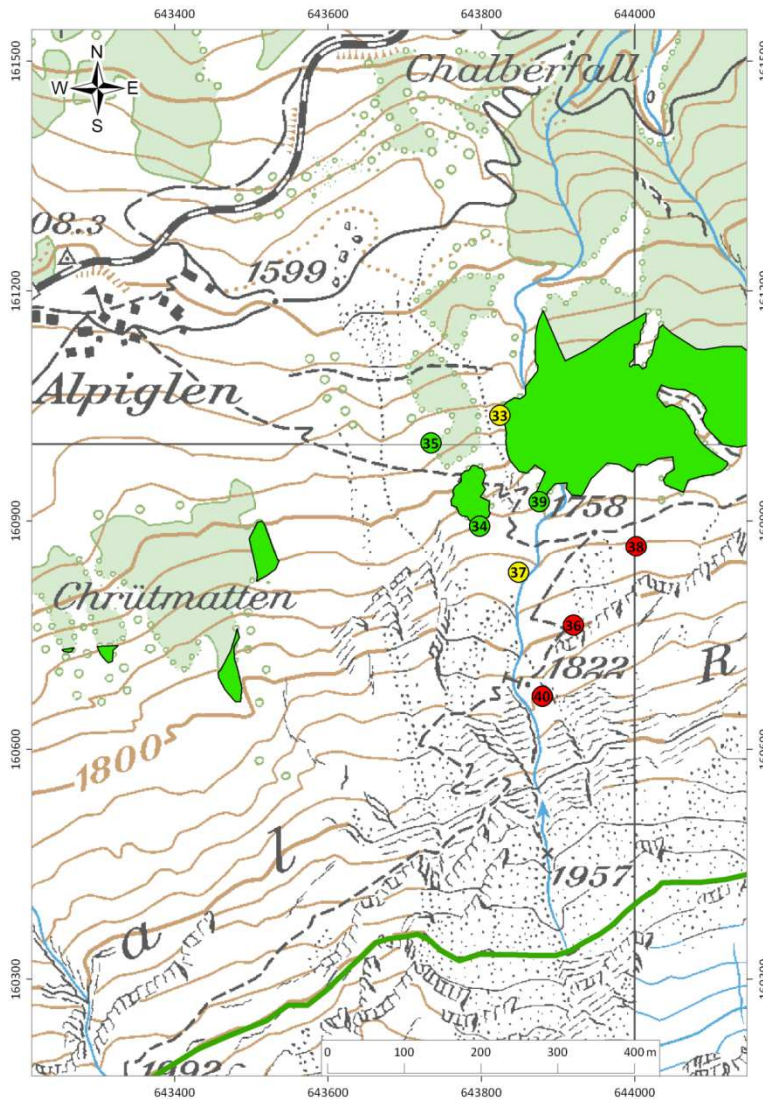
Vegetation relevés attributed to areas showing signs of an upward shift in timber line at Rinderalp

rates classified with GIS (class 1: highest degree, class 3: lowest degree)

1 = highest degree of Vaccinio-Piceion spruce forest invasion: transitional to climax stage

2 = intermediate degree of Vaccinio-Piceion spruce forest invasion: transitional stage

3 = lowest degree of Vaccinio-Piceion spruce forest invasion: initial to transitional stage

average potential timber line altitude at 2000 m a.s.l. for northern Swiss Alps

forest cover increases 1899-2005 at the upper timber line

Figure 33 Vegetation relevés 33-40 at Rinderalp, attributed to areas showing signs of an upward shift in timber line. The proportion of areas with signs of an upward shift in timber line is shown by the progress of spruce forest vegetation (Vaccinio-Piceion) into non-forested areas. Vegetation relevés are ordered according to the rates classified for invasion density of Vaccinio-Piceion spruce forest vegetation. Rates classified as 1 are allocated to areas with highest invasion density of Vaccinio-Piceion (i.e., most advanced stage of spruce forest plant succession), rates classified as 2 are allocated to areas with intermediate invasion density of Vaccinio-Piceion and rates classified as 3 are allocated to areas with lowest invasion density of Vaccinio-Piceion (i.e., initial to transitional stage of spruce forest plant succession). The location and altitude of the 1899 timber line, at 2021 m a.s.l., refers to an interpolated value according to Providoli & Kuhn (2012). The map has been generated with ArcGIS. Note: For map location refer to figure 21 on page 56.
Source: Topographical map: PK25 © 2006 swisstopo; average potential timber line altitude: Landolt 2003, Holtmeier 2009; largest forest cover increases 1899-2005: Providoli & Kuhn 2012; tree species and parameters for intensity of forest progress: own observation of vegetation mappings of the period 2008-2010.
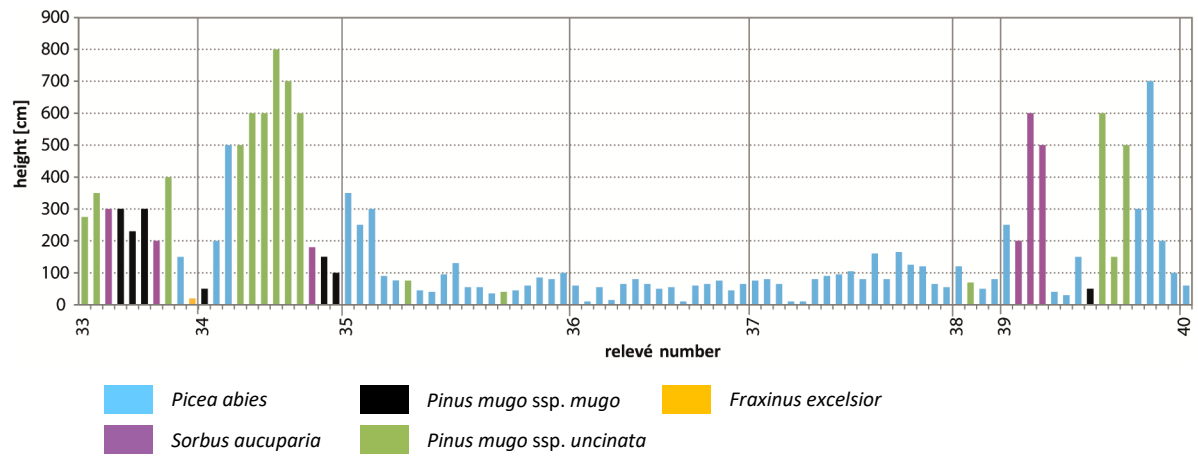
Figure 34 Tree height and type of tree species in each relevé at Rinderalp. The graphic has been generated with Adobe Illustrator.

5 Discussion

This current study tried to answer the question whether the impacts of changes in land-use activity or climate change can be differentiated by means of vegetation mappings according to Braun-Blanquet (1964). Our results showed that Phyto-diversity was found to be more suitable than vegetation structure for understanding the process of progressing forest vegetation at the timber-line ecotone by its non-disturbed/natural character or disturbed/anthropo-zoogenically modified character. In particular, the abundance of Geo montani-Nardetum character species was the test variable that showed the most significant difference between vegetation relevés located above and below the 1899 timber line (Table A 33). The majority of tested mapping variables, however, revealed no sufficient significance differences between the relevés above and below the 1899 timber line (Figures 22 and 29; Table A 33). We therefore draw the conclusion that these causes (land-use changes or climate warming) cannot be clearly disentangled from each other, underlining the difficulty in defining dynamics of vegetation succession for research purposes (Strähl & Burga in prep.). Hence, the results provided by this experimental design remain provisional.

Nevertheless, our results reveal different tendencies in vegetation dynamics within the timber-line ecotone that are thought to be related to the different impacts of climate warming and land-use changes. At some sites we observed dynamics consistent with the initial signs of climate warming, thus providing evidence for an effect of global warming on tree regeneration success and the timber line in subalpine ecosystems of the Swiss Alps. A large proportion of the current timber-line ecotone was found to be following a disturbed process of plant succession, which is determined by pasture reduction; and a minor proportion was found to be following a non-disturbed process, most probably responding to the impact of global warming; although for the majority of relevés the cause of current dynamics in forest vegetation succession is unclear, neither attributable to the impact of global warming nor pasture reduction. Relevés showing a non-disturbed vegetation pattern are limited to localized areas of the timber-line ecotone, as are areas where we propose the timber line will shift upward above its potential limit in the coming decades (Figures 30 and 31).

5.1 Vegetation pattern analysis

5.1.1 Vegetation structure

The results for vegetation structure are according to our expectations, because they evidence younger vegetation in relevés above the 1899 timber line, in that trees in those relevés are predominated by krummholz forms and grow less densely together (Figures 23 and 24; Table A 12). Our surveys and analysis showed significant differences between the means for vegetation relevés above and below the 1899 timber line for the test variables "amount of trees and krummholz" and therefore agree with the studies by Körner and co-authors that trees above the timber line are shorter and krummholz are, on average, more frequent above than below the timber line, because of harsher climate conditions affecting the growth of trees at their upper limit. The higher ratio of krummholz, not only in vegetation relevés above, but also in vegetation relevés below the 1899 timber line (61% of all recorded tree species), but also the lack of significant differences in tree height and shortest tree distance between the sets of relevés above and below the 1899 timber line (Figure 22), however, lends no support to suggestions given by Körner and co-authors (Körner 1998, 2003; Körner & Paulsen 2004; Körner 2012; Table A 11).

In agreement with other calcareous northern alpine regions, the current timber line of the study region is shaped by Norway spruce, while European larch or Cembran pines, which dominate in the crystalline central Alpine regions, are less frequent (Figure 24). Our results showed a wide population of *Pinus cembra* trees at the slope from Itramen towards Kleine Scheidegg and therefore confirm the observations of Imhof (1900) and Rikli (1909) (Figures 25-26 and 28). The wide distribution of *Pinus cembra* krummholz in relation to trees of 2 m and taller, but also the large distribution of *Picea abies*, are evidence of *Picea abies* continuously invading areas of former *Pinus cembra* forests (Figures 24-26 and 28). In only few areas (e.g. relevés 7, 21 and 23; see Figure 24), did we find *Pinus cembra* trees of 2 m and taller, which is evidence of a relict of the upper limit of former Swiss stone pine forests (Figure 28).

5.1.2 Phyto-diversity

The results for phyto-diversity evidence vegetation with a disturbed character in the majority of the mapped relevés, especially for relevés below the 1899 timber line, which is consistent with areas that are easily accessible from the nearest barn being or having been exploited for land-use practices such as pasturing (Tables A 11 and 21). In addition, the recorded vegetation pattern at the timber-line ecotone showed dense patterns of ericaceous dwarf shrubs (*Calluna vulgaris*, *Rhododendron ferrugineum* or *Vaccinium myrtillus*) and single spruces, which is an indication of areas that are not profitable for land-use practices showing reduction in pasture activity and a transition form to the potential coniferous forest. The invaded Geo montani-Nardetum surfaces at the timber-line ecotone

were lacking for the main part in character species. Especially, competitive weak herbs species such as orchids (e.g., *Pseudorchis albida*) were missing in the majority of relevés, while undemanding trivial vegetation with plant species typical of rich meadow communities (*Leontodon helveticus*, *Poa alpina*, *Rumex alpestris* or *Deschampsia cespitosa*) were frequent (Tables A 1-8, 22-23). In contrast, in only few relevés did the vegetation pattern of the current timber-line ecotone show a sign of non-disturbed character, in probable response to global warming, with a wider abundance of character species associated with Geo montani-Nardetum and a scarcity of dwarf shrub species (Tables A 1-8, 22-23). However, in none of our surveyed relevés in the study region was the maximum amount of 9 character species recorded (Braun-Blanquet 1948/1949; Delarze & Gonseth 2008).

Our results were therefore consistent, firstly with our studies of the Lauterbrunnen valley, where a large proportion of mapped Geo montani-Nardetum grassland at the timber-line ecotone showed a transition form with ericaceous dwarf shrubs (Strähl & Burga in prep.; see Tables A 45-46), and secondly with studies that the majority of newly forested area that developed in the Swiss Alps between 1985 and 1997 was a result of ingrowth below the potential regional treeline, indicating land-use as the most likely driver (Gehrig-Fasel et al. 2007). Significant differences in test variables between relevés above and below the 1899 timber line were displayed only in the abundance of Geo montani-Nardetum character species, but not in the density of deteriorated Geo montani-Nardetum to heathland (Figure 29). Hence, our vegetation mapping results do not directly agree with other studies carried out in the northern Swiss Alps that show long-term effects of former pasturing on the composition of the plant communities, where soil degradation and exhaustion cause a continuous transformation of grassland into non-productive heathland (Lüdi 1948; Hegg 1984a, b; Hegg et al. 1992, 1993; Spiegelberger et al. 2006). Nevertheless, our findings that the abundance of Geo montani-Nardetum character species can differentiate naturally determined/undisturbed areas from anthropo-zoogenically determined/disturbed areas demonstrates the potential of using the appearance and abundance of association character species to identify the driving process of vegetation dynamics in a region (Braun-Blanquet 1921, 1964; Dierschke 1994; Ellenberg 1996; Landolt et al. 2010).

5.2 Areas attributed to an upward shift of the Alpine timber line in probable response to global warming

Our vegetation mapping results show a sign of spruce forest progress responding to pasture reduction in fewer than half the relevés (47%) (Figures 30 and 31), even though changes in the organization of agriculture and increasing tourism have led to non-profitable areas for pasture with complicated access being progressively abandoned (Naegeli-Oertle 1986; Liechti et al. in prep.). In addition, there are only few relevés (16%) where global warming may be the predominant driver of spruce forest progression. Those relevés are limited to peripheral areas, where topography (i.e., steep and isolated slope sites) does not allow the pronounced land-use pressure applied in locations with better access to the closest barn (Table A 11). A large proportion of our mapped relevés (38%) cannot be clearly attributed to either pasture reduction or global warming, in which cases the current dynamics of vegetation succession at the timber-line ecotone are likely being determined by other reasons, e.g., site conditions (Figures 30 and 31). The majority of our relevés can only be attributed an initial or intermediate stage of spruce forest development (75%) and are expected to remain at this stage for centuries to come, even in a warmer climate (Figure 31; Table A 36). The test variable "density of deteriorated Geo montani-Nardetum to heathland" is supposed to show a significant difference between areas affected by pasture reduction and areas affected by global warming when forests are reinvading their former terrain after clearance and at the same time progressing beyond their potential limit. Hence, the lack of significant differences between the sets of relevés above and below the 1899 timber line, especially in areas with dense patterns of ericaceous dwarf shrubs supports the observation that a large proportion of our mapped relevés cannot be clearly attributed to either pasture reduction or global warming (Hegg et al. 1993; Holtmeier 2009; Figure 29). Like our main study site, the test area at Rinderalp also shows a large proportion of spruce forest proceeding through the initial or transitional stage of succession, which cannot be attributed to a direct response to land-use changes nor to climate warming (Figure 33; Table A 37).

In our study region, Mesozoic Aalenian schists characterize the common bedrock material (Figure 17; Table A 11). Schists are highly erodible, low in permeability and form soils with high moisture that are prone to landslide activity. In spite of geological substrate allowing soils to develop profoundly and assure root penetration (Hoffmann et al. 2014), the easily and plastically deformable clays produce an unstable substrate, which is unfavourable for the establishment and growth of plant species, in particular more demanding plant species, such as trees (Collet et al. 1938; Lutz & Chandler 1955; Ott et al. 1997; Scheffer et al. 2010). In addition, the effects of trampling produced either by cattle or browsing livestock are likely to enhance surface instability in areas formed out of schists. This is due to frequent trampled surfaces showing a tendency to deepen, while in less trampled surfaces, a large raw humus layer accumulates from decomposition of the dry matter produced by the dwarf shrubs, which are avoided as pasture weeds and produce an abundant A0 (organic)-horizon (Schweingruber 1972). Furthermore, the steep north-facing walls of the Eiger, which border the area of investigation, are prone to avalanche, and also the wide extent of ski slopes, are, together with the bedrock material, likely producing an unfavourable environment for a stable climax forest in the study site (Figure 36).

In agreement with previous observations, we find that some areas along the slopes near Alpiglen have always been vegetated by large patterns of shrubs and ericaceous dwarf shrubs, these areas having never been used as pastures, so this vegetation is rather specific to the site than to a result of a dynamic abandonment process (Naegeli-Oertle 1986; Hegg & Schneiter 1988; Liechti et al., in prep.; Figure 35). Similarly, the existence of widely distributed dwarfed trees, at a markedly low current upper limit (this in spite of topography being shaped by a smooth and not steep surface) is likely to be attributable to unfavorable site conditions (Figures 24 and 34; Tables A 11 and 30).

Figure 35 Dense pattern of ericaceous dwarf shrub heath near Alpiglen. Photo: S.C. Strähl, July 2009

5.3 Fieldwork methods

The present study reinforces the findings of previous studies that vegetation mappings developed by Braun-Blanquet (1964) are important in understanding the potential impact of global warming on a subalpine ecosystem at the scale where trees and other plant species develop. However, short-term changes in the living conditions and growth behaviour of plants, which are important when fingerprinting early signs of the global warming impact within an ecosystem, cannot be analyzed as accurate as, for example, isolated analysis of physiological responses of mature tree growth to thermal conditions, because the plant compositions reacts with a large time lag (Braun-Blanquet 1957; Burga & Perret 2001a; Klötzli 2001; Theurillat & Guisan 2001; Walther et al. 2001; Burga et al. 2007; Burga et al. 2010; Strähl & Burga in prep.; Körner 2012).

The short-term impact of global warming on an ecosystem has been also simulated with other study methods (e.g., pollen analysis, plant phenology, dendrochronology, modeling etc.) (Burga & Perret 1998, 2001b; Theurillat 1998; Zimmermann & Kienast 1999; Kullmann 2000; Defila & Clot 2001; Bolli et al. 2007). Pollen analysis studies have been able to diagnose initial changes in the function of ecosystems. However, this method is time consuming and strongly dependent on how a sample is taken in the peat or lake sediments and stored (Burga 1979, 1988; Burga & Perret 1998). In particular, changes affected by climate impact are often misinterpreted in a pollen diagram, because climate- and anthropogenic-driven impacts often overlap in the pollen analytical profile. For example, natural or anthropo-zoogenically caused forest fires are often misinterpreted in pollen diagrams, because natural or anthropo-zoogenic caused forest fires can change the ratio between tree and non-tree pollen and may mimic a climate fluctuation (Frenzel 1977; Burga & Perret 1998). Plant phenology has been applied as an important method for the purpose of climate and vegetation studies (Defila & Clot 2001; Menzel & Estrella 2001). However, the interpretation quality regarding the measurements of a phenophase is strongly influenced by the number of observation posts and the observing personnel. A lack of observation posts or changing observing personnel can influence the quality of measurements and deteriorate the interpretation quality. As a consequence, measurements of the entire cycles of certain phenophases within a year can be missing and though a general trend of an ecosystem change cannot be mirrored with plant phenology (Defila & Clot 2001). Dendrochronology belongs to one of the most reliable method for the interpretation of short-term impact of global warming. In addition, dendrochronology allows to establish past and present climate variations near the timber line, which are reflected in the age pattern, growth form and rate of increment of the trees. Dendrochronological and dendroclimatological investigations at the upper timber line have been consulted to detect changes in the position of the timber line through the past few decades by analyzing the distribution of tree ages to distinguish between a warming and cooling period, and have been found to be highly suitable for reconstructing past climatic fluctuations.

While studies in dendrochronology are well-suited to monitoring the impact of global ecological change, modest changes in temperature, for example sudden frost or extremely low winter temperatures, are difficult to interpret, because radial growth changes may respond with a certain time lag. Moreover, other locally induced changes that occur over a short-term period, such as topographic or edaphic changes or changes in the intensity of land use, which further alter the timber line position, may also be wrongly interpreted and mimic a climate change. A more precise interpretation can be provided by studies in Herbchronology, which follow the counting of annual growth rings in the secondary root xylem of perennial herbaceous plants. Herbchronology is referring to dendrochronology because of the similarity of the structures investigated. Counting of annual growth rings can be used to estimate plant age, similarly as it is done in trees using dendrochronology (Beniston et al. 1997; Kullmann 2000; Paulsen et al. 2000; Burga & Perret 2001b; Motta & Nola 2001; Dietz & Schweingruber 2002; Bolli et al. 2007; Devi et al. 2008; Kirdyanov et al. 2012; Hagedorn et al. 2014). Modeling is the only available tool that has been demonstrated to be able to assess the impact of long-term climatic change in an ecosystem over several decades (Beniston et al. 1997; Haeberli & Beniston 1998; Zimmermann & Kienast 1999; Heiri et al. 2006; Beniston 2006). Models have been developed and used to show distinct differences in vegetation pattern, to reproduce the impact of long-term climatic change on the diversity of plant species and to analyze changes in land cover density (Theurillat 1995; Allen & Walsh 1996; Jens & Körner 2001; Theurillat & Guisan 2001; Alftine & Malanson 2004; Gehrig-Fasel et al. 2007). Realistic predictions of short-term sequences and spatial changes occurring in transitional areas such as ecotones may need very accurate data (e.g., migration, competition or human disturbance of the landscape, which are crucial to describe dynamics of vegetation succession), which are not always available (Bircher et al. 2015).

For the purpose of long-term monitoring, however, vegetation mappings may lack in accuracy, since repeated observations over several decades on permanent plots are required (Klötzli 2001). A change in observers (e.g., 20 to 30 years later) can affect the data quality. Interpretation regarding type and frequency of plant species may differ among the observers and lead to a less accurate result than less subjective techniques like root-zone measurements (Körner 1998; Körner & Paulsen 2004). In addition, timber lines might be compared to subnival peaks less suited for long-term vegetation monitoring over centuries, because they are often located in areas with better access for human and cattle (Vittoz et al. 2008).

5.4 Experimental design

The locations of our relevés within newly forested area at the timber-line ecotone were chosen to best detect differences between sings of a possible warming impact and signs of pasture reduction and to exclude or keep constant other impacts (e.g., topography, substrate, surface processes, etc.). Moreover, the altitudinal limit of the timber line in the year 1899 was applied as reference to separate a set of relevés most likely responding to the impact of changes in land-use activity from a set, in which a possible warming impact might be recognized. Because the region of Grindelwald has been shaped by varying landscape features that produces a heterogeneous outcome of different substrates, we could only select a limited number of sites for our relevé mappings that satisfied the criteria of our study (Figure 17; Table A 11). Nevertheless, our results have allowed us to map the vegetation patterns at the current timber-line ecotone and to assess differences between non-disturbed and disturbed vegetation patterns at the timber-line ecotone.

However, not all our mapping variables showed significant differences between the set of relevés expected to be non-disturbed influenced by global warming, and the set expected to be disturbed, influenced by changing land-use practices, hence pointing to limitations in this current study. First of all, this study records the vegetation pattern at the timber-line ecotone only at this single moment in time, which may not be sufficient to accurately determine the driving influence. Because plant species are seldom regularly distributed at a site, it might be difficult to gain an accurate result on the significance between the differences of vegetation records. In addition, the large number of non-significant results also emphasizes the difficulty of site selection in this study region, whose complex landscape features make it difficult to identify areas at the timber-line ecotone where signs of a possible warming impact can be disentangled from signs of pasture reduction and other impacts (e.g., topography, substrate, surface processes etc.) are as much as possible excluded or kept constant. Impacts of global warming may not be as distinctive in the Alps as in other high mountain regions of the World (e.g., Rocky Mountains, Russian Ural-mountains, Swedish Scandes), because the timber line of the European Alps has been heavily affected by anthropo-zoogenic impacts over centuries (Burga 1988; Burga & Perret 1998, 2001a; Kullmann 2000; Moiseev & Shiyatov 2003; Wick et al. 2003; Butler et al. 2009). Furthermore, this current study has not considered photographic comparisons between former and current timber lines, as presented by the studies of Moiseev & Shiyatov (2003) in the Russian Ural-mountains. Neither have we incorporated dendroecological analysis, whereas such tree age studies have proven to be useful for reconstructing the process of tree establishment and growth dynamics at the timber line in the northern Central Swiss Alps, and for assessing whether these are in response to recent changes of climate, land-use activity or site properties (Bolli et al. 2007). In addition, other climate parameters

besides the temperature effects should also be considered when discussing vegetation succession dynamics at the Alpine timber line. For example, studies carried out in the Russian Ural have shown that the primary cause of forest advance has been particularly released by increases in snow fall, having a larger impact on tree survival than increases in temperature (Hagedorn et al. 2014).

5.5   Suggestions for future research

In order to overcome the limitations of this study, future research should focus primarily on a long-term monitoring of vegetation pattern on permanent relevés, because recording changes in plant species composition requires multiple observations over decades that must be repeated on permanent relevés, in order to achieve a clearer picture of the magnitude of a possible global warming impact. We therefore suggest that the number of relevé mappings of this current study at the timber-line ecotone be increased and that these relevés be focussed on a certain plant community. Thereby, relevé mappings should also consider areas of pure grassland community, where the impacts of possible climate warming and anthropo-zoogenic effect are interrupted by neither site conditions nor landscape processes and relevés no larger than 4 m^2 should be used to avoid inhomogeneity of too many randomly interspersed plant species. We additionally propose, on the one hand, to monitor changes in species richness and richness of functional plant groups, mean-Landolt-indicator-values, and community mean traits (e.g., specific leaf area, leaf dry-matter content, seed mass, plant height etc.) over time. On the other hand, a calculation of the turnover of species composition in grassland communities, as performed by Fischer & Stöcklin (1997), would also be useful for detecting changes in the intensity of land-use practice over time.

We further suggest that long-term vegetation monitoring also includes other parameter (e.g., precipitation intensity and snow cover pack, type of substrate, type, frequencies and consequences of surface processes) that consider not only how the distribution patterns of plant species are determined by changes in climate warming or intensity of land-use practice over time, but also the ecological requirements of plant species. Including such parameters will allow assessment of ecological factors like surface stability, nutrient availability and drought stress, which are important for plant growth, and enable better understanding of the current and future dynamics of the Alpine timber line.

The inclusion of dendroecological analysis would be an important supplement to the results of vegetation pattern analysis, giving information on the age and evolution of tree growth dynamics within the mapped vegetation relevés at the timber-line ecotone, and helping to better understand the speed of forest invasion into non-forested areas. Moreover, a combined monitoring of vegetation mapping and simulations with remote sensing methods would permit a more accurate interpretation of the dynamics of vegetation succession at the timber line over a long-term period, especially in areas with reduced access for field work studies. Satellite images give an excellent classification of forest surfaces and allow a physiognomic-structural classification of vegetation in the range of sub-formations, but also at the cohort level (Hörsch 2003). Another approach would be to combine GIS-simulation and biomonitoring by developing models of how the topology of a plot of land affects its accessibility and hence the intensity of anthropo-zoogenic practices on it (Liechti et al., in prep.). This approach would help to better understand the non-synchronous behavior of the Alpine timber line with regard to future changes in the disturbance regime, notably in areas in which the forest limit has retreated over the past 100 years (Providoli & Kuhn 2012), and to quantify the area of timber line (e.g., along the steep limestone rock-walls of the Eiger) that is likely to fringe and become more degraded with ongoing environmental change.

6 Outlook

From the results provided by this study, we propose that Vaccinio-Piceion spruce forest will further develop and progress in the study region in the coming 100 years. For the majority of our surveyed relevés, we found a tendency for an upward shift in the timber line, which has been largely attributed to pasture reduction, and thus, spruce forest vegetation is continuously reinvading its former terrain, as noticed in other Alpine regions. In wide areas of our study site, however, we propose that spruce forests are likely to remain at the transitional stage of development and not reach the climax forest stage. The Alpine timber line might therefore not be able to regain its former habitat, even after pasture reduction (Figure 37). The unfavorable site conditions, which are given by the wide extent of Aalenian schists and the high risk of avalanche activity, are expected to strongly hamper the current advance of trees towards their potential limit, even in a warmer climate. As a result, we propose a future invasion of Vaccinio-Piceion spruce forests into non-forested areas in around only 50% of the study region. The majority of these sites are situated near Arvengarten, Bustiglen, as well as between Kleine Scheidegg and Lauberhorn, but some areas are located between Fallboden and the station of the Eiger glacier (Figure 36, 37). In barely 25% of the current timber line do we propose that the altitudinal maximum, at 2200 m a.s.l., will be reached with continuous warming of 0.6 °C per century (IPCC 2013).
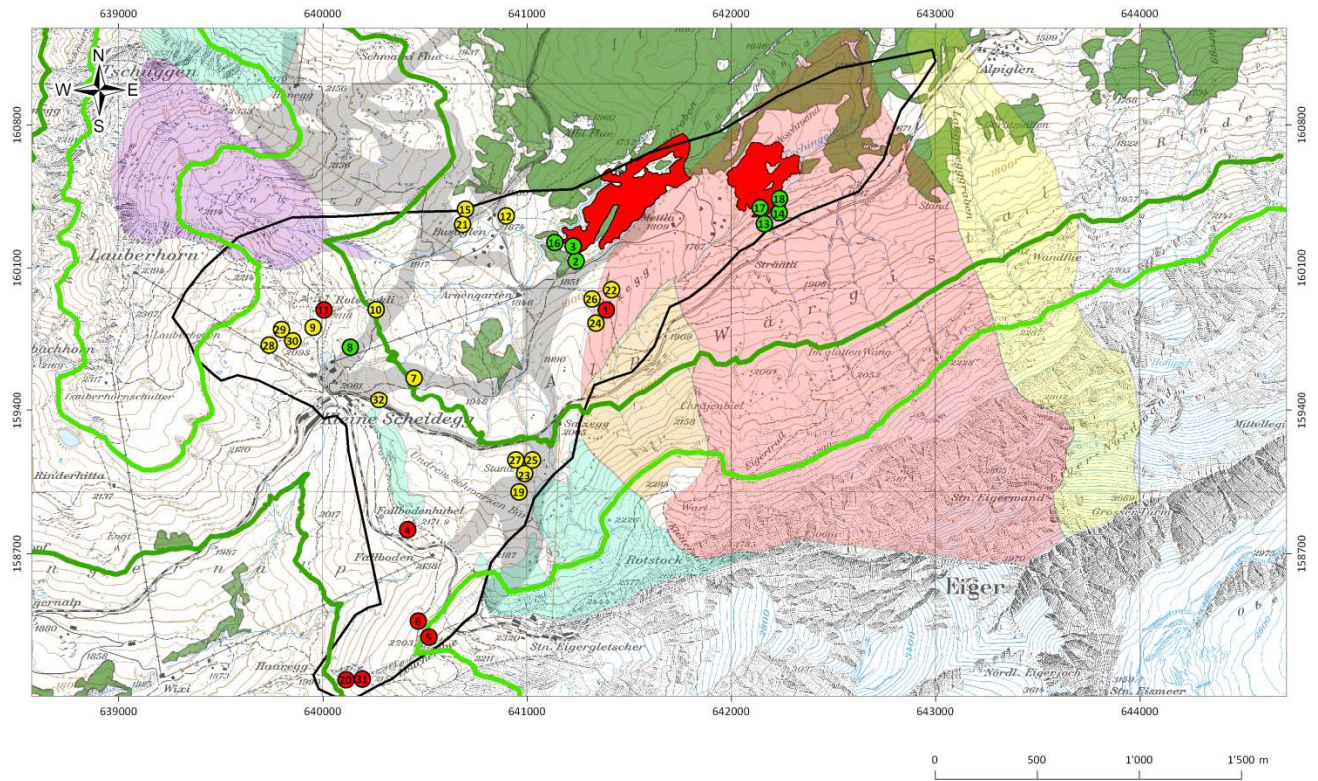
Vegetation relevés attributed to areas showing signs of an upward shift in timber line

rates classified with GIS (class 1: highest degree, class 3: lowest degree)

1 = highest degree of Vaccinio-Piceion spruce forest invasion: transitional to climax stage

2 = intermediate degree of Vaccinio-Piceion spruce forest invasion: transitional stage

3 = lowest degree of Vaccinio-Piceion spruce forest invasion: initial to transitional stage

average potential timber line altitude at 2000 m a.s.l. for northern Swiss Alps

altitudinal maximum of potential timber line at 2200 m a.s.l. for the northwestern Swiss Alps

study region

number of avalanche events with large disturbances: 29

number of avalanche events with large disturbances: 10

number of avalanche events with large disturbances: 7

number of avalanche events with large disturbances: 2

number of avalanche events with large disturbances: 0

ski slopes

forest area in 2007

largest forest cover increases 1899-2005 at the upper timber line

Figure 36 Extent of avalanche tracks and ski slopes within the study region
Source: Topographical map: PK25 © 2006 swisstopo; avalanches: Lawinenkataster des Kantons Bern © Abteilung Naturgefahren des Kantons Bern; ski piste: Bauverwaltung Einwohnergemeinde Grindelwald (2001); forest area in 2007: VECTOR25 © swisstopo; average potential timber line altitude and altitudinal maximum of potential timber line: Landolt 2003, Holmeier 2009; largest forest cover increases 1899-2005 at the upper timber line: Providoli & Kuhn 2012; parameters for the interpretation of vegetation mapping results: own observation of vegetation mappings of the period 2008-2010.

Vegetation relevés attributed to areas showing signs of an upward shift in timber line

rates classified with GIS
(class 1: highest degree, class 3: lowest degree)

● **1 =** highest degree of Vaccinio-Piceion spruce forest invasion: transitional to climax stage

● **2 =** intermediate degree of Vaccinio-Piceion spruce forest invasion: transitional stage

● **3 =** lowest degree of Vaccinio-Piceion spruce forest invasion: initial to transitional stage

— potential natural timber line

‑‑‑ potential of timber line with increasing global warming

— average potential timber line altitude at 2000 m a.s.l. for northern Swiss Alps

— altitudinal maximum of potential timber line at 2200 m a.s.l. for the northwestern Swiss Alps

— study region

▨ forest area in 2007

▮ largest forest cover increases 1899-2005 at the upper timber line

▨ area possible for spruce forest to progress

Figure 37 Possible forest expansion and upward shift in the Alpine timber line in the study region with continued global warming of 0.6 °C and continued reduction in pasture activity in the coming 100 years. Areas are selected as a function of: (a) favorable and unfavorable substrate that respectively favors or restricts forest vegetation (Aalenian schists are considered as unfavorable substrate) and (b) risk potential of avalanche activity. Areas expected to show an upward shift in timber line towards the altitudinal maximum of 2200 m are emphasized by the two black rectangles.
Source: Topographical map: PK25 © 2006 swisstopo; forest area in 2007: VECTOR25 © swisstopo; average potential timber line altitude, altitudinal maximum of potential timber line and potential natural timber line: Landolt 2003, Holmeier 2009; potential of timber line with increasing global warming and area possible for spruce forest to progress: Lawinenkataster des Kantons Bern © Abteilung Naturgefahren des Kantons Bern, Ereigniskataster NGKAT © Abteilung Naturgefahren des Kantons Bern, Collet et al. 1938; largest forest cover increases at the upper timber line: Providoli & Kuhn 2012; parameters for the interpretation of vegetation mapping results: own observation of vegetation mappings of the period 2008-2010.

In the whole region of Grindelwald, we expect the timber line to evolve in a similar way to that proposed for the studied region, behave non-synchronously with and show an uncertain response to the global warming impact (Figures 37 and 38).

We propose an increase in the forest limit to be produced more by pasture reduction and less by global warming. Moreover, site conditions (e.g., edaphic and topographic factors), but also surface processes, are likely affecting large areas of the current forest limit (Figure 38; Table 6). In response to the continuous melting of glaciers ice and permafrost surfaces, surface stability will be affected. As a consequence, rock-falls or landslides (e.g., at the Mettenberg above Stieregg at 2700 m a.s.l.) are expected to be triggered, but also sudden extreme events, since each landscape form exhibits a temporal lifespan that is dependent on the type of bedrock components, type and frequency of surface process and can range from seconds to several centuries (Hörsch 2003; Keusen 2006; Oppikofer et al. 2008; Wagner & Saurer 2008; Werder et al. 2010; Huggel et al. 2011).

Therefore, we propose that forest vegetation will be restricted in completing its succession to the climax stage and that the current forest limit may, despite pasture reduction, not even be able to regain its former limit recorded in 1861, and is likely to persist as an unchanged boundary in a transitionary stage of its vegetation development. We therefore propose that only 11% of the current timber line will be able to reach the potential limit of 2000 m a.s.l. and just 1% the altitudinal maximum at 2200 m a.s.l., with continuous warming of 0.6 °C per century (Figure 38; Table 6).
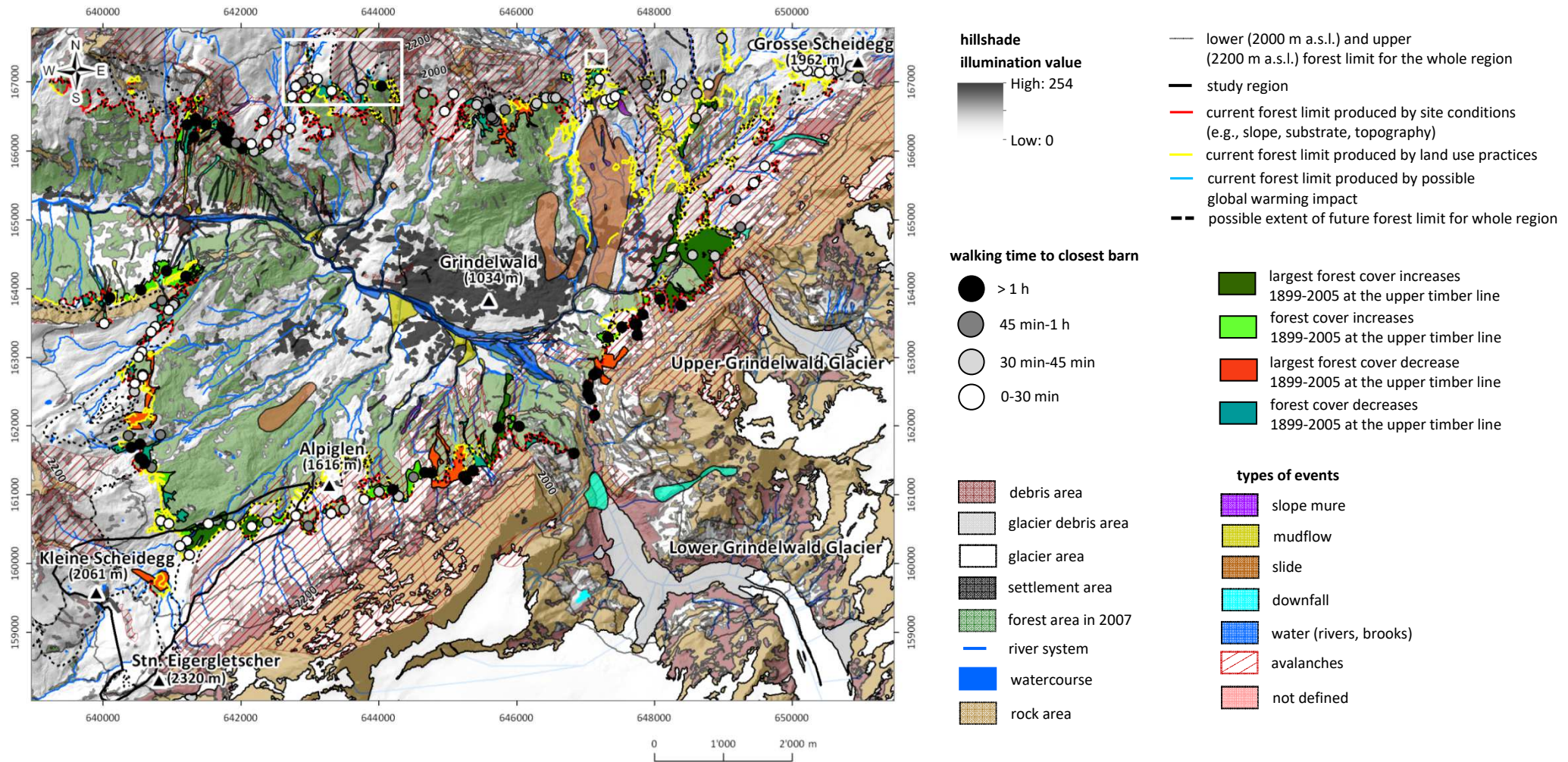
Figure 38 Future development of the Alpine timber line in the Grindelwald region in relation to access and event processes dominating in the region. Areas with current forest limit produced by possible global warming impact are emphasized by white rectangles.

Source: Hillshade and contours: Digitales Geländemodell 2m © swisstopo; river system, watercourse, settlement area, rock area, debris area, glacier debris area, glacier area and forest area in 2007: VECTOR25 © swisstopo; actual forest limit produced by site conditions, possible extent of future forest limit and type of events: Collet et al. 1938, Lawinenkataster des Kantons Bern © Abteilung Naturgefahren des Kantons Bern, Ereigniskataster NGKAT © Abteilung Naturgefahren des Kantons Bern; forest limit for the year 1861: DUFOUR © swisstopo; lower and upper forest limit and actual forest limit produced by possible global warming impact: Landolt 2003, Holtmeier 2009; actual forest limit produced by land use practices: Arealstatistik 1992/97, © BFS GEOSTAT; largest forest cover increases and forest cover increases at the upper timber line: Providoli & Kuhn 2012; walking time to closest barn: Liechti et al., in prep.

Table 6 Current forest limit and expected future development of the Alpine timber line in the region of Grindelwald

current forest limit in the whole region produced by		
land-use practices [%]: 61	site conditions [%]: 38 (e.g., slope, substrate, topography)	possible global warming impact [%]: 1

expected future development of the Alpine timber line in the whole region	
increasing forest limit [%]: 38	unchanged forest limit [%]: 62

increasing forest limit produced by:

pasture reduction [%]: 98	possible global warming impact [%]: 2

increasing forest limit reaching the average potential timber line altitude at 2000 m a.s.l. [%]: 11
increasing forest limit reaching the altitudinal maximum of potential timber line at 2200 m a.s.l. [%]: 1

Source: Current forest limit produced by land use practices: Arealstatistik 1992/97, © BFS GEOSTAT, VECTOR25 © swisstopo; current forest limit produced by site conditions: Collet et al. 1938, Lawinenkataster des Kantons Bern © Abteilung Naturgefahren des Kantons Bern, Ereigniskataster NGKAT © Abteilung Naturgefahren des Kantons Bern; current forest limit produced by possible global warming impact: Landolt 2003, Holtmeier 2009; expected future development of the timber line: Digitales Geländemodell 2m © swisstopo, Collet et al. 1938, Lawinenkataster des Kantons Bern © Abteilung Naturgefahren des Kantons Bern, Ereigniskataster NGKAT © Abteilung Naturgefahren des Kantons Bern, VECTOR25 © swisstopo, Landolt 2003, Holtmeier 2009

This case study in the Grindelwald region (Northern Swiss Alps) was of great value for understanding the current and future dynamics of vegetation succession at the timber line in high mountain ecosystems across the globe with regard to global warming (Beniston et al. 1997; Burga et al. 2003; Walther et al. 2005b; Beniston 2006). Such high mountain ecosystems are important to understand because they are more exposed to atmospheric oscillations, experience a greater availability of thermal energy and the reduced stability of formerly glaciated or perennially-frozen slopes enhances the risk and frequency of extreme events, such as block-debris flows, mud-flows or rock-falls, that are capable of destroying wide areas of the current forest limit (Davies et al. 2001; Haeberli & Burn 2002; Beniston & Stephenson 2004; Gruber et al. 2004; Stoffel et al. 2005; Gruber & Haeberli 2007; Haeberli 2007; Haeberli & Maisch 2007; Haeberli et al. 2007).

The reaction to global warming is complex, especially at the local scale where plant species develop. For example, tree individuals may modify and change local climate conditions, since each tree species has different ecological properties and requirements (e.g., shade tolerant or intolerant, pioneer or climax species, animal or wind mediated seed dispersal, etc.), which influence the development of tree stands and the structure of the timber line. While competitive species (e.g., *Fagus sylvatica*, *Picea abies*) rather form dense stands and abrupt timber lines, less competitive species (e.g., *Larix decidua*, *Pinus cembra*) form open forests that gradually give way to grassland or other subalpine vegetation (Holtmeier 1974, 2009).

In addition, the harsh high-mountain climate prevents the rapid and compete development of forest vegetation, because vegetation generally responds to climate change only decades after a climate impact (e.g., temperature increase) has been established (Burga 1999; Holtmeier & Broll 2007). Similarly, the type of substrate is as important as the climate, because grain size and the water content of the substrate, micro-relief and micro-climate are all crucial for the development of vegetation and soil (Burga et al. 2010).

As a result, newly forested areas at the timber line may not be able to withstand the changing environmental conditions, hence neither reinvade their former limit after pasture reduction nor invade new areas beyond their potential limit, and so the advance of timber lines towards the potential climatically-driven elevation is expected to be strongly hampered or even impeded. The response of timber lines to global warming is therefore rather unpredictable and, in many areas across the globe, in disequilibrium with the current climate conditions (Walther et al. 2002; Nagy et al. 2003; Jones et al. 2009; Brown 2013; Marcias-Fauria & Johnson 2013). Predicted advances of trees towards a given threshold are likely to be driven by geomorphological features and geomorphic processes with climate having only a modulating effect (Hörsch 2003; Butler et al. 2007; Zeng et al. 2007; Holtmeier & Broll 2010).

In our current study, we have found a tendency for forest vegetation to be hardly ever continuous at the timber line, indicating that the Alpine timber line in Grindelwald is responding more to site conditions than to changing climate conditions with elevation. Furthermore, the treeline in cleared areas is likely to remain at a depressed elevation in future, below the potential elevation. We therefore suggest that the Alpine timber line in the Grindelwald region will not directly respond in a uniform manner to ongoing global warming in the coming century, as has been suggested for the purely physics-driven boundary of the snow line, and that the expected timber line will be only able to shift in local areas with ongoing global warming in the coming 1-2 centuries (Körner 1998; Theurillat & Guisan 2001; Kullmann 2002; Körner & Paulsen 2004; Holtmeier & Broll 2005, 2010; Körner 2007b; Harsch et al. 2009; Marcias-Fauria & Johnson 2013).

Compared to the abrupt and thermally controlled snow line, the boundary position of a timber line is expected to be driven rather by local ecological impacts than by the thermal impact alone. Particular important parameters such as, snow cover pack, snow depth, time of snowmelt or snow fungus diverge significantly from the global mean of average temperatures. However, if necessary, mean temperatures may be applied as indicators to roughly describe the thermal conditions at timber lines (e.g., Tuhkanen 1980, 1993; Oshawa 1990; Perret 2005; Holtmeier & Broll 2007).

7 Conclusion

This Ph. D. project studied areas of the timber-line ecotone in the Grindelwald region that had shown the largest [proportional] increases in forest-cover between 1899 and 2005 in order to investigate the importance of vegetation mappings (Braun-Blanquet 1964) for (a) assessing where the vegetation pattern has a non-disturbed (natural) character in probable response to global warming and where it has a disturbed (anthropo-zoogenic) character indicative of pasture reduction and (b) understanding the potential impact of global warming on a subalpine ecosystem at the local scale of tree development.

While previous studies have assumed that the dynamics of vegetation succession differs in both structure and phyto-diversity between areas that have been disturbed by anthropo-zoogenical practices and areas that are non-disturbed, having experienced natural conditions (Lüdi 1921, 1948; Braun-Blanquet 1964; Hegg 1984 a, b; Hegg et al. 1992, 1993, Burga & Perret 2001b; Perret 2005; Strähl & Burga in prep.), our results showed that phyto-diversity is more meaningful than plant structure for determining whether the vegetation pattern has a non-disturbed or a disturbed character. We found that a large proportion of the current timber line shows a disturbed vegetation pattern driven by pasture reduction, whereas only a minor proportion shows the non-disturbed pattern expected of a response to global warming, and this is limited to a few local areas. The majority of studied sites, however, showed a vegetation pattern that was neither clearly disturbed nor clearly non-disturbed, making it impossible to attribute the cause of vegetation succession at the timber-line ecotone to either global warming or pasture reduction. Correspondingly, though we had expected areas of advancing timber line that are at higher altitude (than the 1899 average timber line altitude) to have been driven mainly by temperature rise and areas at lower altitude to have been driven mainly by pasture reduction, the variables measured to characterize the relevés at higher and lower altitudes (e.g., cover and distribution of shrubs and herbs, growth and distribution of trees and phyto-diversity) showed no significant differences in mean values, with the exception of total number of krummholz, total number of trees, total number and density of Geo montani-Nardetum character species (Figures 22 and 29; Table A 33).

We can conclude, therefore, that the temperature rises generated by global warming are not the primary driver of advances in the Alpine timber line in the Grindelwald region observed over the last century. Based on this observation, we predict that the Alpine timber line will not directly respond in a uniform manner to ongoing global warming in the coming century, as has been suggested for the purely physics-driven boundary of the snow line (Körner 1998, 2003 and 2007). Instead, in agreement with previous studies, we expect an upward shift in the timber line in only some locally favored sites (Walther et al. 2001; Kullmann 2002; Holtmeier and Broll 2005, 2010; Burga et al. 2007; Harsch et al. 2009).

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8.3 GIS-data

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8.5 Applied software

Adobe Illustrator CS2 Artwork 12.0.1: design of figures and correction of photos.

Adobe Photoshop CS2 Version 9.0.2: design of figures and correction of photos.

ESRI ArcGIS 10: design of maps

IBM SPSS statistics Version 22: calculation of statistics

Acknowledgments

Appendix

Table of Contents

List of Figures

List of Tables

A.1 Field work raw data for relevés no. 1-32

A.1.1 Vegetation mapping results

Table A 1 Vegetation mapping results for the tree and shrub cover of vegetation relevés no. 1 to 16. Plant species are ordered alphabetically (without indication of family). Note: Tree cover comprises all trees, small trees and tree seedlings; shrub cover comprises all shrub-, dwarf shrub- and shrublet species.

relevé no. / species	S1		S2		S3		S4		S5		S6		S7		S8		S9		S10		S11		S12		S13		S14		S15		S16	
trees in percent (left column) and according to the abundance-dominance index of Braun-Blanquet (right column)																																
Betula pendula																									5	2.1						
Picea abies	< 1	r.1	15	2.2	10	2.2							1	+.1	4	1.1									7	2.1	12	2.2	1	+.1	15	2.2
Pinus cembra	1-2	+.1	20	2.2	5	2.1							10	2.2	1-2	+.1	1-2	+.1	5	2.1					1	+.1	1	+.1	3	1.1	5	2.1
Pinus mugo ssp. *uncinata*							< 1	r.1													1	+.1										
Sorbus aucuparia													< 1	r.1											3	1.1	4	1.1			1-2	+.1
total trees [%]	**2**		**35**		**15**		**< 1**						**11**		**6**		**2**		**5**		**1**				**13**		**13**		**4**		**22**	
shrubs in percent (left column) and according to the abundance-dominance index of Braun-Blanquet (right column)																																
Alnus viridis																											4	1.1				
dwarf shrubs in percent (left column) and according to the abundance-dominance index of Braun-Blanquet (right column)																																
Calluna vulgaris	12	2.3	< 1	r.1	4	1.2	25	2.3			5	2.2	3	1.2	6	2.3	5	2.3	15	2.3	15	2.4	5	2.4					18	2.3		
Erica carnea																	5	2.3			1	+.1										
Juniperus nana	8	2.3					1-2	+.1					10	2.3	4	1.3	8	2.3	4	1.3												
Lonicera caerulea			5	2.3	10	2.3																			10	2.3	10	2.3			5	2.3
Rhododendron ferrugineum	8	2.2	1-2	+.2	4	1.3			3	1.3	4	1.3	7	2.3	7	2.3	7	2.3	8	2.3	3	1.2	1-2	+.1	10	2.2	7	2.3	5	2.1	5	2.1
Vaccinium gaultherioides	5	2.1																														
Vaccinium myrtillus	10	2.3	5	2.3	22	2.3	3	1.1			6	2.3	25	2.3	30	3.3	15	2.3	5	2.3	5	2.3	15	2.4	20	2.3	5	2.3	15	2.4	20	2.3
Vaccinium uliginosum													2	1.1	9	2.2	6	2.3	< 1	r.1	1	+.1	4	1.3	3	1.2						
Vaccinium vitis-idaea	3	1.3			5	2.3					5	2.1	7	2.3	20	2.3	10	2.3	20	2.3	3	1.2	4	1.2					7	2.1	3	1.3
shrublets in percent (left column) and according to the abundance-dominance index of Braun-Blanquet (right column)																																
Dryas octopetala																											8	2.3				
Loiseleuria procumbens							10	2.3			3	1.3	3	1.3					1-2	+.2	3	1.3	10	2.4								
Salix retusa									3	1.3																						
total shrubs [%]	**46**		**12**		**45**		**40**		**6**		**25**		**64**		**73**		**52**		**56**		**41**		**29**		**40**		**34**		**45**		**33**	

Table A 2 Vegetation mapping results for the herb cover of vegetation relevés no. 1 to 16. Plant species are ordered according to their family.

Family	species (relevé no.)	S1		S2		S3		S4		S5		S6		S7		S8		S9		S10		S11		S12		S13		S14		S15		S16	
		herbs in percent (left column) and according to the abundance-dominance index of Braun-Blanquet (right column)																															
Poaceae	*Anthoxanthum alpinum*	1-2	+.2	5	2.2	1	+.1							< 1	r.1	< 1	r.1	1	+.1	1	+.1	1-2	+.1							4	1.1	4	1.2
	Avenella flexuosa/ Deschampsia flexuosa			7	2.2	4	1.1																									5	2.2
	Calamagrostis villosa			3	1.1	1	+.2																			1	+.1	< 1	r.1			< 1	r.1
	Deschampsia cespitosa			1	+.1	< 1	r.1																			5	2.2	1	+.1			3	1.1
	Festuca rubra	3	1.2					3	1.2	3	1.2	3	1.2	1-2	+.2	1	+.1	4	1.2	3	1.2	1	+.1					< 1	r.1	6	2.4		
	Helictotrichon versicolor									1-2	+.1											1	+.1										
	Nardus stricta	15	2.2	8	2.2	6	2.2	5	2.2	4	1.2	6	2.2	4	1.2	4	1.2	4	1.2	5	2.2	5	2.2	15	2.2	6	2.2	4	1.2	12	2.2	10	2.2
	Phleum alpinum																															1-2	+.1
	Poa alpina	4	1.2	3	1.1																			4	1.1							1	+.1
Cyperaceae	*Carex sempervirens*	4	1.2							1-2	+.1			1	+.1	3	1.2	1-2	+.1	1-2	+.1	4	1.2										
Juncaceae	*Juncus trifidus*																	1-2	+.1														
	Luzula multiflora	6	2.2					< 1	r.1			1-2	+.1	< 1	r.1			1	+.1	1	+.1	1	+.1	4	1.1			1-2	+.1	< 1	r.1		
	Luzula sylvatica ssp. *sieberi*			4	1.1	3	1.2																			< 1	r.1					1	+.1
Liliaceae	*Paradisea liliastrum*																											3	1.2				
	Veratrum album ssp. *album*							1-2	+.1			7	2.2	4	1.2	< 1	r.1	< 1	r.1	1	+.1	1-2	+.1										
Irdaceae	*Crocus albiflorus*							1-2	+.2	3	1.2	3	1.2	1	+.1			1	+.1	1-2	+.2	4	1.2										
Orchidaceae	*Pseudorchis albida*							1-2	+.1			1	+.1			< 1	r.1			< 1	r.1												
	Nigritella nigra									< 1	r.1																						
Polygonaceae	*Rumex alpestris*																											3	1.1				
	Polygonum bistorta															< 1	r.1																
	Polygonum viviparum																							1-2	+.1								

Table A 2 (continued)

Family	species (relevé no.)	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16
	herbs in percent (left column) and according to the abundance-dominance index of Braun-Blanquet (right column)																
Caryphyllaceae	*Silene vulgaris* ssp. *vulgaris*			3 1.1													
Ranunculaceae	*Pulsatilla alpina* ssp. *alpina*					1 +.1											
Ranunculaceae	*Ranunculus alpestris*					1-2 +.1	1 +.1										
Ranunculaceae	*Trollius europaeus*						< 1 r.1										
Rosaceae	*Alchemilla alpina*		3 1.3	1 +.1		1 +.1								14 2.2	1 +.1	1-2 +.1	
Rosaceae	*Alchemilla monticola*		10 2.3	14 2.3			3 1.1									2 1.2	
Rosaceae	*Alchemilla pentaphyllea*														5 2.2	< 1 r.1	
Rosaceae	*Geum montanum*		< 1 r.1	< 1 r.1	5 2.2	1-2 +.1	2 1.1	1-2 +.1	1 +.1	< 1 r.1	< 1 r.1	3 1.1	3 1.1	< 1 r.1	3 1.2	1-2 +.1	1 +.1
Rosaceae	*Potentilla aurea*	< 1 r.1	8 2.3	1 +.1	3 1.1	1 +.1	3 1.1	1 +.1	1 +.1		3 1.1		1-2 +.1	1-2 +.1		1 +.1	3 1.2
Rosaceae	*Potentilla erecta*	< 1 r.1	7 2.3	10 2.2	1-2 +.1	1 +.1	3 1.1	< 1 r.1	1-2 +.2		1-2 +.1			6 2.2	4 1.1	1 +.1	4 1.2
Fabaceae	*Anthyllis vulneraria* spp. *alpestris*														6 2.2		
Fabaceae	*Hippocrepis comosa*					3 1.1											
Fabaceae	*Trifolium alpinum*				1 +.1	1-2 +.1	1 +.1	3 1.1	1 +.1	1 +.1	1-2 +.1	3 1.1		1-2 +.1			
Fabaceae	*Trifolium pratense* ssp. *pratense*			1 +.1		1 +.2	1-2 +.1										1 +.2
Geraniaceae	*Geranium rivulare*	1 +.2															
Geraniaceae	*Geranium sanguineum*														5 2.2		
Violaceae	*Viola cenisia*						1 +.1										
Onagraceae	*Epilobium angustifolium*														< 1 r.1		

Table A 2 (continued)

species (relevé no.)		S1		S2		S3		S4		S5		S6		S7		S8		S9		S10		S11		S12		S13		S14		S15		S16	
		herbs in percent (left column) and according to the abundance-dominance index of Braun-Blanquet (right column)																															
Apiaceae	Astrantia major																									1	+.1	1-2	+.1				
	Ligusticum mutellina													1	+.1			1	+.1														
	Ligusticum mutellinoides									4	1.2	4	1.2																				
Oxalidaceae	Oxalis acetosella			6	2.3	5	2.3																			5	2.3					8	2.3
Pyrolaceae	Pyrola rotundifolia																											< 1	r.1				
Primulaceae	Primula farinosa									4	1.1	1	+.1																				
Gentianaceae	Gentiana acaulis							1	+.1	1	+.1	1-2	+.1	1	+.1																		
	Gentiana asclepiadea	3	1.1																														
	Gentiana purpurea	3	1.2															< 1	r.1			1	+.1										
	Gentiana verna									5	2.1																						
Lamiaceae	Ajuga pyramidalis									8	2.1	4	1.1																				
Orobanchaceae	Bartsia alpina									10	2.2																						
	Euphrasia rostkoviana					4	1.2																										
	Pedicularis tuberosa															1-2	+.2			1	+.1	1	+.1							5	2.1		
	Pedicularis verticillata																																

Table A 2 (continued)

Family	species	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16
	relevé no.																
	species — herbs in percent (left column) and according to the abundance-dominance index of Braun-Blanquet (right column)																
Plantaginaceae	*Plantago alpina*		1-2 +.1	1 +.1	1-2 +.1	3 1.1	1-2 +.1	<1 r.1	<1 r.1			1 +.1	5 2.2	4 1.1	4 1.2	5 2.1	3 1.1
Dipsacaceae	*Scabiosa lucida*													<1 r.1	1 +.1		
Campanulaceae	*Campanula barbata*				<1 r.1		1-2 +.1		<1 r.1								
	Campanula rhomboidalis			<1 r.1													
	Phyteuma spicatum											1 +.1					
Asteraceae	*Achillea millefolium*							1 +.1									
	Adenostyles alliariae													<1 r.1	3 1.1		
	Arnica montana	1 +.1	1-2 +.1		1-2 +.1	5 2.2	3 1.1	1 +.1	1 +.1	1 +.1	5 2.2	1-2 +.2	3 1.1	3 1.1		6 2.2	
	Carduus personata														<1 r.1		
	Cirsium acaule												3 1.1				
	Cirsium helenioides					1 +.1											
	Crepis aurea								<1 r.1	1 +.1	6 2.2						
	Hieracium alpinum			<1 r.1										1-2 +.1			
	Hieracium prenanthoides	1-2 +.1															
	Homogyne alpina	1 +.1	5 2.3		3 1.1	1 +.1	3 1.1	1 +.1	<1 r.1	1-2 +.1	1 +.1	1-2 +.1	8 2.3		10 2.2	3 1.1	4 1.2
	Leucanthemum adustum						1-2 +.1							<1 r.1			
	Senecio ovatus			<1 r.1													
	Leontodon helveticus	3 1.1	1-2 +.1	1 +.1	1 +.1	3 1.2		1-2 +.1	1-2 +.1	1 +.1	1-2 +.1	1 +.1	1 +.1	3 1.1		<1 r.1	4 1.2
	Taraxacum alpinum												9 2.1				

Table A 3 Vegetation mapping results for the pteridophyte cover of vegetation relevés no. 1 to 16. Plant species are ordered alphabetically (without indication of family).

relevé no. / species	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16
pteridophytes	pteridophytes in percent (left column) and according to the abundance-dominance index of Braun-Blanquet (right column)															
Athyrium distentifolium		< 1 r.1	3 1.1										< 1 r.1			1 +.1
Blechnum spicant														1-2 +.1		
Gymnocarpium dryopteris														< 1 r.1		
Huperzia selago									1 +.1					3 1.2		
total herbs & pteridophytes [%]	**48**	**76**	**59**	**35**	**73**	**61**	**25**	**18**	**23**	**37**	**35**	**65**	**51**	**59**	**52**	**55**

Table A 4 Vegetation mapping results for the mosses and lichens cover of vegetation relevés no. 1 to 16. Plant species are ordered alphabetically (without indication of family).

relevé no. / species	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16
mosses & lichens	mosses & lichens in percent (left column) and according to the abundance-dominance index of Braun-Blanquet (right column)															
Cetraria islandica					3 1.3	5 2.3	< 1 r.1				< 1 r.1			5 2.5		5 2.2
Cladonia rangiferina			5 2.3	15 2.3				< 1 r.1	5 2.3	5 2.3	4 1.3		10 2.4		10 2.3	1 +.3
Polytrichum sexangulare	20 2.3	15 2.3	15 2.3	5 2.3	4 1.3	5 2.3	5 2.3	5 2.3	15 2.3	3 1.3	1 +.1	4 1.3	15 2.4	20 2.5		20 2.4
Rhizocarpon geographicum											5 2.3					
total mosses & lichens [%]	**20**	**15**	**20**	**20**	**7**	**10**	**5**	**5**	**20**	**8**	**10**	**4**	**25**	**25**	**10**	**26**

6

Table A 5 Vegetation mapping results for the tree and shrub cover of vegetation relevés no. 17 to 32. Plant species are ordered alphabetically (without indication of family). Note: Tree cover comprises all trees, small trees and tree seedlings; shrub cover comprises all shrub-, dwarf shrub- and shrublet species.

relevé no.	S17	S18	S19	S20	S21	S22	S23	S24	S25	S26	S27	S28	S29	S30	S31	S32
species	trees in percent (left column) and according to the abundance-dominance index of Braun-Blanquet (right column)															
Larix decidua								< 1 r.1								
Picea abies	25 2.2	30 3.3		5 2.2	5 2.1				1 +.1	1-2 +.1	< 1 r.1	3 1.1	4 1.2	3 1.1	9 2.2	
Pinus cembra		7 2.2			10 2.1	6 2.1	5 2.1	3 1.1		3 1.1	1 +.1					< 1 r.1
Sorbus aria	< 1 r.1															
Sorbus aucuparia	1 +.1	3 1.1								< 1 r.1						
total trees [%]	**25**	**37**		**5**	**15**	**6**	**5**	**3**	**1**	**5**	**1**	**3**	**4**	**3**	**9**	**< 1**
species	shrubs in percent (left column) and according to the abundance-dominance index of Braun-Blanquet (right column)															
Alnus incana		< 1 r.1														
Alnus viridis	1 +.1	1-2 +.2		4 1.3												
dwarf shrubs	dwarf shrubs in percent (left column) and according to the abundance-dominance index of Braun-Blanquet (right column)															
Calluna vulgaris			3 1.3	6 2.3	15 2.3	1-2 +.1	< 1 r.1	15 2.3	7 2.3	7 2.2	10 2.3	10 2.3	15 2.3	23 2.4		
Empetrum hermaphroditum		1 +.1								9 2.2						
Erica carnea				5 2.3											4 1.3	
Juniperus nana			1 +.3	5 2.3	20 2.3	7 2.3		5 2.3	3 1.3	6 2.3	< 1 r.1	18 2.4	20 2.4	10 2.4	5 2.3	
Lonicera caerulea	15 2.4	5 2.4														
Rhododendron ferrugineum	4 1.3	5 2.3	10 2.3	3 1.1	10 2.1	10 2.3	13 2.3	10 2.3	15 2.3	8 2.3	10 2.3	6 2.2	5 2.2	4 1.1	6 2.3	15 2.3
Vaccinium gaultherioides			6 2.3			15 2.4	25 2.3	10 2.3	8 2.3	8 2.3	6 2.3					
Vaccinium myrtillus	20 2.4	10 2.4	12 2.3		10 2.4	25 2.4	15 2.3	15 2.3	13 2.3	18 2.3	15 2.3	18 2.4	10 2.3	22 2.3	3 1.1	10 2.3
Vaccinium uliginosum														7 2.2		1 +.1
Vaccinium vitis-idaea	3 1.1		6 2.3		5 2.2	5 2.3	5 2.2	1-2 +.1	5 2.2	3 1.3	4 1.1	7 2.2	4 1.1	1-2 +.1	1-2 +.1	4 1.2
shrublets	shrublets in percent (left column) and according to the abundance-dominance index of Braun-Blanquet (right column)															
Dryas octopetala				6 2.3											5 2.3	
Polygala chamaebuxus				10 2.3											5 2.3	
total shrubs [%]	**43**	**22**	**39**	**39**	**60**	**64**	**58**	**57**	**51**	**59**	**45**	**59**	**61**	**61**	**30**	**30**

Table A 6 Vegetation mapping results for the herb cover of vegetation relevés no. 17 to 32. Plant species are ordered according to their family.

Family	relevé no. / species	S17		S18		S19		S20		S21		S22		S23		S24		S25		S26		S27		S28		S29		S30		S31		S32	
		herbs in percent (left column) and according to the abundance-dominance index of Braun-Blanquet (right column)																																
Poaceae	Anthoxanthum alpinum					1	+.1	3	1.2	1	+.1	3	1.2	1-2	+.1	4	1.2	1-2	+.1	1	+.1	3	1.1	6	2.2	3	1.1	5	2.1	3	1.2		
	Avenella flexuosa/ Deschampsia flexuosa			1	+.1																												
	Calamagrostis villosa	1-2	+.1	3	1.1																												
	Deschampsia cespitosa	1-2	+.1	4	1.1																												
	Festuca rubra	1-2	+.1			3	1.1					5	2.2	4	1.2	5	2.2	3	1.2	1	+.1	3	1.2	4	1.2	3	1.2	3	1.1				
	Nardus stricta	3	1.2			8	2.2	4	1.2	10	2.2	8	2.2	10	2.2	9	2.2	15	2.2	10	2.2	12	2.2	4	1.2	5	1.2	6	2.2	6	2.2	8	2.2
	Oreochloa disticha							1-2	+.1																								
	Phleum alpinum															4	1.1																
	Poa alpina											1	+.1			1	+.1	8	2.2	1	+.1	5	2.2									4	1.2
Cyperaceae	Carex curvula spp. curvula																													2	1.2	3	1.2
	Carex sempervirens					6	2.1	3	1.2					3	1.2			5	2.2	3	1.1	4	1.1	1	+.1	1	+.1					1	+.1
	Trichophorum alpinum													< 1	r.1																		
Juncaceae	Luzula multiflora	1	+.1			3	1.1	1	+.1					1	+.1							1	+.1	4	1.1					1	+.1	1	+.1
	Luzula sylvatica ssp. sieberi			1	+.1																												
Liliaceae	Veratrum album ssp. album																							1	+.1	1	+.1					1	+.1
Irdaceae	Crocus albiflorus																															3	1.2
Orchidaceae	Dactylorhiza maculata									1	+.1																			< 1	r.1		
	Pseudorchis albida					1	+.1													1	+.1												
Polygonaceae	Rumex alpestris	1	+.1																														
	Polygonum viviparum									1	+.1																						

Table A 6 (continued)

	relevé no.	S17		S18		S19		S20		S21		S22		S23		S24		S25		S26		S27		S28		S29		S30		S31		S32	
species		herbs in percent (left column) and according to the abundance-dominance index of Braun-Blanquet (right column)																														
Caryphyllaceae	Silene vulgaris ssp. vulgaris									1	+.1															3	1.1	4	1.1				
Ranunculaceae	Anemone narcissiflora							< 1	r.1																								
	Pulsatilla alpina ssp. alpina											3	1.1											1	+.1	< 1	r.1	3	1.1				
	Ranunculus alpestris							1-2	+.1																					1	+.1	1-2	+.1
	Ranunculus lanuginosus					4	1.1																										
	Trollius europaeus																															1	+.1
Saxifragaceae	Saxifraga exarata ssp. moschata																													4	1.3		
Rosaceae	Alchemilla alpina	1	+.1	10	2.3	1-2	+.1	4	1.3	7	2.1	3	1.2	5	2.2	1-2	+.1	< 1	r.1			1	+.1			1	+.1			3	1.3	4	1.2
	Alchemilla monticola	1	+.1	3	1.2					5	2.2																						
	Alchemilla vulgaris					1	+.1							1	+.2			3	1.2			3	1.2										
	Geum montanum					1-2	+.1	3	1.1	< 1	r.1	1	+.1	< 1	r.1	< 1	r.1	1	+.1	1	+.1	1	+.1	< 1	r.1	< 1	r.1	< 1	r.1	2	1.1	3	1.2
	Potentilla aurea			1	+.1	3	1.1			1	+.1							1	+.1	1-2	+.1	1	+.1	1	+.1	1	+.1	1	+.1	3	1.2	3	1.1
	Potentilla erecta			< 1	r.1			4	1.2	1-2	+.1			< 1	r.1	< 1	r.1	< 1	r.1	3	1.1	1	+.1	1-2	+.1	1	+.1	1-2	+.1	3	1.2	1-2	+.1
Fabaceae	Hippocrepis comosa							1-2	+.1																								
	Trifolium alpinum	< 1	r.1					4	1.1	1-2	+.1	< 1	r.1			1	+.1													3	1.1		
	Trifolium pratense ssp. pratense																															1	+.1
Geraniaceae	Geranium rivulare	1	+.1											1	+.2																		
	Geranium sanguineum							1	+.1																								
Violaceae	Viola cenisia																					< 1	r.1									4	1.2

Table A 6 (continued)

Family	species / relevé no.	S17	S18	S19	S20	S21	S22	S23	S24	S25	S26	S27	S28	S29	S30	S31	S32
		herbs in percent (left column) and according to the abundance-dominance index of Braun-Blanquet (right column)															
Apiaceae	Peucedanum ostruthium									1 +.1							
	Ligusticum mutellina			1-2 +.1				3 1.1		1 +.1		3 1.1					3 1.2
Oxalidaceae	Oxalis acetosella	6 2.4	4 1.3														
Primulaceae	Androsace chamaejasme				1-2 +.1			<1 r.1								1-2 +.1	
	Primula farinosa															1-2 +.1	
	Primula veris				3 1.1											2 1.1	
Gentianaceae	Gentiana acaulis			1 +.1	4 1.1							<1 r.1			1 +.1	3 1.1	4 1.1
	Gentiana asclepiadea						<1 r.1		1-2 +.1								
	Gentiana purpurea			<1 r.1			1 +.1	<1 r.1	1 +.1		1 +.1	<1 r.1	2 1.1		3 1.1		
	Gentiana verna															1 +.1	
Lamiaceae	Ajuga pyramidalis															2 1.1	
Orobanchaceae	Pedicularis tuberosa			3 1.1	1-2 +.1					<1 r.1	<1 r.1		<1 r.1	<1 r.1	<1 r.1		
Plantaginaceae	Plantago alpina	3 1.1		3 1.1		1 +.1	1-2 +.1		3 1.1	1-2 +.1	1 +.1		1 +.1	1 +.1	4 1.2		3 1.1

Table A 6 (continued)

	relevé no. → species	S17	S18	S19	S20	S21	S22	S23	S24	S25	S26	S27	S28	S29	S30	S31	S32
		herbs in percent (left column) and according to the abundance-dominance index of Braun-Blanquet (right column)															
Globulariaceae	*Globularia nudicaulis*				1-2 +.1											3 1.1	
Dipsacaceae	*Scabiosa lucida*														< 1 r.1		
Campanulaceae	*Campanula barbata*			1 +.1									1 +.1	1 +.1	1 +.1		
Asteraceae	*Achillea millefolium*					1 +.1										2 1.1	1-2 +.1
	Adenostyles alliariae	1 +.1	1-2 +.1														
	Adenostyles leucophylla			< 1 r.1													
	Arnica montana			1 +.1	1 +.1	< 1 r.1	1 +.1	1-2 +.1	4 1.2	1-2 +.1	4 1.1	1-2 +.1	3 1.1	3 1.1	1 +.1	1 +.1	1 +.1
	Carduus personata	3 1.2															
	Carlina acaulis ssp. *caulescens forma nana*														< 1 r.1		
	Cirsium acaule					4 1.1											
	Cirsium helenioides	1-2 +.1	1-2 +.1													1 +.1	
	Crepis aurea						1 +.1										
	Hieracium prenanthoides						< 1 r.1	1 +.1	< 1 r.1	3 1.1		3 1.1			3 1.1		
	Homogyne alpina	5 2.3	15 2.3	5 2.2	1-2 +.1	1 +.1		1-2 +.1		6 2.2	5 2.2	3 1.1	4 1.2	3 1.2	3 1.2		5 2.2
	Leucanthemum adustum				1 +.1											2 1.1	
	Leontodon helveticus	< 1 r.1				1-2 +.1						1 +.1	3 1.1	3 1.1	1 +.1		3 1.1
	Leontodon hispidus			3 1.2													

Table A 7 Vegetation mapping results for the pteridophyte cover of vegetation relevés no. 17 to 32. Plant species are ordered alphabetically (without indication of family).

relevé no. / species	S17	S18	S19	S20	S21	S22	S23	S24	S25	S26	S27	S28	S29	S30	S31	S32
	pteridophytes in percent (left column) and according to the abundance-dominance index of Braun-Blanquet (right column)															
Athyrium distentifolium	1 +.1	1-2 +.2														
Blechnum spicant	3 1.1															
Botrychium lunaria		1 +.1														
Gymnocarpium dryopteris	< 1 r.1	1 +.1														
Lycopodium annotinum						3 1.4										
Selaginella selaginoides					1-2 +.3											
total herbs & pteridophytes [%]	**38**	**50**	**57**	**48**	**40**	**32**	**35**	**36**	**53**	**34**	**47**	**38**	**30**	**41**	**52**	**62**

Table A 8 Vegetation mapping results for the mosses and lichens cover of vegetation relevés no. 17 to 32. Plant species are ordered alphabetically (without indication of family).

relevé no. / species	S17	S18	S19	S20	S21	S22	S23	S24	S25	S26	S27	S28	S29	S30	S31	S32
	mosses & lichens in percent (left column) and according to the abundance-dominance index of Braun-Blanquet (right column)															
Cetraria islandica			3 1.3			5 2.4										< 1 r.1
Cladonia rangiferina		< 1 r.1	6 2.3			1 +.3		5 2.3	5 2.3	12 2.4	5 2.3	1 +.1	< 1 r.1	< 1 r.1	< 1 r.1	
Polytrichum sexangulare	30 2.5	30 3.4	6 2.3	5 2.3	5 2.3	25 2.5	20 2.4	15 2.5	5 2.3	10 2.3	10 2.3		4 1.3		5 2.3	5 2.3
Rhizocarpon geographicum		< 1 r.1										7 2.4	1 +.3	3 1.1		
total mosses & lichens [%]	**30**	**30**	**15**	**5**	**5**	**31**	**20**	**20**	**10**	**22**	**15**	**8**	**5**	**3**	**5**	**5**

Table A 9 Evaluation of vegetation pattern for the vegetation relevés no. 1-16
Note: The value expressing the cumulative species cover includes parts of vegetation layers (i.e., tree-, shrub-, herb- and moss layer) that overlap, hence a density value of more than 100% can occur in general.

Vegetation pattern	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16
total trees [%]	2	35	15	< 1			11	6	2	5	1		16	17	4	22
total shrubs [%]	46	12	45	40	6	25	64	73	52	56	41	29	40	34	45	33
total herbs and pteridophytes [%]	48	76	59	35	73	61	25	18	23	37	35	65	51	59	52	55
total mosses & lichens [%]	20	15	20	20	7	10	5	5	20	8	10	4	25	25	10	26
cumulative species cover [%]	**116**	**138**	**139**	**95**	**86**	**96**	**105**	**102**	**97**	**106**	**87**	**98**	**132**	**135**	**111**	**136**
total number of flowering plants, ferns, mosses & lichens	24	25	30	23	30	32	30	28	28	27	29	19	27	33	23	27

Table A 10 Evaluation of vegetation pattern for the vegetation relevés no. 17-32
Note: The value expressing the cumulative species cover includes parts of vegetation layers (i.e., tree-, shrub-, herb- and moss layer) that overlap, hence a density value of more than 100% can occur in general.

Vegetation pattern	S17	S18	S19	S20	S21	S22	S23	S24	S25	S26	S27	S28	S29	S30	S31	S32
total trees [%]	26	40		5	15	6	5	3	1	5	1	3	4	3	9	< 1
total shrubs [%]	43	22	39	39	60	64	58	57	51	59	45	59	61	61	30	30
total herbs and pteridophytes [%]	38	50	57	48	40	32	35	36	53	34	47	38	30	41	52	62
total mosses & lichens [%]	30	30	15	5	5	31	20	20	10	22	15	8	5	3	5	5
cumulative species cover [%]	**137**	**142**	**111**	**97**	**120**	**133**	**118**	**116**	**115**	**120**	**108**	**108**	**100**	**108**	**96**	**97**
total number of flowering plants, ferns, mosses & lichens	29	26	32	30	24	25	24	24	26	26	29	25	27	27	33	29

Table A 11 Summary of the habitat properties of the relevés no. 1-32

relevee ID	coordinates		elevation [m a.s.l.]	slope [°]	exposure	geology & substrate	soil depth [cm]	micro relief	type of land use	accessibility [value]
	x	y								
1	641412	159935	1910	16	E	Mesozoicum Aalenian schists	41	wavy	pasture	0.34
2	641240	160170	1816	17	S	Quaternary moraine	47	planar	pasture	0.28
3	641200	160180	1813	5	W	Quaternary moraine	47	planar	pasture	0.29
4	640415	158817	2160	13	SW	Mesozoicum Aalenian schists	31	planar	extensive pasture	0.75
5	640572	158321	2227	24	NW	Quaternary moraine	31	planar	extensive pasture	1.03
6	640468	158371	2176	24	NW	Mesozoicum Aalenian schists	31	light-humped	extensive pasture	0.99
7	640447	159562	1996	23	NE	Quaternary moraine	40	wavy	pasture	0.47
8	640134	159712	2038	24	S	Mesozoicum iron sandstones	40	wavy	pasture	0.42
9	639960	159853	2121	16	SE	Mesozoicum iron sandstones	31	humped	extensive pasture	0.60
10	640261	159897	1997	24	E	Mesozoicum iron sandstones	40	wavy	pasture	0.29
11	639948	159852	2124	15	SE	Mesozoicum iron sandstones	31	light-humped	extensive pasture	0.59
12	640898	160354	1872	28	SE	Quaternary moraine	41	light-humped	pasture	0.04
13	642191	160342	1745	26	N	Quaternary moraine	49	humped	forestry	0.25
14	642235	160371	1741	26	N	Quaternary moraine	49	humped	forestry	0.25
15	640698	160387	1913	27	SE	Mesozoicum iron sandstones	41	wavy	pasture	0.16
16	641200	160200	1811	13	W	Quaternary moraine	47	planar	pasture	0.29
17	642197	160400	1733	21	E	Quaternary moraine	49	humped	forestry	0.23
18	642219	160402	1731	14	N	Quaternary moraine	49	humped	forestry	0.65
19	640961	159026	2045	17	N	Quaternary moraine	33	light-wavy	extensive pasture	0.77
20	640035	158099	2022	24	SW	Quaternary moraine	31	light-humped	extensive pasture	1.07
21	640689	160329	1898	29	SE	Mesozoicum iron sandstones	41	wavy	pasture	0.09
22	641422	159985	1906	7	NE	Mesozoicum Aalenian schists	41	wavy	pasture	0.34
23	640988	159107	2028	12	NE	Quaternary moraine	33	humped	extensive pasture	1.16
24	641398	159919	1913	13	E	Mesozoicum Aalenian schists	41	wavy	pasture	0.32
25	641027	159157	2023	11	N	Quaternary moraine	33	humped	extensive pasture	0.77
26	641411	159966	1909	10	NE	Mesozoicum Aalenian schists	41	wavy	pasture	0.34
27	640977	159193	2026	11	N	Quaternary moraine	33	light-humped	extensive pasture	0.66
28	639737	159734	2137	14	S	Quaternary moraine	31	light-humped	extensive pasture	0.65
29	639813	159752	2128	21	S	Mesozoicum iron sandstones	31	light-humped	extensive pasture	0.66
30	639853	159744	2118	26	S	Mesozoicum iron sandstones	31	light-humped	extensive pasture	0.62
31	640140	158084	2030	29	SW	Quaternary moraine	31	light-humped	extensive pasture	1.08
32	640275	159452	2041	12	NE	Mesozoicum Aalenian schists	40	wavy	pasture	0.49

A.1.2 Tree height and density

Table A 12 Vegetation growth expressed by tree height and density (including all trees, small trees and tree seedlings). Height is recorded for each tree species and displayed separately for trees (growing ≥ 2 m) and krummholz (growing < 2 m). Density is expressed for each tree species within the tree layer by the shortest distances to the neighbouring trees, small trees and tree seedlings in cm. Each recorded tree species of a relevé (no. 1 to 32) is displayed in the following tables.
*Note: Shortest tree distance values with less than 5 cm were not able to be calculated and are not displayed in the table. The same applies to relevés with only one recorded tree species where there are no distance values shown. **In relevés 5, 6, 12 and 19 no tree species were recorded.

relevee ID	coordinates		number	krummholz height [cm]	tree height [cm]	species	shortest tree distance [cm]*
	x	y					
1	641412	159935	B1	20		*Pinus cembra*	36
	641412	159935	B2	50		*Pinus cembra*	36
	641413	159936	B3	10		*Picea abies*	83
2	641242	160175	B1		500	*Pinus cembra*	112
	641243	160176	B2		200	*Pinus cembra*	11
	641243	160176	B3		1000	*Pinus cembra*	11
	641243	160176	B4		1000	*Picea abies*	5
	641243	160176	B5		1000	*Pinus cembra*	5
	641244	160171	B6		800	*Pinus cembra*	68
	641244	160171	B7		1000	*Picea abies*	68
	641250	160174	B8		500	*Picea abies*	611
3	641206	160189	B1	130		*Picea abies*	360
	641209	160189	B2		500	*Picea abies*	301
	641209	160186	B3		700	*Pinus cembra*	76
	641209	160185	B4		650	*Picea abies*	76
	641209	160183	B5		700	*Picea abies*	226
	641210	160180	B6		250	*Picea abies*	226
	641207	160182	B7		450	*Picea abies*	238
	641204	160182	B8		500	*Picea abies*	290
4	640410	158817	B1	25		*Pinus mugo ssp. unicinata*	
5**							
6**							
7	640435	159561	B1	150		*Picea abies*	583
	640440	159558	B2		210	*Pinus cembra*	583
	640439	159552	B3		300	*Pinus cembra*	608
	640447	159553	B4		400	*Pinus cembra*	806
	640441	159565	B5	15		*Sorbus aucuparia*	707
8	640127	159712	B1	80		*Picea abies*	224
	640132	159716	B2	35		*Picea abies*	316
	640135	159715	B3	90		*Picea abies*	224
	640136	159717	B4	155		*Picea abies*	224
	640127	159715	B5	140		*Picea abies*	141
	640128	159714	B6	95		*Pinus cembra*	141
9	639956	159842	B1	45		*Pinus cembra*	

Table A 12 (continued)

relevee ID	coordinates		number	krummholz height [cm]	tree height [cm]	species	shortest tree distance [cm]*
	x	y					
10	640262	159901	B1	15		*Pinus cembra*	412
	640267	159900	B2	20		*Pinus cembra*	141
	640266	159898	B3	25		*Pinus cembra*	100
	640266	159899	B4	50		*Pinus cembra*	100
	640264	159897	B5	30		*Pinus cembra*	
	640266	159895	B6	40		*Pinus cembra*	
	640264	159895	B7	10		*Pinus cembra*	
	640264	159897	B8	10		*Pinus cembra*	
	640264	159897	B9	15		*Pinus cembra*	
	640263	159897	B10	10		*Pinus cembra*	100
	640261	159888	B11	90		*Pinus cembra*	447
	640263	159892	B12	65		*Pinus cembra*	224
	640265	159891	B13	40		*Pinus cembra*	224
	640266	159894	B14	80		*Pinus cembra*	100
	640264	159895	B15	85		*Pinus cembra*	
	640266	159895	B16	35		*Pinus cembra*	
	640267	159894	B17	25		*Pinus cembra*	100
	640269	159893	B18	10		*Pinus cembra*	224
	640267	159890	B19	15		*Pinus cembra*	224
11	639947	159850	B1	35		*Pinus mugo* ssp. *unicinata*	1204
	639934	159852	B2	25		*Pinus mugo* ssp. *unicinata*	1315
12**							
13	642191	160352	B1		600	*Betula pendula*	78
	642191	160351	B2		500	*Picea abies*	51
	642191	160351	B3		450	*Picea abies*	51
	642191	160344	B4		200	*Sorbus aucuparia*	206
	642191	160342	B5	56		*Pinus cembra*	206
	642193	160347	B6	67		*Picea abies*	323
	642197	160342	B7	62		*Betula pendula*	265
	642198	160344	B8	30		*Betula pendula*	265

Table A 12 (continued)

relevee ID	coordinates		number	krummholz height [cm]	tree height [cm]	species	shortest tree distance [cm]*
	x	y					
14	642237	160372	B1		600	*Picea abies*	105
	642237	160372	B2		300	*Picea abies*	105
	642236	160375	B3		500	*Picea abies*	189
	642236	160377	B4		350	*Sorbus aucuparia*	32
	642237	160379	B5		700	*Picea abies*	152
	642240	160372	B6	25		*Picea abies*	30
	642240	160372	B7	35		*Picea abies*	30
	642244	160373	B8	40		*Pinus cembra*	261
	642240	160374	B9	45		*Picea abies*	210
	642243	160375	B10	60		*Sorbus aucuparia*	50
	642243	160375	B11	15		*Sorbus aucuparia*	50
	642244	160376	B12	23		*Picea abies*	70
	642244	160376	B13	27		*Sorbus aucuparia*	56
	642244	160377	B14	34		*Picea abies*	56
	642244	160377	B15	50		*Picea abies*	81
	642242	160376	B16	55		*Picea abies*	122
	642240	160376	B17	45		*Picea abies*	175
	642238	160378	B18	25		*Picea abies*	45
	642236	160377	B19	35		*Picea abies*	32
	642236	160377	B20	50		*Picea abies*	41
	642238	160379	B21	20		*Picea abies*	45
	642239	160379	B22	40		*Picea abies*	10
	642239	160379	B23	25		*Picea abies*	10
15	640699	160388	B1	15		*Picea abies*	140
	640702	160389	B2	45		*Pinus cembra*	215
	640704	160389	B3	60		*Pinus cembra*	150
	640706	160389	B4	20		*Pinus cembra*	150
	640699	160390	B5	25		*Pinus cembra*	50
	640700	160390	B6	30		*Picea abies*	50
	640701	160391	B7	40		*Pinus cembra*	99
	640702	160392	B8	30		*Pinus cembra*	222
16	641202	160200	B1		600	*Picea abies*	397
	641205	160203	B2		300	*Picea abies*	45
	641205	160203	B3		600	*Pinus cembra*	45
	641207	160204	B4	80		*Sorbus aucuparia*	130
	641205	160205	B5		700	*Picea abies*	175
	641208	160205	B6		900	*Picea abies*	36
	641207	160205	B7		500	*Picea abies*	36

Table A 12 (continued)

relevee ID	coordinates		number	krummholz height [cm]	tree height [cm]	species	shortest tree distance [cm]*
	x	y					
17	642204	160401	B1		800	*Picea abies*	80
	642204	160402	B2		600	*Picea abies*	63
	642204	160402	B3	80		*Picea abies*	
	642205	160403	B4	75		*Picea abies*	51
	642204	160402	B5	80		*Picea abies*	21
	642205	160405	B6	40		*Sorbus aucuparia*	41
	642205	160405	B7	30		*Sorbus aria*	41
	642205	160406	B8		230	*Picea abies*	65
	642204	160407	B9		600	*Picea abies*	84
	642205	160407	B10		700	*Picea abies*	25
	642205	160407	B11	50		*Sorbus aucuparia*	25
	642207	160410	B12	80		*Picea abies*	305
	642199	160410	B13	80		*Picea abies*	296
	642199	160407	B14		520	*Picea abies*	296
	642198	160403	B15		1020	*Picea abies*	412
18	642223	160405	B1		1200	*Picea abies*	20
	642224	160405	B2		600	*Picea abies*	20
	642204	160402	B3		1200	*Picea abies*	
	642225	160404	B4		500	*Sorbus aucuparia*	172
	642228	160404	B5		1000	*Picea abies*	300
	642220	160407	B6		650	*Pinus cembra*	284
	642221	160410	B7		650	*Pinus cembra*	134
	642222	160411	B8		700	*Pinus cembra*	134
	642224	160409	B9		1100	*Picea abies*	103
	642225	160410	B10		900	*Picea abies*	54
	642224	160411	B11		250	*Picea abies*	54
	642226	160411	B12		500	*Pinus cembra*	63
	642226	160411	B13		1000	*Picea abies*	50
	642226	160411	B14		450	*Picea abies*	50
	642228	160411	B15		900	*Picea abies*	170
	642229	160408	B16		1050	*Picea abies*	318
19**							
20	640034	158101	B1	45		*Picea abies*	500
	640029	158101	B2	40		*Picea abies*	100
	640028	158101	B3	50		*Picea abies*	100
	640028	158103	B4	110		*Picea abies*	200
	640026	158102	B5	195		*Picea abies*	224
	640027	158100	B6	180		*Picea abies*	141
	640023	158102	B7	95		*Picea abies*	300

Table A 12 (continued)

relevee ID	coordinates		number	krummholz height [cm]	tree height [cm]	species	shortest tree distance [cm]*
	x	y					
21	640689	160329	B1		800	*Picea abies*	218
	640691	160331	B2		500	*Picea abies*	10
	640691	160331	B3		500	*Pinus cembra*	10
	640691	160331	B4	50		*Pinus cembra*	10
	640691	160330	B5		1000	*Pinus cembra*	10
	640691	160330	B6		500	*Picea abies*	20
	640691	160330	B7	40		*Pinus cembra*	10
	640691	160331	B8	50		*Pinus cembra*	10
	640691	160331	B9		500	*Picea abies*	10
	640692	160330	B10	160		*Picea abies*	85
	640691	160331	B11	15		*Pinus cembra*	25
	640689	160336	B12		400	*Picea abies*	90
	640690	160336	B13	25		*Pinus cembra*	90
22	641422	159985	B1	100		*Pinus cembra*	361
	641426	159987	B2	116		*Pinus cembra*	200
	641424	159988	B3	70		*Pinus cembra*	141
	641425	159989	B4	60		*Pinus cembra*	141
	641430	159985	B5	60		*Pinus cembra*	193
	641431	159986	B6	45		*Pinus cembra*	146
	641431	159987	B7	10		*Pinus cembra*	146
	641432	159991	B8	50		*Pinus cembra*	376
	641428	159991	B9	10		*Pinus cembra*	20
	641428	159991	B10	25		*Pinus cembra*	20
	641427	159992	B11	40		*Pinus cembra*	156
	641424	159992	B12	30		*Pinus cembra*	130
	641423	159993	B13	50		*Pinus cembra*	64
	641422	159993	B14	60		*Pinus cembra*	64
	641422	159995	B15	60		*Pinus cembra*	204
23	640988	159107	B1		500	*Pinus cembra*	
24	641398	159919	B1	140		*Pinus cembra*	753
	641400	159926	B2	30		*Larix decidua*	235
	641401	159929	B3	100		*Pinus cembra*	235
	641403	159926	B4	40		*Pinus cembra*	250
	641406	159926	B5	100		*Pinus cembra*	250
25	641027	159157	B1	80		*Picea abies*	
26	641413	159967	B1	50		*Picea abies*	162
	641411	159966	B2	100		*Pinus cembra*	22
	641411	159966	B3	30		*Pinus cembra*	22
	641418	159968	B4	33		*Picea abies*	128
	641421	159969	B5	88		*Pinus cembra*	226
	641417	159969	B6	28		*Sorbus aucuparia*	128
	641415	159971	B7	69		*Pinus cembra*	171
	641416	159973	B8	50		*Pinus cembra*	171

Table A 12 (continued)

relevee ID	coordinates		number	krummholz height [cm]	tree height [cm]	species	shortest tree distance [cm]*
	x	y					
27	640977	159193	B1	45		*Pinus cembra*	775
	640978	159201	B2	70		*Pinus cembra*	446
	640983	159200	B3	40		*Picea abies*	446
28	639737	159734	B1	180		*Picea abies*	400
	639741	159734	B2	45		*Picea abies*	400
29	639817	159754	B1		300	*Picea abies*	121
	639816	159753	B2	190		*Picea abies*	121
	639816	159756	B3	75		*Picea abies*	187
30	639863	159745	B1	60		*Picea abies*	304
	639860	159746	B2	50		*Picea abies*	211
	639858	159747	B3	63		*Picea abies*	211
	639863	159754	B4		200	*Picea abies*	825
31	640135	158096	B1	160		*Picea abies*	361
	640138	158093	B2	50		*Picea abies*	
	640141	158093	B3		250	*Picea abies*	100
	640142	158092	B4		230	*Picea abies*	100
	640143	158093	B5		210	*Picea abies*	141
	640141	158092	B6		260	*Picea abies*	100
	640139	158094	B7	150		*Picea abies*	100
	640138	158093	B8	170		*Picea abies*	
	640138	158094	B9		300	*Picea abies*	100
	640135	158092	B10		210	*Picea abies*	100
	640135	158091	B11	160		*Picea abies*	
	640135	158091	B12	140		*Picea abies*	
	640140	158087	B13	50		*Picea abies*	510
32	640280	159441	B1	15		*Pinus cembra*	

A.2 Field work raw data for additionally surveyed area (relevés no. 33-40)

A.2.1 Vegetation mapping results

Table A 13 Vegetation mapping results for the tree and shrub cover of vegetation relevés no. 33 to 40. Plant species are ordered alphabetically (without indication of family).
Note: Tree cover comprises all trees, small trees and tree seedlings; shrub cover comprises all shrub-, dwarf shrub- and shrublet species.

relevé no.	S33		S34		S35		S36		S37		S38		S39		S40	
species	**trees in percent (left column) and according to the abundance-dominance index of Braun-Blanquet (right column)**															
Fraxinus excelsior	< 1	r.1														
Picea abies	3	1.1	6	2.1	14	2.2	8	2.1	10	2.1	3	1.1	10	2.2	1	+.1
Pinus mugo ssp. uncinata	7	2.2	12	2.2	1	+.1					< 1	r.1	8	2.1		
Pinus mugo ssp. mugo	6	2.2	4	1.2									< 1	r.1		
Sorbus aucuparia	5	2.1	3	1.1									6	2.2		
total trees [%]	**21**		**25**		**15**		**8**		**10**		**3**		**24**		**1**	
relevé no.	S33		S34		S35		S36		S37		S38		S39		S40	
species	**shrubs in percent (left column) and according to the abundance-dominance index of Braun-Blanquet (right column)**															
Alnus viridis	5	2.1	10	2.1	3	1.1	< 1	r.1			5	2.1	< 1	r.1		
	dwarf shrubs in percent (left column) and according to the abundance-dominance index of Braun-Blanquet (right column)															
Calluna vulgaris	1-2	+.1	< 1	r.1												
Daphne mezereum													< 1	r.1		
Erica carnea	3	1.3	10	2.3	4	1.1			1-2	+.1			5	2.3		
Rhododendron hirsutum	6	2.1	5	2.1	6	2.3	5	2.3	6	2.3	20	2.3	8	2.2	10	2.3
Vaccinium myrtillus	3	1.1	4	1.1	15	2.3	3	1.1	1-2	+.1	< 1	r.1	12	2.3	< 1	r.1
Vaccinium vitis-idaea	1	+.1	< 1	r.1	2	1.2					< 1	r.1				
	shrublets in percent (left column) and according to the abundance-dominance index of Braun-Blanquet (right column)															
Dryas octopetala							7	2.3	5	2.3	6	2.3			10	2.3
Salix retusa	5	2.3	5	2.1	5	2.1							5	2.2		
total shrubs [%]	**25**		**34**		**35**		**15**		**14**		**30**		**30**		**20**	

Table A 14 Vegetation mapping results for the herb cover of vegetation relevés no. 33 to 40. Plant species are ordered according to their family.

Family	relevé no. / species	S33		S34		S35		S36		S37		S38		S39		S40	
		herbs in percent (left column) and according to the abundance-dominance index of Braun-Blanquet (right column)															
Poaceae	Anthoxanthum alpinum					5	2.2										
	Festuca rubra					4	1.2										
	Nardus stricta	7	2.2	3	1.2	5	2.2					< 1	r.1	4	1.2	4	1.2
	Poa alpina	3	1.2	4	1.2									3	1.2		
Cyperaceae	Carex curvula spp. curvula					3	1.2	1-2	+.1	3	1.2	1-2	+.1			1-2	+.1
	Carex ferruginea							1	+.2	2-3	1.2					< 1	r.1
	Carex parviflora							1	+.2								
	Carex sempervirens											4	1.1			4	1.2
Juncaceae	Luzula multiflora			1	+.1	4	1.2	1	+.1	1	+.1			1	+.1		
Irdaceae	Crocus albiflorus									5	2.3						
Orchidaceae	Dactylorhiza majalis											< 1	r.1				
	Pseudorchis albida											< 1	r.1			< 1	r.1
Polygonaceae	Polygonum viviparum											< 1	r.1			1-2	+.1
Caryphyllaceae	Silene vulgaris ssp. vulgaris	1	+.1											1	+.1		
Ranunculaceae	Pulsatilla alpina ssp. alpina							< 1	r.1								
	Ranunculus alpestris									1	+.1						
	Trollius europaeus									4	1.2	1-2	+.1				
Saxifragaceae	Saxifraga exarata ssp. moschata							8	2.3	3	1.3						
Rosaceae	Alchemilla alpina	6	2.2	5	2.2	15	2.3	10	2.3	5	2.3	8	2.3	10	2.3	8	2.3
	Alchemilla monticola	1-2	+.1														
	Alchemilla vulgaris					10	2.2										
	Geum montanum			1	+.1					< 1	r.1			< 1	r.1		
	Potentilla aurea	3	1.2					1	+.1	1-2	+.1			1	+.1		
	Potentilla erecta	1-2	+.1	1-2	+.1					1-2	+.1			3	1.1		

Table A 14 (continued)

	relevé no.	S33		S34		S35		S36		S37		S38		S39		S40	
species		herbs in percent (left column) and according to the abundance-dominance index of Braun-Blanquet (right column)															
Fabaceae	*Astragalus alpinus*															5	2.1
	Hippocrepis comosa									3	1.1						
	Trifolium alpinum									3	1.1						
	Trifolium pratense ssp. *nivale*											< 1	r.1				
	Trifolium rubens											< 1	r.1				
	Vicia cracca									1-2	+.1						
Geraniaceae	*Geranium sylvaticum*	4	1.1	10	2.2									12	2.2		
Cistaceae	*Helianthemum nummularium ssp. grandiflorum*											5	2.2			3	1.1
Apiaceae	*Astrantia major*			1	+.1									< 1	r.1		
Primulaceae	*Androsace chamaejasme*							< 1	r.1								
	Primula veris							4	1.1	< 1	r.1						
Gentianaceae	*Gentiana acaulis*			< 1	r.1			< 1	r.1	1-2	+.1					< 1	r.1
	Gentiana asclepiadea			7	2.2							1	+.1				
	Gentiana punctata			< 1	r.1												
Orobanchaceae	*Veronica bellidioides*											1	+.1				
Plantaginaceae	*Plantago alpina*	4	1.2	1-2	+.1			1-2	+.1	4	1.2			1	+.1	3	1.1

Table A 14 (continued)

relevé no.		S33		S34		S35		S36		S37		S38		S39		S40	
species		herbs in percent (left column) and according to the abundance-dominance index of Braun-Blanquet (right column)															
Globulariaceae	*Globularia nudicaulis*							5	2.2	< 1	r.1						
Dipsacaceae	*Knautia arvensis*					3	1.1										
	Scabiosa lucida	1-2	+.1	3	1.1	< 1	r.1					< 1	r.1	< 1	r.1	4	1.1
Campanulaceae	*Campanula barbata*			< 1	r.1												
	Campanula scheuchzeri											1-2	+.1			3	1.1
	Phyteuma orbiculare											< 1	r.1				
Asteraceae	*Arnica montana*	< 1	r.1	3	1.1	< 1	r.1			1-2	+.1	< 1	r.1	1	+.1	1-2	+.1
	Carlina acaulis ssp. caulescens forma nana													< 1	r.1		
	Cirsium helenioides	4	1.1			3	1.1										
	Hieracium pilosella			4	1.1												
	Hieracium prenanthoides			3	1.1									5	2.2		
	Homogyne alpina	15	2.2	6	2.2	1-2	+.1	1-2	+.1	4	1.3	8	2.2	8	2.3	5	2.1
	Leucanthemum adustum			3	1.1	3	1.1	1	+.1	1-2	+.1	3	1.1	< 1	r.1		
	Leontodon helveticus	3	1.1	1-2	+.1							8	2.2			5	2.1

Table A 15 Vegetation mapping results for the pteridophyte cover of vegetation relevés no. 33 to 34.
Plant species are ordered alphabetically (without indication of family).

relevé no.		S33		S34		S35		S36		S37		S38		S39		S40	
species		pteridophytes in percent (left column) and according to the abundance-dominance index of Braun-Blanquet (right column)															
pteridophytes	*Athyrium distentifolium*	3	1.1			3	1.2										
	Blechnum spicant			1	+.1									< 1	r.1		
total herbs & pteridophytes [%]		S33		S34		S35		S36		S37		S38		S39		S40	
		55		**60**		**60**		**38**		**50**		**45**		**50**		**50**	

Table A 16 Vegetation mapping results for the mosses of vegetation relevés no. 33 to 40

relevé no. species		S33		S34		S35		S36		S37		S38		S39		S40	
		mosses in percent (left column) and according to the abundance-dominance index of Braun-Blanquet (right column)															
mosses	*Polytrichum sexangulare*	8	2.3	15	2.3	15	2.3	1	+.3	2-3	1.3	5	2.3	20	2.3	1	+.3
total mosses [%]		**8**		**15**		**15**		**1**		**3**		**5**		**20**		**1**	

Table A 17 Evaluation of vegetation pattern for the vegetation relevés no. 33 to 40
Note: The value expressing the cumulative species cover includes parts of vegetation layers (i.e., tree-, shrub-, herb- and moss layer) that overlap, hence a density value of more than 100% can occur in general.

Vegetation pattern	S33	S34	S35	S36	S37	S38	S39	S40
total trees [%]	21	25	15	8	10	3	24	1
total shrubs [%]	25	34	35	15	14	30	30	20
total herbs and pteridophytes [%]	55	60	60	38	50	45	50	50
total moss [%]	8	15	15	1	3	5	20	1
cumulative species cover [%]	**109**	**134**	**125**	**62**	**77**	**83**	**124**	**72**
total number of flowering plants, ferns, mosses & lichens	28	33	23	21	27	28	29	21

A.2.2 Tree height and density

Table A 18 Vegetation growth expressed by tree height and density (including all trees, small trees and tree seedlings). Height is recorded for each tree species and displayed separately for trees (growing ≥ 2 m) and krummholz (growing < 2 m). Density is expressed for each tree species within the tree layer by the shortest distances to the neighboring trees, small trees and tree seedlings in cm. Each recorded tree species of a relevé (no. 33 to 40) is displayed in the following tables.

*Note: Distance values with less than 5 cm were not able to be calculated and are not displayed in the table. The same applies to relevés with only one recorded tree species where there are no distance values shown.

relevé ID	coordinates		number	krummholz height [cm]	tree height [cm]	species	shortest tree distance [cm]*
	x	y					
33	643787	160985	B1		275	*Pinus mugo* ssp. *unicinata*	364
	643785	160989	B2		350	*Pinus mugo* ssp. *unicinata*	89
	643784	160990	B3		300	*Sorbus aucuparia*	89
	643785	160991	B4		300	*Pinus mugo* ssp. *mugo*	152
	643786	160989	B5		230	*Pinus mugo* ssp. *mugo*	50
	643786	160989	B6		300	*Pinus mugo* ssp. *mugo*	50
	643789	160991	B7		200	*Sorbus aucuparia*	201
	643791	160991	B8		400	*Pinus mugo* ssp. *unicinata*	76
	643791	160991	B9	150		*Picea abies*	76
	643790	160987	B10	20		*Fraxinus excelsior*	364
34	643761	160955	B1	50		*Pinus mugo* ssp. *mugo*	502
	643762	160946	B2		200	*Picea abies*	224
	643762	160949	B3		500	*Picea abies*	100
	643762	160950	B4		500	*Pinus mugo* ssp. *uncinata*	40
	643763	160950	B5		600	*Pinus mugo* ssp. *uncinata*	110
	643764	160947	B6		600	*Pinus mugo* ssp. *uncinata*	212
	643763	160948	B7		800	*Pinus mugo* ssp. *uncinata*	141
	643765	160950	B8		700	*Pinus mugo* ssp. *uncinata*	200
	643766	160945	B9		600	*Pinus mugo* ssp. *uncinata*	250
	643762	160950	B10	180		*Sorbus aucuparia*	40
	643770	160949	B11	150		*Pinus mugo* ssp. *mugo*	461
	643767	160952	B12	100		*Pinus mugo* ssp. *mugo*	283

Table A 18 (continued)

relevé ID	coordinates		number	krummholz height [cm]	tree height [cm]	species	shortest tree distance [cm]*
	x	y					
35	643738	160971	B1		350	*Picea abies*	230
	643738	160973	B2		250	*Picea abies*	
	643738	160973	B3		300	*Picea abies*	
	643738	160973	B4	90		*Picea abies*	
	643740	160983	B5	76		*Picea abies*	300
	643740	160978	B6	75		*Pinus mugo* ssp. *uncinata*	54
	643739	160986	B7	45		*Picea abies*	300
	643741	160974	B8	40		*Picea abies*	255
	643741	160978	B9	95		*Picea abies*	54
	643743	160971	B10	130		*Picea abies*	262
	643743	160974	B11	55		*Picea abies*	180
	643744	160976	B12	55		*Picea abies*	136
	643745	160974	B13	35		*Picea abies*	117
	643747	160972	B14	40		*Pinus mugo* ssp. *uncinata*	40
	643746	160972	B15	45		*Picea abies*	40
	643746	160972	B16	60		*Picea abies*	56
	643746	160973	B17	85		*Picea abies*	30
	643745	160973	B18	80		*Picea abies*	30
	643746	160971	B19	100		*Picea abies*	123
36	643941	160863	B1	60		*Picea abies*	100
	643941	160864	B2	10		*Picea abies*	100
	643945	160864	B3	55		*Picea abies*	
	643946	160863	B4	15		*Picea abies*	
	643945	160864	B5	65		*Picea abies*	
	643946	160863	B6	80		*Picea abies*	
	643950	160862	B7	65		*Picea abies*	100
	643951	160862	B8	50		*Picea abies*	100
	643952	160867	B9	55		*Picea abies*	412
	643948	160866	B10	10		*Picea abies*	360
	643939	160866	B11	60		*Picea abies*	100
	643942	160869	B12	65		*Picea abies*	200
	643942	160867	B13	75		*Picea abies*	100
	643941	160867	B14	45		*Picea abies*	100
	643940	160866	B15	65		*Picea abies*	100

Table A 18 (continued)

relevé ID	coordinates		number	krummholz height [cm]	tree height [cm]	species	shortest tree distance [cm]*
	x	y					
37	643895	160790	B1	75		*Picea abies*	640
	643891	160795	B2	80		*Picea abies*	200
	643889	160795	B3	65		*Picea abies*	200
	643881	160792	B4	10		*Picea abies*	224
	643880	160794	B5	10		*Picea abies*	224
	643875	160803	B6	80		*Picea abies*	300
	643873	160799	B7	90		*Picea abies*	224
	643866	160798	B8	95		*Picea abies*	316
	643867	160795	B9	105		*Picea abies*	316
	643866	160789	B10	80		*Picea abies*	355
	643871	160793	B11	160		*Picea abies*	424
	643874	160796	B12	80		*Picea abies*	316
	643875	160800	B13	165		*Picea abies*	224
	643879	160804	B14	125		*Picea abies*	412
	643880	160790	B15	120		*Picea abies*	224
	643881	160798	B16	65		*Picea abies*	316
	643882	160801	B17	55		*Picea abies*	316
38	643886	160902	B1	120		*Picea abies*	305
	643930	160902	B2	70		*Pinus mugo* ssp. *uncinata*	305
	643861	160926	B3	50		*Picea abies*	869
	643804	160940	B4	80		*Picea abies*	869
39	643798	160980	B1		250	*Picea abies*	78
	643798	160982	B2		200	*Sorbus aucuparia*	150
	643798	160983	B3		600	*Sorbus aucuparia*	150
	643800	160984	B4		500	*Sorbus aucuparia*	175
	643799	160980	B5	40		*Picea abies*	78
	643800	160980	B6	30		*Picea abies*	51
	643800	160980	B7	150		*Picea abies*	42
	643800	160979	B8	50		*Pinus mugo* ssp. *mugo*	42
	643800	160978	B9		600	*Pinus mugo* ssp. *uncinata*	120
	643807	160978	B10	150		*Pinus mugo* ssp. *uncinata*	414
	643804	160981	B11		500	*Pinus mugo* ssp. *uncinata*	414
	643805	160986	B12		300	*Picea abies*	81
	643805	160986	B13		700	*Picea abies*	10
	643805	160986	B14		200	*Picea abies*	10
	643807	160986	B15	100		*Picea abies*	148
40	643881	160723	B1	60		*Picea abies*	

A.3 Analysis of vegetation pattern for relevés no. 1-32

A.3.1 Analysis of vegetation structure

Table A 19 Vegetation cover showing the cover and distribution of shrubs and herbs. Shrub cover includes all shrub, dwarf shrub and shrublet species; herb cover includes all herb and pteridophyte species. Each value is expressed in percent of the whole surface mapped. Values are expressed separately, for relevés beyond the 1899 limit of the timber line (≥ 2021 m a.s.l.) (left table) and for relevés below (< 2021 m a.s.l.) (right table). Mean values are marked in bold, for both, relevés beyond and below 2021 m a.s.l.

relevés (100 m^2) ≥ 2021 [m a.s.l.]	shrub cover [%]	herb cover [%]	relevés (100 m^2) < 2021 [m a.s.l.]	shrub cover [%]	herb cover [%]
4	40	35	1	46	48
5	6	73	2	12	76
6	25	61	3	45	59
8	73	18	7	64	25
9	52	23	10	56	37
11	41	35	12	29	65
19	39	57	13	40	51
20	39	48	14	34	59
23	58	35	15	45	52
25	51	53	16	33	55
27	45	47	17	43	38
28	59	38	18	22	50
29	61	30	21	60	40
30	61	41	22	64	32
31	30	52	24	57	36
32	30	62	26	59	34
Ø	**44**	**44**	**Ø**	**44**	**47**

Table A 20 Vegetation growth expressing the growth and distribution of trees (including small trees and tree seedlings). Growth shows the height of trees (including small trees and tree seedlings) in cm. Distribution illustrates: (a) the frequency of trees (≥ 2m) and krummholz (< 2 m; including all small trees and tree seedlings), and (b) shortest tree distance (average shortest distance between all neighboring trees, small trees and tree seedlings) in cm. Values are expressed separately for relevés beyond the 1899 limit of the timber line (≥ 2021 m a.s.l.) (upper table) and for relevés below (< 2021 m a.s.l.) (lower table). Mean values are marked in bold for relevés both beyond and below 2021 m a.s.l.

relevés (100 m^2) ≥ 2021 [m a.s.l.]	tree height [cm]	number of krummholz [< 2 m]	number of trees [≥ 2 m]	shortest tree distance [cm]
4	25	1	0	(-)
5	0	0	0	(-)
6	0	0	0	(-)
8	95	6	0	212
9	45	1	0	(-)
11	30	2	0	1260
19	0	0	0	(-)
20	100	7	0	224
23	500	0	1	(-)
25	80	1	0	(-)
27	50	3	0	555
28	110	2	0	400
29	180	2	1	143
30	90	3	1	388
31	180	7	6	124
32	15	1	0	(-)
Ø	**94**	**2**	**1**	**413**
relevés (100 m^2) < 2021 [m a.s.l.]	tree height [cm]	number of krummholz [< 2 m]	number of trees [≥ 2 m]	shortest tree distance [cm]
1	25	3	0	52
2	750	0	8	111
3	485	1	7	224
7	215	2	3	658
10	35	19	0	126
12	0	0	0	(-)
13	245	4	4	181
14	135	18	5	85
15	30	8	0	135
16	520	1	6	123
17	330	8	7	120
18	790	0	16	120
21	340	6	7	46
22	50	15	0	157
24	80	5	0	345
26	55	8	0	129
Ø	**255**	**6**	**4**	**174**

A.3.2 Analysis of phyto-diversity

Table A 21 Phyto-diversity expressed by the effect of plant species immigration into Geo montani-Nardetum grassland. The pattern of non-disturbed/naturally shaped vegetation of Geo montani-Nardetum is determined by the abundance of Geo montani-Nardetum character species (i.e., total number and density of character species), whereas the pattern of anthropo-zoogenically disturbed vegetation of Geo montani-Nardetum is determined by the intensity of deteriorated Geo montani-Nardetum to heathland. Values are expressed separately for relevés beyond the 1899 limit of the timber line (≥ 2021 m a.s.l.) (upper table) and for relevés below (< 2021 m a.s.l.) (lower table). Mean values are marked in bold for relevés both beyond and below 2021 m a.s.l.
Note: According to Braun-Blanquet (1948/1949) and Delarze & Gonseth (2008) the natural and undisturbed vegetation pattern of Geo montani-Nardetum grassland shows 9 character species.

relevés (100 m^2) ≥ 2021 [m a.s.l.]	total number of Geo montani-Nardetum character species	density of Geo montani-Nardetum character species [%]	density of deteriorated Geo montani-Nardetum to heathland [%]
4	5	11	34
5	4	16	11
6	5	12	21
8	4	3	49
9	2	2	33
11	2	5	29
19	5	6	37
20	3	8	17
23	2	3	47
25	3	4	60
27	3	4	57
28	3	5	41
29	3	5	39
30	4	4	56
31	4	8	18
32	3	8	47
Ø	**3**	**6**	**37**
relevés (100 m^2) < 2021 [m a.s.l.]	total number of Geo montani-Nardetum character species	density of Geo montani-Nardetum character species [%]	density of deteriorated Geo montani-Nardetum to heathland [%]
1	1	1	49
2	2	3	24
3	1	1	39
7	3	4	42
10	3	6	35
12	2	6	42
13	2	4	58
14	1	3	21
15	2	8	53
16	1	1	43
17	0	0	32
18	0	0	34
21	2	1	54
22	2	2	49
24	2	5	52
26	3	6	44
Ø	**2**	**3**	**42**

Table A 22 Recorded plant species associated to Geo montani-Nardetum for vegetation relevés no. 1-32. Herb plant species are displayed in the order of their family and alphabetically within their family (first pteridophytes then herbaceous angiosperms). Shrub species are ordered alphabetically (without indication of family).

Note: Plant species marked in bold refer to dominant plant species of the vegetation layer. Values are expressed in percent for each mapped plant species. Plant species showing a density cover of < 1% are attributed with a value of 0.5%. Plant species with an interval percent range, e.g., 1-2%, are rounded up to 2%.

shrub species	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16	S17	S18	S19	S20	S21	S22	S23	S24	S25	S26	S27	S28	S29	S30	S31	S32
Calluna vulgaris	12	0.5	4	25		5	3	6	5	15	15	5			18				3	6	15	1-2	0.5	15	7	7	10	10	15	23		
Rhododendron ferrugineum	8	1-2	4		3	4	7	7	7	8	3	1-2	10	7	5	5	4	5	10	3	10	10	13	10	15	8	10	6	5	4	6	15
Vaccinium myrtillus	10	5	22	3		6	25	30	15	5	5	15	20	5	15	20	20	10	12		10	25	15	15	13	18	15	18	10	22	3	10

herb & pteridophyte species	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16	S17	S18	S19	S20	S21	S22	S23	S24	S25	S26	S27	S28	S29	S30	S31	S32
Botrychium lunaria																		1														
Anthoxanthum alpinum	1-2	5	1				0.5	0.5	1	1	1-2				4	4			1	3	1	3	1-2	4	1-2	1	3	6	3	5	3	
Avenella flexuosa		7	4													5		1														
Festuca rubra s.str.	3			3	3	3	1-2	1	4	3	1			0.5	6		1-2		3			5	4	5	3	1	3	4	3	3		
Nardus stricta	**15**	**8**	**6**	**5**	**4**	**6**	**4**	**4**	**4**	**5**	**5**	**15**	**6**	**4**	**12**	**10**	**3**		**8**	**4**	**10**	**8**	**10**	**9**	**15**	**10**	**12**	**4**	**5**	**6**	**6**	**8**
Luzula multiflora	6			0.5		1-2	0.5		1	1	1	4		1-2	0.5		1		3	1			1				1	4			1	1
Nigritella nigra					0.5																											
Pseudorchis albida				1-2		1		0.5		0.5									1						0.5	0.5						
Pulsatilla alpina ssp. *apiifolia*					1																	3								3		
Alchemilla alpina		1-2	1		1								14	1	1-2		1	15	1-2	4	7	3	5	1-2	0.5		1		1		3	4
Potentilla aurea	0.5	8	1	3	1	3	1	1		3		1-2	1-2		1	3		1	3		1				1	1-2	1	1	1	1	3	3
Potentilla erecta	0.5	7	10	1-2	1	3	0.5	1-2		1-2		6	3	4	1	4		0.5	4		1-2		0.5	0.5	0.5	3	1	1-2	1	1-2	3	1-2
Geum montanum		**0.5**	**0.5**	**5**	**1-2**		**1-2**	**1**	**0.5**	**0.5**	**3**	**3**	**0.5**	**3**	**1-2**	**1**			**1-2**	**3**	**0.5**	**1**	**0.5**	**0.5**	**1**	**1**	**1**	**0.5**	**0.5**	**0.5**	**2**	**3**
Trifolium alpinum				1-2	1	3	1	1	1	1-2	3		1-2				0.5			4	1-2	0.5		1							3	
Gentiana acaulis			1	1	1-2	1													1	4						0.5				1	3	4
Gentiana purpurea	3							0.5		1									0.5			1	0.5	1		1	0.5	2		3		
Ajuga pyramidalis					8	4																									2	
Pedicularis tuberosa							1-2			1	1				5				3	1-2					0.5	0.5		0.5	0.5	0.5		
Plantago alpina		1-2	1	1-2	3	1-2	0.5	0.5		1	5	4	4	5	3	3			3		1	1-2		3	1-2	1		1	1	4		3
Campanula barbata			0.5		1-2		0.5												1									1	1	1		
Arnica montana	**1**	**1-2**		**1-2**	**5**	**3**	**1**	**1**	**1**	**5**	**1-2**	**3**	**3**		**6**				**1**	**1**	**0.5**	**1**	**1-2**	**4**	**1-2**	**4**	**1-2**	**3**	**3**	**1**	**1**	**1**
Homogyne alpina	1	5		3	1	3	1	0.5	1-2	1	1-2	8		10	3	4	5	17	5	1-2	1			1-2		6	5	3	4	3	3	5
Leontodon helveticus		**1-2**	**1**	**1**	**3**		**1-2**	**1-2**	**1**	**1-2**	**1**	**1**	**3**		**0.5**	**4**	**0.5**				**1-2**							**1**	**3**	**3**	**1**		**3**
total density [%]	62	56	56	58	40	50	54	61	43	55	46	69	68	41	86	63	40	51	67	37	63	65	56	70	69	63	65	70	56	84	39	62

Source: Braun-Blanquet 1948/1949; Delarze & Gonseth 2008; plant species displayed for Geo montani-Nardetum is according to Figure 14 on page 39.

Table A 23 Evaluation of non-disturbed/natural vs. disturbed/anthropo-zoogenically influenced Geo montani-Nardetum grassland, expressed by: (a) abundance of Geo montani-Nardetum character species and (b) density of deteriorated Geo montani-Nardetum to heathland, in percent, for vegetation relevés no. 1-32. Herb plant species are displayed in the order of their family and alphabetically within their family (first pteridophytes then herbaceous angiosperms). Shrub species are ordered alphabetically (without indication of family).

Note: Plant species marked in bold refer to dominant plant species of the vegetation layer. Values are expressed in percent for each mapped plant species. Plant species showing a density cover of < 1% are attributed with a value of 0.5%. Plant species with an interval percent range, e.g., 1-2%, are rounded up to 2%.

abundance of Geo montani-Nardetum character species	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16	S17	S18	S19	S20	S21	S22	S23	S24	S25	S26	S27	S28	S29	S30	S31	S32
herb species																																
Pseudorchis albida				1-2		1		0.5		0.5									1						0.5	0.5						
Geum montanum		0.5	0.5	5	1-2		1-2	1	0.5	0.5	3	3	0.5	3	2	1			1-2	3	0.5	1	0.5	0.5	1	1	1	0.5	0.5	0.5	2	3
Gentiana acaulis				1	1	1-2	1												1	4					0.5					1	3	4
Ajuga pyramidalis				8	4																											2
Campanula barbata				0.5		1-2		0.5											1									1	1	1		
Arnica montana	1	1-2		1-2	5	3	1	1	1	5	1-2	3	3		6				1	1	0.5	1	1-2	4	1-2	4	1-2	3	3	1	1	1
total density [%]	1	3	1	11	16	12	4	3	2	6	5	6	4	3	8	1	0	0	6	8	1	2	3	5	4	6	4	5	5	4	8	8

density of deteriorated Geo montani-Nardetum to heathland	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16	S17	S18	S19	S20	S21	S22	S23	S24	S25	S26	S27	S28	S29	S30	S31	S32
shrub species																																
Calluna vulgaris	12	0.5	4	25		5	3	6	5	15	15	5			18				3	6	15	1-2	0.5	15	7	7	10	10	15	23		
Rhododendron ferrugineum	8	1-2	4		3	4	7	7	7	8	3	1-2	10	7	5	5	4	5	10	3	10	10	13	10	15	8	10	6	5	4	6	15
Vaccinium myrtillus	10	5	22	3		6	25	30	15	5	5	15	20	5	15	20	20	10	12		10	25	15	15	13	18	15	18	10	22	3	10
herb species																																
Deschampsia cespitosa		1	0.5										5	1		3	1-2	4														
Nardus stricta	15	8	6	5	4	6	4	4	4	5	5	15	6	4	12	10	3		8	4	10	8	10	9	15	10	12	4	5	6	6	8
Poa alpina	4	3									4					1					1			1	8	1	5					4
Rumex alpestris														3			1															
Alchemilla alpina		1-2	1		1							14	1	1-2		1	15		1-2	4	7	3	5	1-2	0.5		1		1		3	4
Ligusticum mutellina							1		1										1-2				3		1			3				3
Leontodon helveticus		1-2	1	1	3		1-2	1-2	1	1-2	1	1	3		0.5	4	0.5				1-2							1	3	3	1	3
total density [%]	49	24	39	34	11	21	42	49	33	35	29	42	58	21	53	43	32	34	37	17	54	49	47	52	60	44	57	41	39	56	18	47

Geo montani-Nardetum	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16	S17	S18	S19	S20	S21	S22	S23	S24	S25	S26	S27	S28	S29	S30	S31	S32
evaluation																																
amount of character species	1	2	1	5	4	5	3	4	2	3	2	2	2	1	2	1			5	3	2	2	2	2	3	3	3	3	3	4	4	3
density of character species [%]	1	3	1	11	16	12	4	3	2	6	5	6	4	3	8	1			6	8	1	2	3	5	4	6	4	5	5	4	8	8
density of deterioration to heathland [%]	49	24	39	34	11	21	42	49	33	35	29	42	58	21	53	43	32	34	37	17	54	49	47	52	60	44	57	41	39	56	18	47

Source: Braun-Blanquet 1948/1949; Delarze & Gonseth 2008; plant species displayed for non-disturbed vs. disturbed Geo montani-Nardetum is according to Figure 14 on page 39.

A.3.3 Intensity of spruce forest progress into areas of grassland vegetation

Table A 24 Spruce forest progress is shown by the invasion density of recorded plant species associated to Vaccinio-Piceion, for vegetation relevés no. 1-32. Herb plant species are displayed in the order of their family and alphabetically within their family (first pteridophytes then herbaceous angiosperms). Tree and shrub species are ordered alphabetically (without indication of family).
Note: Plant species marked in bold refer to dominant plant species of the vegetation layer. Values are expressed in percent for each mapped plant species. Plant species showing a density cover of < 1% are attributed with a value of 0.5%. Plant species with an interval percent range, e.g., 1-2%, are rounded up to 2%.

tree species	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16	S17	S18	S19	S20	S21	S22	S23	S24	S25	S26	S27	S28	S29	S30	S31	S32
Picea abies	0.5	15	10				1	4					7	12	1	15	25	30		5	5				1	1-2	0.5	3	4	3	9	
Larix decidua																								0.5								
Sorbus aucuparia							0.5						3	4		1-2	1	3									0.5					
shrub species	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16	S17	S18	S19	S20	S21	S22	S23	S24	S25	S26	S27	S28	S29	S30	S31	S32
Lonicera caerulea		5	10										10	10		5	15	5														
Rhododendron ferrugineum	8	1-2	4		3	4	7	7	7	8	3	1-2	10	7	5	5	4	5	10	3	10	10	13	10	15	8	10	6	5	4	6	15
Vaccinium myrtillus	10	5	22	3		6	25	30	15	5	5	15	20	5	15	20	20	10	12		10	25	15	15	13	18	15	18	10	22	3	10
Vaccinium vitis-idaea	3		5			5	7	20	10	20	3	4	10		7	3	3	5	6		5	5	5	1-2	5	3	4	7	4	1-2	1-2	4
herb & pteridophyte species	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16	S17	S18	S19	S20	S21	S22	S23	S24	S25	S26	S27	S28	S29	S30	S31	S32
Athyrium distentifolium		0.5	3										0.5			1	1	1-2														
Blechnum spicant														1-2			3															
Avenella flexuosa		7	4													5		1														
Calamagrostis villosa		3	1										1	0.5		0.5	1-2	3														
Luzula sylvatica ssp. *sieberi*		4	3										0.5			1		1														
Oxalis acetosella		6	5										5			8	6	4														
Pyrola rotundifolia														0.5																		
Veronica urticifolia																																
Adenostyles alliariae													0.5	3			1	1-2														
Homogyne alpina	1	5		3	1	3	1	0.5	1-2	1	1-2	8		10	3	4	5	15	5	1-2	1		1-2		6	5	3	4	3	3		5
total density [%]	**23**	**53**	**67**	**6**	**4**	**18**	**42**	**62**	**34**	**34**	**13**	**29**	**68**	**54**	**31**	**70**	**86**	**86**	**33**	**10**	**31**	**40**	**35**	**28**	**40**	**37**	**33**	**38**	**26**	**34**	**20**	**34**

Source: Delarze & Gonseth 2008; plant species displayed for Vaccinio-Piceion is according to Figure 14 on page 39.

A.3.4 Analysis of habitat conditions

Table A 25 Ecological plant indicator values showing the climate factors (light (L), temperature (T) and continentality (K)). Factors for light and continentality follow a scale of five units ranging from 1 to 5, whereas temperature follows a scale of nine units ranging from 1 to 5.

scale	light (L)	temperature (T)	continentality (K)
1	deep shade (plant tolerates even less than 3 % of relative illumination)	alpine and nival	oceanic (very high relative air humidity; very small daily and annual variation in temperature, relatively mild winters)
1.5		lower alpine, supra subalpine and upper subalpine	
2	shade (plant rarely tolerates below 3 %, but often below 10 % of relative illumination)	subalpine	suboceanic (high relative air humidity; small daily and annual variation in temperatrue, rather mild winters)
2.5		lower subalpine and upper montane	
3	semi-shade (plant rarely tolerates below 10 % of relative illumination)	montane	suboceanic to subcontinental (medium relative air humidity; moderate daily and annual variation of temperature; medium winter temperatures)
3.5		lower montane and upper colline	
4	well-lit places (plant tolerates light shade only occasionally or for short periods)	colline	subcontinental (low relative air humidity; large daily and annual variation of temperature; rather cool winters)
4.5		warm colline	
5	full light (plant grows only in open and sunny places)	very warm colline	continental (very low relative air humidity; very large daily and annual variation in temperature; relatively cold winters)

Source: Landolt et al. 2010

Table A 26 Ecological plant indicator values showing the soil factors (moisture (F), soil reaction (R), nutrients (N), humus (H) and aeration (D)). Factors for soil reaction and nutrients follow a scale of five units ranging from 1 to 5, whereas moisture follows a scale of nine units ranging from 1 to 5. Humus and aeration follow a scale of 3 units (1, 3, 5). Additionally, the value for root depth specifies the depth of the root penetration in the soil, where small values indicate superficial and high values deep root penetration. Values follow a scale of nine units ranging from 1 to 5.

scale	moisture (F)	soil reaction (R)	nutrients (N)	humus (H)	aeration (D)	root depth (WT)
1	very dry	extremely acid pH 2.5-5.5	very infertile	little or no humus	bad areation (compacted or wet soil)	< 25 cm
1.5	dry					at most 20 % of the root depth in class 2
2	moderately dry	acid, pH 3.5-6.5	infertile			25-50 cm
2.5	fresh					at most 20 % of the root depth in class 3
3	moderately moist	weakly acid to weakly neutral pH 4.5-7.5	medium infertile to medium fertile	moderate humus content (mostly as mull)	moderate areation	50-100 cm
3.5	moist					at most 10 % of the root depth in class 4
4	very moist	neutral or alkaline pH 5.5-8.5	fertile			100-200 cm
4.5	wet					at most 5 % of the root depth in class 5
5	flooded, i.e. submerged	alkaline, high pH pH 6.5-8.5	very fertile and over-rich	high humus content (mostly as raw humus, moder or peat)	good areation (loose, often rocky or sandy soil)	> 200 cm

Source: Landolt et al. 2010

Table A 27 The ecological behavior for each relevé is given by the mean ecological plant indicator values of all recorded plant species. Average values are displayed for climate (L: light, T: temperature, K: continentality) and soil indicators (F: moisture, R: reaction, N: nutrients, H: humus and D: aeration) as well as values for root depth (WT).

relevé ID	climate indicators			soil indicators					root depth
	L	T	K	F	R	N	H	D	WT
1	3.21	2.01	2.90	2.81	1.98	2.10	3.67	1.74	1.73
2	2.94	2.10	2.94	2.99	2.03	2.17	3.83	2.16	1.98
3	2.97	2.19	2.89	2.88	1.96	2.04	3.84	2.17	1.90
4	3.58	1.90	2.95	2.78	1.95	1.82	3.54	1.81	1.64
5	3.90	1.97	3.07	2.99	2.80	2.12	3.30	2.18	1.71
6	3.59	2.12	2.89	3.03	2.26	2.09	3.85	1.86	1.58
7	3.21	1.95	2.79	2.73	1.92	1.98	3.76	1.94	1.81
8	2.89	1.93	2.60	2.65	1.65	1.84	3.66	1.73	1.73
9	3.33	1.96	2.98	2.67	2.03	1.91	3.74	2.00	1.65
10	3.43	2.02	2.97	2.80	1.98	2.03	3.88	1.88	1.71
11	3.52	2.07	2.98	2.82	2.06	2.01	3.93	1.97	1.74
12	3.46	2.12	2.85	3.06	1.95	2.24	3.93	1.87	1.67
13	2.99	2.10	2.85	2.88	2.01	1.97	3.49	2.09	2.49
14	3.13	2.01	2.84	2.91	2.52	2.21	3.50	2.06	2.47
15	3.32	2.06	2.86	2.88	1.93	2.09	3.88	1.97	1.69
16	3.01	2.16	3.01	3.00	2.10	2.04	3.89	2.28	2.11
17	2.70	2.13	2.74	2.96	1.99	2.34	3.63	1.98	2.06
18	2.73	2.09	2.85	3.02	2.09	2.28	3.87	2.23	2.27
19	3.43	2.01	2.92	2.88	1.98	2.00	3.80	1.79	1.62
20	3.57	1.95	3.08	2.64	2.82	2.06	3.34	2.58	2.06
21	3.28	2.02	2.96	2.76	2.09	2.13	3.72	2.41	2.08
22	3.28	1.93	2.99	2.84	2.07	1.96	3.61	2.06	1.77
23	3.16	1.91	2.80	2.80	1.84	1.98	3.62	1.91	1.64
24	3.33	1.91	2.88	2.84	1.99	1.92	3.52	1.85	1.89
25	3.24	1.93	2.89	2.89	2.02	2.17	3.62	1.90	1.69
26	3.36	1.93	2.94	2.93	1.83	1.91	3.98	1.73	1.77
27	3.23	1.90	2.78	2.89	1.98	2.09	3.53	1.88	1.61
28	3.25	2.09	2.89	2.84	2.00	2.09	4.00	1.95	1.87
29	3.21	2.06	2.80	2.85	1.96	2.00	3.82	1.90	1.92
30	3.18	2.01	2.87	2.72	2.12	2.06	3.59	2.09	2.00
31	3.60	1.94	3.11	2.65	2.76	1.98	3.38	2.58	1.88
32	3.64	1.87	2.82	2.94	2.23	2.15	3.47	2.29	1.67

Source: Landolt 1977, Landolt et al. 2010

In this table, the ecological behavior of each relevé was determined by the mean ecological plant indicator values, which has been measured by the total amount of recorded plant species (including flowering plants, ferns, mosses and lichens) for each relevé (no. 1-32). Average values have been calculated for climate (L: light, T: temperature, K: continentality) and soil indicators (F: moisture, R: reaction, N: nutrients, H: humus and D: aeration), as well as values for root depth (WT). Landolt et al. (2010) suggests that average values are more accurate for evaluating a habitat by its ecology than only considering separate values of a plant species. For all vegetation records we calculated the mean for each ecological plant indicator value over species weighted by abundance, as suggested by Landolt (1977), in order to account for the greater importance of dominant plant species over rare ones. Species with abundance "+" were weighted one, species with abundance "1" were weighted two, "2" were weighted three, "3" were weighted four, "4" were weighted five and "5" were weighted six. Plant species with a very low abundance "r" were weighted 0.5.

A.4 Analysis of vegetation pattern for additionally surveyed area (relevés no. 33-40)

A.4.1 Intensity of forest progress into areas of grassland vegetation

Table A 28 The intensity of forest progress into areas of grassland vegetation is displayed by the density of recorded plant species associated to the dominant forest communities (cohorts: Vaccinio-Piceion and Erico-Pinion mugo), for vegetation relevés no. 33-40. Tree and shrub species are ordered alphabetically (without indication of family).
Note: Plant species marked in bold refer to dominant plant species of the vegetation layer. Values are expressed in percent for each mapped plant species. Plant species showing a density cover of < 1% are attributed with a value of 0.5%. Plant species with an interval percent range, e.g., 1-2%, are rounded up to 2%.

Vaccinio-Piceion								
tree species	S33	S34	S35	S36	S37	S38	S39	S40
Picea abies	**6**	**3**	**14**	**8**	**10**	**3**	**10**	**1**
Sorbus aucuparia	3	5					6	
shrub species	S1	S2	S3	S4	S5	S6	S7	S8
Vaccinium myrtillus	**4**	**3**	**15**	**3**	**1-2**	**0.5**	**12**	**0.5**
Vaccinium vitis-idaea	0.5	1	2			0.5		
herb and pteridophyte species	S1	S2	S3	S4	S5	S6	S7	S8
Homogyne alpina	6	15	1-2	1-2	4	8	8	5
total density [%]	**20**	**27**	**33**	**13**	**16**	**12**	**36**	**7**
Erico-Pinion mugo								
tree species	S33	S34	S35	S36	S37	S38	S39	S40
Picea abies	6	3	14	8	10	3	10	1
Pinus mugo ssp. *mugo*	4	6					0.5	
Pinus mugo ssp. ***unicinata***	**12**	**7**	**1**			**0.5**	**8**	
shrub species	S33	S34	S35	S36	S37	S38	S39	S40
Erica carnea	**10**	**3**	**4**		**1-2**		**5**	
Rhododendron hirsutum	**5**	**6**	**6**	**5**	**6**	**20**	**8**	**10**
Vaccinium myrtillus	4	3	15	3	1-2	0.5	12	0.5
Vaccinium vitis-idaea	0.5	1	2			0.5		
total density [%]	**42**	**29**	**42**	**16**	**20**	**25**	**44**	**12**

Source: Delarze & Gonseth (2008)

A.4.2 Recorded plant species with signs of pasturing and signs of undemanding/pioneer vegetation

Table A 29 Evaluation of vegetation pattern at the timber-line ecotone of the study region of vegetation relevés no. 33-40. Recorded plant species with signs of pasturing (plant species associated to the cohort Poion alpinae) and with signs of undemanding/pioneer vegetation are shown for vegetation relevés no. 33-40. Herb plant species are displayed in the order of their family and alphabetically within their family (first pteridophytes then herbaceous angiosperms). Shrub species are ordered alphabetically (without indication of family).
Note: Plant species marked in bold refer to dominant plant species of the vegetation layer. Values are expressed in percent for each mapped plant species. Plant species showing a density cover of < 1% are attributed with a value of 0.5%. Plant species with an interval percent range, e.g., 1-2%, are rounded up to 2%. Shrub cover comprises all shrub-, dwarf shrub- and shrublet species. The value expressing the cumulative species cover includes parts of vegetation layers (i.e., tree-, shrub-, herb- and moss layer) that overlap, hence a density value of more than 100% can occur in general.

recordet plant species with signs of pasturing	S33	S34	S35	S36	S37	S38	S39	S40	
herb species									
Festuca rubra **s.str.**			**4**						
Poa alpina	**4**	**3**					**3**		
Alchemilla vulgaris			10						
Trifolium pratense ssp. *nivale*						0.5			
Plantago alpina	2	4		2	4		1	3	
total density [%]	**6**	**7**	**14**	**2**	**4**	**< 1**	**4**	**3**	

recordet plant species with signs of undemanding / pioneer vegetation	S33	S34	S35	S36	S37	S38	S39	S40	preferred habitat
shrubs (including all shrubs, dwarf shrubs & shrublets)									
Alnus viridis	10	5	3	0.5		5	0.5		stony rocks, slopes and gullies
Daphne mezereum							0.5		forests, rock-debris
Dryas octopetala				7	5	6		10	rock-debris, rocks
Salix retusa	5	5	5				5		rock, debris, stony pastures
herb species									
Saxifraga exarata ssp. *moschata*				8	3				rock-debris, rocks
Alchemilla alpina	5	6	15	10			10	8	rocks
Androsace chamaejasme				0.5					stony grass
Globularia nudicaulis				5	0.5				meadows, stony slopes
Scabiosa lucida	3	2	0.5			0.5	0.5	4	alpine meadows on stony soils
total density [%]	**23**	**18**	**24**	**31**	**9**	**12**	**17**	**22**	

evaluation									
	S33	S34	S35	S36	S37	S38	S39	S40	
cumulative species cover [%]	113	135	125	62	77	83	124	72	
total cover of undemanding / pioneer plant species [%]	23	18	24	31	9	12	17	22	
total density of plant species with signs of pasturing [%]	6	7	14	2	4	1	4	3	

Source: Recorded plant species with signs of pasturing, signs of undemanding/pioneer vegetation, as well as the interpretation of preferred habitat corresponds to the publications "Lebensräume der Schweiz" (Delarze & Gonseth 2008), "Flora Helvetica" (Lauber & Wagner 2012) and "Unsere Alpenflora" (Landolt 2003)

Table A 30 Summary of the habitat properties of the relevés no. 33-40

relevé ID	coordinates		geology & substrate	slope [°]	elevation [m a.s.l.]	type of land use	accessibility [value]
	x	y					
33	643783	160982	tertiary (coalic limestones)	11	1691	extensive pasture	0.29
34	643761	160945	tertiary (coalic limestones)	37	1701	extensive pasture	0.29
35	643737	160970	tertiary (coalic limestones)	21	1685	extensive pasture	0.24
36	643941	160871	tertiary (limestone breccia)	19	1762	not used	0.40
37	643880	160796	tertiary (limestone breccia)	22	1781	extensive pasture	0.39
38	643939	160897	tertiary (limestone breccia)	19	1754	extensive pasture	0.38
39	643797	160977	tertiary (coalic limestones)	28	1696	extensive pasture	0.31
40	643881	160723	mesozoic (berriacien, Oehrli-calc)	24	1812	not used	0.44
Ø				23	1735		0.34

relevé ID	tree height [cm]	shortest tree distance [cm]	cumulative species cover [%]	plant community	Erico-Pinion mugo [%]	Vaccinio-Piceion [%]	total cover of undemanding/pioneer plant species [%]	total density of plant species with signs of pasturing [%]
33	253	214	113	Erico-Pinetum mugi	42	20	23	6
34	415	151	135	Erico-Pinetum mugi	29	27	18	7
35	106	116	125	Erico-Pinetum mugi	42	33	24	14
36	52	118	62	Rhododendro hisuti-mugetum	16	13	31	2
37	86	308	77	Rhododendro hisuti-mugetum	20	16	9	4
38	80	587	83	Rhododendro hisuti-mugetum	25	12	12	< 1
39	291	131	124	Erico-Pinetum mugi	44	36	17	4
40	60	(-)	72	rock and debris vegetation	12	7	22	3
Ø	168	232	99		29	20	19	6

Source: Coordinates, altitude, slope and exposition: Digitales Geländemodell 2m © swisstopo; substrate: Collet et al. 1938; type of land use: Hoffmann et al. 2014; accessibility: Liechti et al., in prep.

A.5 Statistical analysis

Table A 31 Tests produced by IBM SPSS-Statistics program for (a) normality and (b) homogeneity of variance for test variables for vegetation cover, vegetation growth and phyto-diversity. Significance value (p) is two-tailed. Test variables are normally distributed if the distributions of their values are not significantly different from a normal distribution ($p > 0.05$).
Note: *The value 0.200 shows a minimum level of the effective significance. Several test variables show for vegetation growth inconsistent results (marked in red bold in the table) for the calculated significances of the Kolmogorov-Smirnov and Shapiro-Wilk test. Since the Shapiro-Wilk test has more power to detect differences from normality, the results of the Shapiro-Wilk output table are applied for the interpretation of normal and non-normal data distribution (Field 2009). The Levene's test shows that the variances in different groups are roughly equal if $p > 0.05$. In spite of some variables showing equal variances (marked in blue bold in the table), a non-parametric test is more appropriate, since parametric tests always require normally distributed samplings (Field 2009).

| test variables | (a) Tests of Normality | | | | | | (b) Test of Homogeneity of Variance | | assumption of data |
| | Kolmogorov-Smirnov | | Shapiro-Wilk | | distribution | | Levene's test | interpretation | |
	relevés ≥ 2021 [m a.s.l.] (p)	relevés < 2021 [m a.s.l.] (p)	relevés ≥ 2021 [m a.s.l.] (p)	relevés < 2021 [m a.s.l.] (p)	relevés ≥ 2021 [m a.s.l.]	relevés < 2021 [m a.s.l.]	(p) is based on mean	based on the Test of Homogeneity of Variance	
vegetation cover									
shrub cover	.200*	.200*	.807	.417	normal	normal	.772	equal variances	parametric
herb cover	.200*	.200*	.982	.861	normal	normal	.653	equal variances	parametric
vegetation growth									
tree height	.200*	**.200***	.339	**.023**	normal	**non-normal**	.003	different variances	non-parametric
number of krummholz	.038	**.081**	.019	**.028**	non-normal	**non-normal**	.042	different variances	non-parametric
number of trees	.001	.044	.000	.010	non-normal	non-normal	.038	different variances	non-parametric
shortest tree distance	**.106**	.002	**.011**	.000	**non-normal**	non-normal	.065	**equal variances**	non-parametric
phyto-diversity									
total number of Geo montani-Nardetum character species	.027	.007	.049	.046	non-normal	non-normal	.581	**equal variances**	non-parametric
density of Geo montani-Nardetum character species	.138	.200*	.062	.303	normal	normal	.097	equal variances	parametric
density of deteriorated Geo montani-Nardetum to heathland	.200*	.200*	.630	.678	normal	normal	.152	equal variances	parametric

Table A 32 Exploratory data analysis produced by IBM SPSS-Statistics program showing descriptive statistics, such as number of pairs (*n*), mean (*m*), standard deviation (*sd*) and standard error (*se*) for test variables for vegetation cover, vegetation growth and phyto-diversity.

test variables	number of pairs (*n*)		mean (*m*)		standard deviation (*sd*)		standard error (*se*)	
	relevés ≥ 2021 [m a. s. l.]	relevés < 2021 [m a. s. l.]	relevés ≥ 2021 [m a. s. l.]	relevés < 2021 [m a. s. l.]	relevés ≥ 2021 [m a. s. l.]	relevés < 2021 [m a. s. l.]	relevés ≥ 2021 [m a. s. l.]	relevés < 2021 [m a. s. l.]
vegetation cover								
shrub cover	16	16	44	44	16.8	15.4	4.2	3.9
herb cover	16	16	44	47	15.04	13.6	3.8	3.4
vegetation growth								
tree height	16	16	94	255	53.8	259.6	19.03	67.02
number of krummholz	16	16	2	6	2.3	6.3	0.8	1.6
number of trees	16	16	1	4	2.07	4.5	0.7	1.2
shortest tree distance	16	16	413	174	372.43	152.07	131.7	39.3
phyto-diversity								
total number of Geo montani-Nardetum character species	16	16	3	2	1.03	0.95	0.26	0.24
density of Geo montani-Nardetum character species	16	16	6	3	3.9	2.45	0.98	0.6
density of deteriorated Geo montani-Nardetum to heathland	16	16	37	42	15.06	10.7	3.8	2.7

The output of the tests for normality and tests of homogeneity of variance show that the data for the shrub-, herb cover, density of Geo montani-Nardetum character species and density of deteriorated Geo montani-Nardetum to heathland are parametric. We applied for the interpretation of significance, the dependent *t*-test (Paired Samples Test). In contrast, the data for tree height, number of krummholz and trees, shortest tree distance and total number of Geo montani-Nardetum character species are non-parametric. We applied for the interpretation of significance, the non-parametric equivalent of the dependent *t*-test, i.e., the Wilcoxon-signed-rank test (Table A 31).

Table A 33 Significance tests produced by IBM SPSS-Statistics program for (a) Wilcoxon-Test, showing the exact significance (required for most accurate results in small samples) of calculated *z*-score for test variables for vegetation cover, vegetation growth and phyto-diversity with non-normal distribution and different variances; and (b) Paired Samples Test showing the significance of calculated *t*-value for test variables for vegetation cover, vegetation growth and phyto-diversity with normal distribution and equal variances. Significance value (*p*) is two-tailed. Values *p* < 0.05 are significant. Values *p* ≥ 0.05 are not significant. Significance values applied for the interpretation of mean differences are pointed out in bold.
Note: (-)* The Paired Samples Test is only displayed for parametric data.

test variables for vegetation cover	(a) Wilcoxon-Test exact significance of *z*-score (*p*)	(b) Paired Samples Test significance of *t*-value (*p*)	Interpretation of mean differences
shrub cover	.990	**.988**	non-significant
herb cover	.280	**.406**	non-significant
test variables for vegetation growth	(a) Wilcoxon-Test exact significance of *z*-score (*p*)	(b) Paired Samples Test significance of *t*-value (*p*)	Interpretation of mean differences
tree height	**.050**	(-)*	non-significant
number of krummholz	**.026**	(-)*	significant
number of trees	**.020**	(-)*	significant
shortest tree distance	**.578**	(-)*	non-significant
test variables for phyto-diversity	(a) Wilcoxon-Test exact significance of *z*-score (*p*)	(b) Paired Samples Test significance of *t*-value (*p*)	Interpretation of mean differences
total number of Geo montani-Nardetum character species	**.001**	(-)*	significant
density of Geo montani-Nardetum character species	.030	**.024**	significant
density of deteriorated Geo montani-Nardetum to heathland	.291	**.243**	non-significant

A.6 Expected prognosis of current study by means of ArcGIS

A.6.1 For relevés no. 1-32

Table A 34 GIS-classification for areas where we propose a climate warming impact. The expected response of possible warming impact is expressed by the degree of non-disturbed/natural vegetation pattern of dominant grassland community of the study region (i.e., abundance of Geo montani-Nardetum character species). Vegetation relevés are classified according to the different rates for abundance of Geo montani-Nardetum character species. Classes are categorized with ESRI ArcGIS and are marked in bold. Rates classified as 1 are allocated to areas with highest abundance rates, rates classified as 2 are allocated to areas with intermediate abundance rates, and rates classified as 3 are allocated to areas with lowest abundance rates and clearest signs of recessive pasture activity.
Note: Average rate of 2.5 are rounded up to 3, whereas average rates of 1.5 are rounded down to 1.

relevé ID	GIS-class for total number of Geo montani-Nardetum character species	GIS-class for density of Geo montani-Nardetum character species	average rates	GIS-class according to average rate	degree of non-disturbed/natural vegetation pattern of Geo montani-Nardetum
1	3	3	3.0	**3**	lowest degree: clearest signs of pasture reduction
2	2	3	2.5	**3**	lowest degree: clearest signs of pasture reduction
3	3	3	3.0	**3**	lowest degree: clearest signs of pasture reduction
4	1	1	1.0	**1**	highest degree: most probably related to global warming
5	1	1	1.0	**1**	highest degree: most probably related to global warming
6	1	1	1.0	**1**	highest degree: most probably related to global warming
7	2	3	2.5	**3**	lowest degree: clearest signs of pasture reduction
8	1	3	2.0	**2**	intermediate degree: possible reduction in pasture activity and other reasons (e.g., site conditions)
9	2	3	2.5	**3**	lowest degree: clearest signs of pasture reduction
10	2	2	2.0	**2**	intermediate degree: possible reduction in pasture activity and other reasons (e.g., site conditions)
11	2	2	2.0	**2**	intermediate degree: pasture reduction and other reasons (e.g. site conditions)
12	2	2	2.0	**2**	intermediate degree: possible reduction in pasture activity and other reasons (e.g., site conditions)
13	2	3	2.5	**3**	lowest degree: clearest signs of pasture reduction
14	3	3	3.0	**3**	lowest degree: clearest signs of pasture reduction
15	2	2	2.0	**2**	intermediate degree: possible reduction in pasture activity and other reasons (e.g., site conditions)
16	3	3	3.0	**3**	lowest degree: clearest signs of pasture reduction

Table A 34 (continued)

relevé ID	GIS-class for total number of Geo montani-Nardetum character species	GIS-class for density of Geo montani-Nardetum character species	average rates	GIS-class according to average rate	degree of non-disturbed/natural vegetation pattern of Geo montani-Nardetum
17	3	3	3.0	**3**	lowest degree: clearest signs of pasture reduction
18	3	3	3.0	**3**	lowest degree: clearest signs of pasture reduction
19	1	2	1.5	**1**	highest degree: most probably related to global warming
20	2	2	2.0	**2**	intermediate degree: possible reduction in pasture activity and other reasons (e.g., site conditions)
21	2	3	2.5	**3**	lowest degree: clearest signs of pasture reduction
22	2	3	2.5	**3**	lowest degree: clearest signs of pasture reduction
23	2	3	2.5	**3**	lowest degree: clearest signs of pasture reduction
24	2	2	2.0	**2**	intermediate degree: possible reduction in pasture activity and other reasons (e.g., site conditions)
25	2	3	2.5	**3**	lowest degree: clearest signs of pasture reduction
26	2	2	2.0	**2**	intermediate degree: possible reduction in pasture activity and other reasons (e.g., site conditions)
27	2	3	2.5	**3**	lowest degree: clearest signs of pasture reduction
28	2	2	2.0	**2**	intermediate degree: possible reduction in pasture activity and other reasons (e.g., site conditions)
29	2	2	2.0	**2**	intermediate degree: possible reduction in pasture activity and other reasons (e.g., site conditions)
30	1	3	2.0	**2**	intermediate degree: possible reduction in pasture activity and other reasons (e.g., site conditions)
31	1	2	1.5	**1**	highest degree: most probably related to global warming
32	2	2	2.0	**2**	intermediate degree: possible reduction in pasture activity and other reasons (e.g., site conditions)

Table A 35 GIS-classification for the proportion of areas where we propose an upward shift in timber line. The expected proportion of areas showing progress of spruce forest vegetation into non-forested areas is expressed by the appearance of plant species that are allocated to Vaccinio-Piceion. Vegetation relevés are classified according to the different rates for invasion density of Vaccinio-Piceion spruce forest vegetation. Classes are categorized with ESRI ArcGIS and are marked in bold. Rates classified as 1 are allocated to areas with highest invasion density of Vaccinio-Piceion (i.e., most advanced stage of spruce forest plant succession), rates classified as 2 are allocated to areas with intermediate invasion density of Vaccinio-Piceion and rates classified as 3 are allocated to areas with lowest invasion density of Vaccinio-Piceion (i.e., initial to transitional stage of spruce forest plant succession).

relevé ID	GIS-class for density of Vaccinio-Piceion	intensity of forest progress	relevé ID	GIS-class for density of Vaccinio-Piceion	intensity of forest progress
1	1	initial to transitional stage	17	3	transitional to climax stage
2	3	transitional to climax stage	18	3	transitional to climax stage
3	3	transitional to climax stage	19	2	transitional stage
4	1	initial to transitional stage	20	1	initial to transitional stage
5	1	initial to transitional stage	21	2	transitional stage
6	1	initial to transitional stage	22	2	transitional stage
7	2	transitional stage	23	2	transitional stage
8	3	transitional to climax stage	24	2	transitional stage
9	2	transitional stage	25	2	transitional stage
10	2	transitional stage	26	2	transitional stage
11	1	initial to transitional stage	27	2	transitional stage
12	2	transitional stage	28	2	transitional stage
13	3	transitional to climax stage	29	2	transitional stage
14	3	transitional to climax stage	30	2	transitional stage
15	2	transitional stage	31	1	initial to transitional stage
16	3	transitional to climax stage	32	2	transitional stage

Table A 36 Evaluation of GIS-analysis for: (a) current shape of timber line in probable response to global warming/pasture reduction, (b) areas proposed to show an upward shift in timber line

relevé ID	current shape of timber line with		signs in probable response to global warming			areas proposed to show an upward shift in timber line		
	signs of global warming impact	signs of pasture reduction	clear signs	intermediate signs	lowest signs	initial to transitional stage	transitional stage	transitional to climax stage
1		x			x	x		
2		x			x			x
3		x			x			x
4	x		x			x		
5	x		x			x		
6	x		x			x		
7		x			x		x	
8		x		x				x
9		x			x		x	
10		x		x			x	
11		x		x		x		
12		x		x			x	
13		x			x			x
14		x			x			x
15		x		x			x	
16		x			x			x
17		x			x			x
18		x			x			x
19	x		x				x	
20		x		x		x		
21		x			x		x	
22		x			x		x	
23		x			x		x	
24		x		x			x	
25		x			x		x	
26		x		x			x	
27		x			x		x	
28		x		x			x	
29		x		x			x	
30		x		x			x	
31	x		x			x		
32		x		x			x	
in percent	16	84	16	38	47	22	53	25

A.6.2 For relevés no. 33-40

Table A 37 GIS-classification for the proportion of areas where we propose an upward shift in timber line. The expected proportion of areas showing a progress of spruce forest vegetation into non-forested areas is expressed by the appearance of plant species that are allocated to Vaccinio-Piceion. Vegetation relevés are classified according to the different rates for invasion density of Vaccinio-Piceion spruce forest vegetation. Classes are categorized with ESRI ArcGIS and are marked in bold. Rates classified as 1 are allocated to areas with highest invasion density of Vaccinio-Piceion (i.e., most advanced stage of spruce forest plant succession), rates classified as 2 are allocated to areas with intermediate invasion density of Vaccinio-Piceion and rates classified as 3 are allocated to areas with lowest invasion density of Vaccinio-Piceion (i.e., initial to transitional stage of spruce forest plant succession).

relevé ID	GIS-class for density of Vaccinio-Piceion	intensity of forest progress
33	2	transitional stage
34	3	transitional to climax stage
35	3	transitional to climax stage
36	1	initial to transitional stage
37	2	transitional stage
38	1	initial to transitional stage
39	3	transitional to climax stage
40	1	initial to transitional stage

A.7 Further important records

hillshade illumination value

High: 254

Low: 0

glacier debris area

glacier area

contours displayed for the following altitudinal boundaries:
1400 m a.s.l. upper limit of broadleaved forests
1800-2000 m a.s.l. forest limit / timber line
2200-2300 m a.s.l. tree limit / treeline
2400 m a.s.l. Krummholz limit
3000 m a.s.l. nival belt, snow line

current forest limit

possible extend of future forest limit for whole region

vegetation

forests

broadleaved forests

subalpine coniferous forests

afforested area

natural stage of growth

shrubs

shrubs

subalpine dwarf shrub heath

grassland

rich meadows and pastures

thermophilic dry meadow

dry meadows on limestone

meager pastures

subalpine and alpine meadows

subalpine and alpine pastures

alpine grassland

peat bogs and swamps

subalpine and alpine mega forbs

richly manured alpine pasture

snow pocket vegetation

rock and debris vegetation

rock and debris vegetation on limestone

not defined units

Figure A 1 Vegetation of the whole region of Grindelwald according to Hegg & Schneiter (1988)
Source: Hillshade and contours: Digitales Geländemodell 2m © swisstopo; actual forest limit, glacier debris and glacier area: VECTOR25 © swisstopo; vegetation: Hegg & Schneiter 1988; possible extend of future forest limit for whole region: Collet et al. 1938, Lawinenkataster des Kantons Bern © Abteilung Naturgefahren des Kantons Bern, Ereigniskataster NGKAT © Abteilung Naturgefahren, Amt für Wald des Kantons Bern, Landolt 2003, Holtmeier 2009; contours displayed for the selected altitudinal boundaries are according to tables 1 and 2 (page 17).

Table A 38 Vegetation of the whole region of Grindelwald according to Hegg & Schneiter (1988)

type of vegetation	in [m²]	in [%]
broadleaved forests	2787986.529	2.9
subalpine coniferious forests	17640354.09	18.3
afforested area	182269.462	0.2
natural stage of growth (pioneer spruce forest with *Melampyrum sylvaticum*)	70327.427	0.1
shrubs	2231139.029	2.3
subalpine dwarf shrub heath	4044907.771	4.2
rich meadows and pastures	20893946.68	21.7
thermophilic dry meadow	758803.062	0.8
dry meadows on limestone	1267193.969	1.3
meager pastures	1108560.325	1.1
subalpine and alpine meadows	12941291	13.4
subalpine and alpine pastures	4694830.099	4.9
alpine grassland	767439.133	0.8
peat bogs and swamps	2179463.333	2.3
subalpine and alpine mega forbs	1601207.521	1.7
richly manured alpine pasture	724077.846	0.8
snow pocket vegetation	4172623.393	4.3
rock and debris vegetation	15371744.49	15.9
not undefined units	3012655.857	3.1
total area of vegetation in the community	**96450821.02**	**100**

Source: Hegg & Schneiter 1988; Delarze & Gonseth 2008

Methods of vegetation classification:

The MAB (Man and Biosphere) is an interdisciplinary research program of UNESCO that has focussed its research on the equilibrium between the ecological balance of the area and human activity. Switzerland has decided to contribute in one part (i.e., research program no. 6: "The study of Man's impact on mountain ecosystems") of the worldwide studied research projects, investigating all fundamental habitats of the earth. In addition, this research program was taken over by the Swiss National Science Foundation (SNF) under the title "Socioeconomic development and ecological resilience in mountainous areas" (NFP 55). The aim of this research project was to analyse, in selected regions (Grindelwald, Pays-d'Enhaut, Aletsch, Davos): (1) the interdependency between economical activities, land use and the ecological balance of the area and (2) determine the processes that affect the long-term security of a mountainous area in the sense of living, economic and recreation areas (Swiss National Science Foundation 2015). In the region of Grindelwald, vegetation mappings belong to a sub-project among many others. For the region of Grindelwald, several spatial units of different vegetation groups have been identified that are more or less homogeneous areas of about 1-5 ha and cover the whole inventory of plant communities. According to the traditional vegetation mapping method of Braun-Blanquet (1964), different vegetation types were defined within the spatial units. In the mapping entities, plant communities of different plant sociological levels, specifically the levels of subassociation, association and cohort, are considered. For specific research purposes of the MAB-project, the different plant physiognomic aspects were additionally recorded in the sense of their formation or appearances, according to the dominance of certain plant species or groups of certain plant species (e.g., variants or facies). For the whole test area of Grindelwald, there have been a total of around 5600 spatial units.

The vegetation map, showing the dominant plant communities in the region of Grindelwald, has been produced by selecting the values out of the attribute table that show the dominant vegetation groups (including forests and non-forest areas) within the spatial units. In order to select the most dominant vegetation groups (i.e., the plant communities with strongest abundance), the attribute values of "DVEG1" have been selected (Hegg & Schneiter 1988).
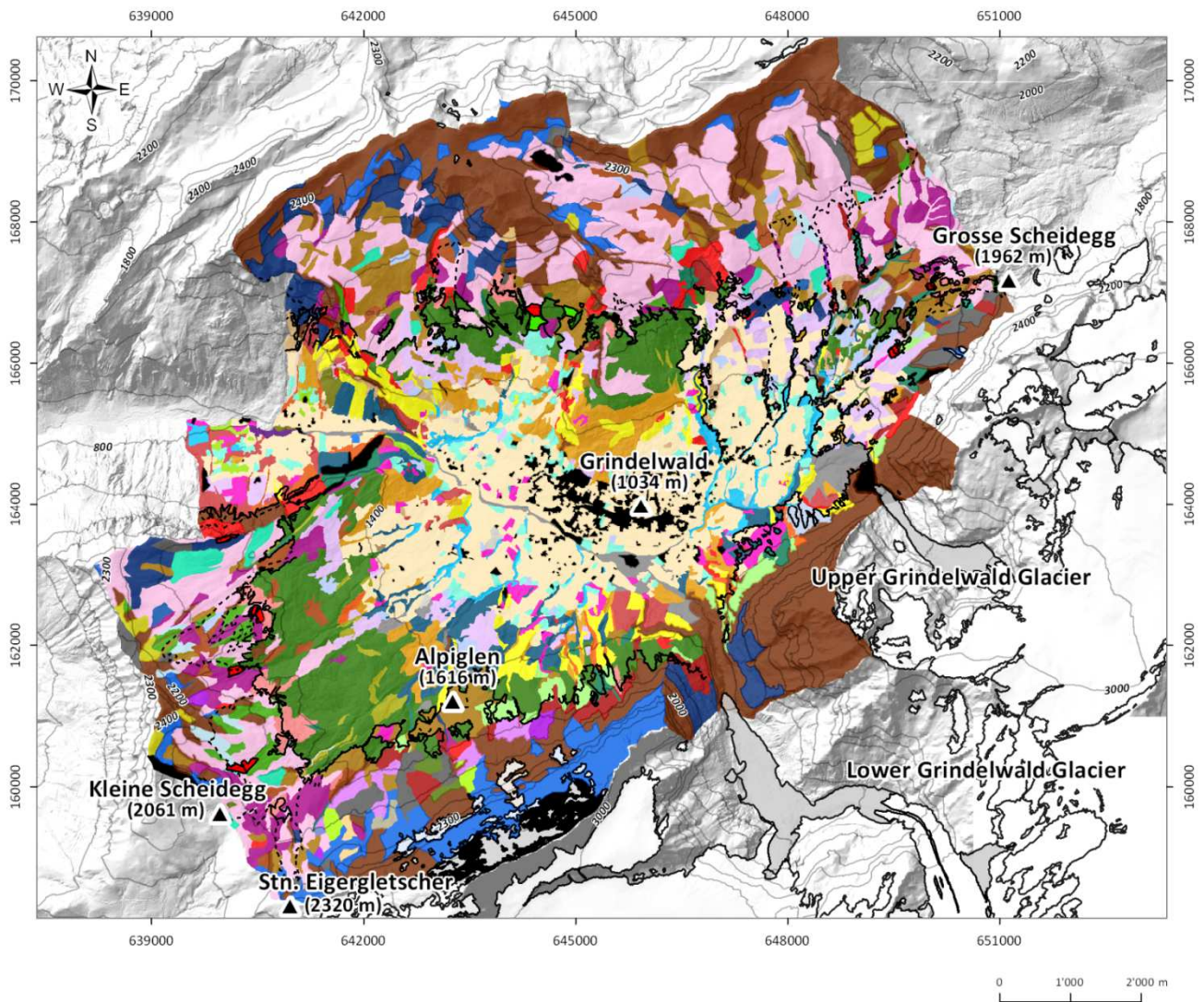
Figure A 2 Dominant plant communities in the whole region of Grindelwald. For the legend, see following pages (53-54).

Note: Abbreviation "V" stands for cohort and "A" for association.

Source: Hillshade and contours: Digitales Geländemodell 2m © swisstopo; actual forest limit, glacier debris and glacier area: VECTOR25 © swisstopo; vegetation: Hegg & Schneiter 1988; possible extend of future forest limit for whole region: Collet et al. 1938, Digitales Geländemodell 2m © swisstopo, Lawinenkataster des Kantons Bern © Abteilung Naturgefahren des Kantons Bern, Ereigniskataster NGKAT © Abteilung Naturgefahren, Amt für Wald des Kantons Bern, Landolt 2003, Holtmeier 2009; contours displayed for the selected altitudinal boundaries are according to tables 1 and 2 (page 17).

broadleaved forests

V: Fagion
A: Galio odorati-Fagetum luzuletosum
percentage out of all broadleaved forests: 2.1%

V: Fagion
A: Tilio-Fagetum
percentage out of all broadleaved forests: 7.4%

V: Fagion
A: Carici-Fagetum and Calamagrostio variae-Fagetum
percentage out of all broadleaved forests: 4.2%

V: Abieti-Fagion
A: Abieti-Fagetum festucetosum, Abieti-Fagetum luzuletosum, Abietetum festucetosum, Abieti-Piceetum mercurialietosum and Abieti-Piceetum dryopteridetosum
percentage out of all broadleaved forests: 40.1%

V: Lunario-Acerion
A: Ulmo-Aceretum, Arunco-Aceretum and Aceri-Fraxinetum tilietosum
percentage out of all broadleaved forests: 8.9%

V: Alno-Fraxinion
A: Aceri-Fraxinetum typicum
percentage out of all broadleaved forests: 37.3%

subalpine coniferous forests

V: Piceo-Abietion
A: Aceri-Piceetum mercurialietosum, Aceri-Piceetum aconitetosum vulpariae, Aceri-Piceetum chaerophylletosum cicutariae and Aceri-Piceetum calamagrostietosum variae
percentage out of all coniferous forests: 11.5%

V: Piceo-Abietion
A: Calamagrostio variae-Piceetum and Carici-Piceetum
percentage out of all coniferous forests: 13%

V: Vaccinio-Piceion
A: Myrtillo-Piceetum typicum, Myrtillo-Piceetum prenanthetosum and Asplenio-Piceetum
percentage out of all coniferous forests: 17%

V: Vaccinio-Piceion
A: Sphagno-Piceetum
percentage out of all coniferous forests: 0.2%

V: Vaccinio-Piceion
A: Veronico latifoliae-Piceetum, Homogyno-Piceetum typicum, Homogyno-Piceetum sphagnetosum and Homogyno-Piceetum asplenietosum
percentage out of all coniferous forests: 46.3%

V: Vaccinio-Piceion
A: Adenostylo-Piceetum
percentage out of all coniferous forests: 2.1%

V: Vaccinio-Piceion
A: Rhododendro-Pinetum sorbetosum chamaemespili and Rhododendro-Pinetum juniperetosum nanae
percentage out of all coniferous forests: 5.4%

V: Erico-Pinion
A: Erico-Pinetum mugi, Rhododendro hirsuti-Pinetum mugi typicum and Rhododendro hirsuti-Pinetum mugi betuletosum
percentage out of all coniferous forests: 4.6%

afforestation and natural growth

afforested area
percentage out of all increased forest areas: 72%

natural stage of growth (pioneer spruce forest with *Melampyrum sylvaticum*)
percentage out of all increased forest areas: 28%

shrubs

V: Alnion
A: Alnetum viridis adenostyletosum and Alnetum viridis rhododendretosum
percentage out of all shrubs: 33.9%

V: Salicion
A: Salicetum appendiculatae
percentage out of all shrubs: 9%

V: Corylion
A: Coryletum avellanae
percentage out of all shrubs: 2.2%

V: Alnion
A: Calamagrostio-Alnetum mercurialietosum, Calamagrostio-Alnetum stellarietosum, Calamagrostio-Alnetum petasitetosum, Calamagrostio-Alnetum scirpetosum and Salici-Alnetum incanae
percentage out of all shrubs: 54.2%

hedges and single bushes
percentage out of all shrubs: 0.7%

subalpine dwarf shrub heath

V: Rhododendro-Vaccinion
A: Rhododendro-Vaccinietum
percentage out of all subalpine dwarf shrub heath: 65%

V: Juniperion nanae
A: Junipero-Callunetum
percentage out of all subalpine dwarf shrub heath: 18%

V: Rhododendro-Vaccinion
A: Empetro-Vaccinietum
percentage out of all subalpine dwarf shrub heath: 3.6%

V: Loiseleurio-Vaccinion
A: Cetrario-Loiseleurietum
percentage out of all subalpine dwarf shrub heath: 0.4%

stocks of Dryadetum
percentage out of all subalpine dwarf shrub heath: 2%

V: Rhododendro-Vaccinion
A: stocks of Rhododendro hirsuti-mugetum
percentage out of all subalpine dwarf shrub heath: 11%

rich meadows and pastures

V: Arrhenatherion
A: Alchemillo-Arrhenatheretum, Anthrisco-Trisetetum and Phleo-Trisetetum
percentage out of all rich meadows and pastures: 58%

V: Cynosurion
A: Alchemillo-Cynosuretum
percentage out of all rich meadows and pastures: 8%

V: Cynosurion
A: Crepido-Cynosuretum and Crepido-Festucetum
percentage out of all rich meadows and pastures: 14%

V: Poion alpinae
A: Poetum alpinae
percentage out of all rich meadows and pastures: 1%

V: Poion alpinae
A: Crepido-Festucetum
percentage out of all rich meadows and pastures: 19%

thermophilic dry meadow

V: Mesobromion and Seslerio-Mesobromion

dry meadows on limestone

mixed stocks of Crepido-Festucetum-Nardetum

meager pastures

A: Agrostio-Festucetum rubrae and Alchemillo-Poetum alpinae

subalpine and alpine meadows

V: Nardion
A: Geo montani-Nardetum
percentage out of all subalpine and alpine meadows: 96.6%

V: Nardion
A: Luzulo-Nardetum
percentage out of all subalpine and alpine meadows: 3.1%

V: Nardion
A: Hypochoero-Nardetum
percentage out of all subalpine and alpine meadows: 0.3%

subalpine and alpine pastures

V: Seslerion
A: Oxytropo-Sesleretum, Astero-Seslerietum and Trifolio-Seslerietum
percentage out of all subalpine and alpine meadows: 66.9%

V: Caricion ferruginae
A: Festuco pulchellae-Caricetum ferrugineae and Heracleo-Caricetum ferrugineae
percentage out of all subalpine and alpine meadows: 24.8%

V: Caricion ferruginae
A: Arnica montana-Carex ferruginae and Sesleria coerulea-Carex sempervirens
percentage out of all subalpine and alpine meadows: 4.1%

V: Festucion variae
A: Trifolio-Festucetum violaceae
percentage out of all subalpine and alpine meadows: 4.2%

alpine grassland

V: Caricion firmae
A: Caricetum firmae
percentage out of all alpine grassland: 20%

V: Elynion
A: Elynetum
percentage out of all alpine grassland: 13%

V: Caricion curvulae
A: Caricetum curvulae
percentage out of all alpine grassland: 67%

peat bogs and swamps

neutral and basiphyle wet vegetation
A: Bartsio-Caricetum davallianae, Junco-Caricetum davallianae, Nardo-Caricetum pulicaris and Molinietum litoralis
percentage out of all peat bogs and swamps: 36%

V: Caricion fuscae
A: Caricetum fuscae and Valeriano-Caricetum fuscae
percentage out of all peat bogs and swamps: 52%

V: Molinion
A: Trollio-Cirsietum, Polygono-Cirsietum, Scirpetum silvaticae and Filipendulo-Juncetum inflexi
percentage out of all peat bogs and swamps: 11%

wet vegetation general not further defined
percentage out of all peat bogs and swamps: 1%

subalpine and alpine mega forbs

V: Adenostylion
A: Adenostylo-Cicerbitetum, Calamagrostietum villosae, Calamagrostietum variae, Brachypodietum pinnatae, Chaerophylletum villarsi and Trifolietum medii
percentage out of all subalpine and alpine mega forbs: 86%

V: Epilobion angustifolii
A: Epilobietum angustifoliium
percentage out of all subalpine and alpine mega forbs: 14%

richly manured alpine pasture

V: Rumicion alpini
A: Rumicetum alpini, Cirsietum spinosissimi and Poetum supinae

snow pocket vegetation

A: Salicetum herbaceae, Salicetum retuso-reticulatae, Arabido-Rumicetum nivalis, Polytrichetum sexangularis and Poo-Cerastietum cerastoidis

rock and debris vegetation

A: Androsacetum helveticae, Potentillo-Hieracietum humilis, Asplenio-Primuletum hirsutae, Sedo-Sclerathion, Dryopteridetum robertianae, Petasitetum paradoxi, Athamanto-Trisetetum distichophylli, Thlaspietum rotundifolii, Leontodontetum montani, Androsacetum alpinae, Oxyretum digynae and Tussilago-Flur

not defined units

glacier debris area

glacier area

hillshade illumination value
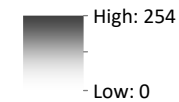
High: 254

Low: 0

contours displayed for the following altitudinal boundaries:
1400 m a.s.l. upper limit of broadleaved forests
1800-2000 m a.s.l. forest limit / timber line
2200-2300 m a.s.l. tree limit / treeline
2400 m a.s.l. Krummholz limit
3000 m a.s.l. nival belt, snow line

current forest limit
possible extend of future forest limit for whole region

The nomenclature of plant communities for the cohort level corresponds to the publication "Lebensräume der Schweiz" (Delarze & Gonseth 2008).

For the association level, the nomenclature of plant communities corresponds to the publication and data file "Die Vegetation als Grundlage von Alp-und Forstwirtschaft, Tourismus und Naturschutz im MAB-Testgebiet Grindelwald" (Hegg & Schneiter 1988) and to the publication "Die subalpinen Zwergstrauchgesellschaften im Einzugsgebiet der Aare" (Schweingruber 1972). The percentage values calculated for an association are taken from the AREA column (showing m^2 values) in the attribute table "DVEG1" (Hegg & Schneiter 1988).

The nomenclature "Geo montani-Nardetum" was applied according to the publications "Übersicht über die Pflanzengesellschaften Rätiens" (Braun-Blanquet 1948/1949) and "Lebensräume der Schweiz" (Delarze & Gonseth 2008). Hegg & Schneiter (1988) identifies this plant community as Sieversio-Nardetum. However, the plant species content within the plant community remains unchanged between the two different designations of nomenclature.

Table A 39 Land-use practices in the region of Grindelwald

intensively used agricultural land: 24%		cultivated area (24%)
vegetation	**in [m^2]**	
thermophilic dry meadow	758803.062	
dry meadows on limestone	1267193.969	
rich meadows and pastures	20893946.68	
total area of cultivated fields	**22919943.72**	
extensively used agricultural land: 14%		total area of pastures, meadows and grassland (20%)
vegetation	**in [m^2]**	
Elynetum	98979.088	
Geo montani-Nardetum	12503947.56	
Luzulo-Nardetum	399042.192	
Hypochoero-Nardetum	38301.254	
Caricetum curvulae	516640.638	
Trifolio-Festucetum violaceae	195545.323	
total area of extensive used land	**13752456.05**	
lean pastures: 6%		
vegetation	**in [m^2]**	
meager pastures	1108560.325	
Seslerion	2509376.216	
occasionally grazed Seslerion	632142.888	
Caricion ferruginae	1164310.46	
Arnica montana-Carex ferruginae	193455.212	
Caricetum firmae	151819.407	
total area of lean pastures	**5759664.508**	

Source: Hegg & Schneiter 1988; Käsermann 2007. Nomenclature of plant communities is applied according to Hegg & Schneiter 1988 and Delarze & Gonseth 2008.

Table A 40 Geological time scale in the study region, modified according to Collet et al. 1938 and Käsermann 2007

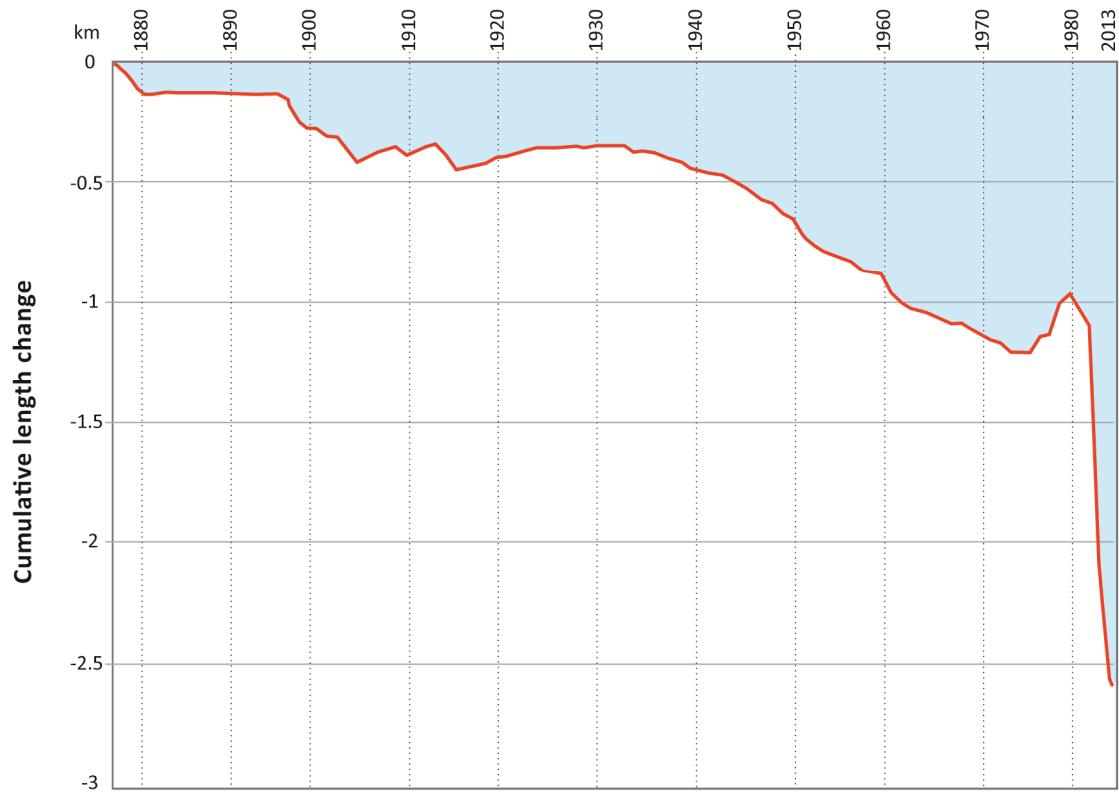| era	period	epoch	age (mio. years)	stratigraphy & lithogenesis			
Cainozoic	Quaternary	Holocene	0.01	**Quaternary features** -slope debris -rock fall & scree material -settling & landslides -aggradation & alluvial terrace			Post-glacial period
Cainozoic	Quaternary	Pleistocene	1.75	-moraines with ramparts of present glaciers (e.g. Eiger glacier, Lower & Upper Grindelwald Glacier) -local moraines (deposits from local glaciers of Männlichen & Faulhorn chains) -moraines with ramparts of the main glacier (glacial debris)			Glacial period
Cainozoic	Tertiary	Pliocene	5	**Paraautochthonous imbrication** -Flysch -coalic limestones -quarzit -Mürren limestone breccias -Bohnerz formation (siderolithic breccias, e.g. Grindelwald marble)			Main alpine folding
Cainozoic	Tertiary	Miocene	24				Main alpine folding
Cainozoic	Tertiary	Oligocene	37				Main alpine folding
Cainozoic	Tertiary	Eocene	58				
Cainozoic	Tertiary	Paleocene	65				
Mesozoic	Cretaceous	Upper Cretaceous	98	-Hauterivien (sandy limestones) -Berriacien (Oehrli-limestones) -Malm limestones -Argovien breccias (limestones & schists)	**Ultrahelvetic nappe (Doldenhorn)** -Wildflysch (clay-slate interspersed with unregulraly often tectonically disrupted by sandstone benches)	**Helvetic nappe (Wildhorn)** -Berriasien-marl -Argovien-limestones -Argovien-Callovien-schists -Bajocien-Echinodermen breccia -Bajocien-sandy limestones -iron sandstone (gnarled, sandy and irony slate) -Aalenian schist (clay-slate with iron content)	Initial alpine folding
Mesozoic	Cretaceous	Lower Cretanous	140				Initial alpine folding
Mesozoic	Jura	Malm	160				Initial alpine folding
Mesozoic	Jura	Dogger	175				Initial alpine folding
Mesozoic	Jura	Lias	203	Lias depositions are not existent because of emersion			Initial alpine folding
Mesozoic	Trias	Keuper	230	Trias & Perm are also only partly existent due to degradation during the Lias-drainage			Initial alpine folding
Mesozoic	Trias	Muschelkalk	240				
Mesozoic	Trias	Bunter sandstone	245				
Paleozoic	Permian	not itemized	290	**Autochthonous Aar massif** Crystallin -Innertkirchner Granite (ortho-rock going over to mixed gneiss) -Erstfelder Gneiss (ortho-rock, parly going over to mixed gneiss) -Lötschental-Fernigen-schists (mixed gneiss)			Hercynic folding
Paleozoic	Carbon	not itemized	360				Hercynic folding
Paleozoic	Devonian	not itemized	408				Hercynic folding
Paleozoic	Silurian	not itemized	438				Hercynic folding
Paleozoic	Ordovician	not itemized	500				Hercynic folding
Paleozoic	Cambrian	not itemized	570				Hercynic folding

Figure A 3 Cumulative length change of glacier tongue of the Lower Grindelwald Glacier since A.D. 1879
Source: Glaciological reports 1881-2009; Holzhauser & Zumbühl 2003
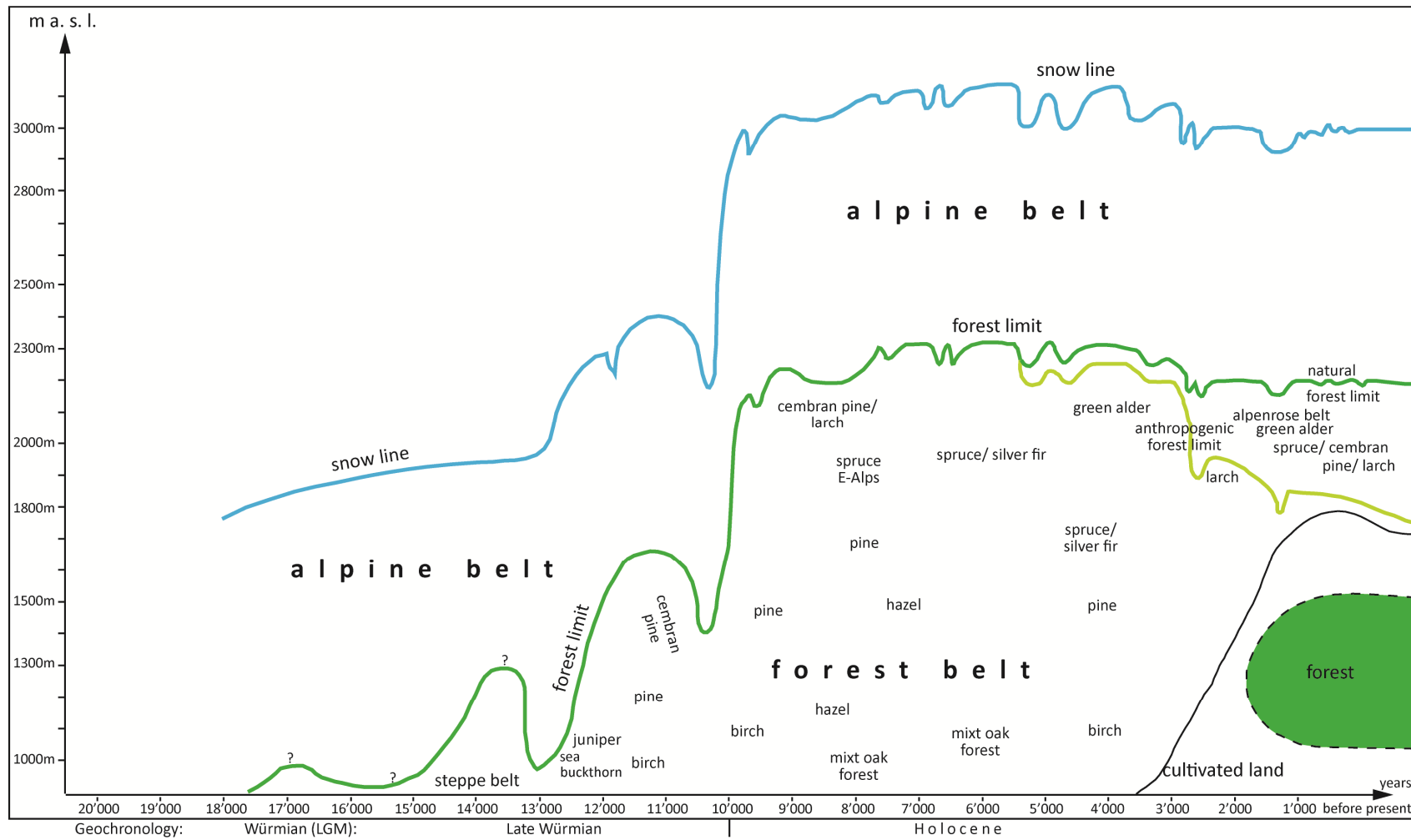
Figure A 4 Development of the Central Alpine forest belt of the Central Grisons since the Late Würmian
Source: Modified according to Burga C. A. (1999)

Table A 41 Scheme relating dominant geological features of the study region to pedogenesis, soil type, land cover and type of plant community

geology	substrates & components	soils	location	land cover
Quaternary -landslide	→ coarsely-finely grained material → instable → badly weathering	→ neutral-basic → immature soils (e.g. rendzina, syrosem-rendzina)	locally distributed between Alpiglen & Kleine Scheidegg	rock, sand, scree alternating with pasture, meadow
Quaternary -debris	→ coarsely-finely grained loose material → instable → badly weathering	→ neutral-basic → immature soils (e.g. rendzina, syrosem-rendzina)	locally distributed between Alpiglen & Kleine Scheidegg	rock, sand, scree alternating with pasture, meadow
Quaternary -moraine	→ coarsely-finely grained material → stable → weathering weathering intensity depending on grain size of fraction	→ neutral-basic → cambisols & podsols	widely spread along smooth slopes between Kleine Scheidegg & Grindelwald	forest, open forest, shrubs, bushes, pasture with shrubs, grassland, farmland
Tertiary -Flysch	→ rapid change of strata → alternating grained fraction (clay-larger stones) → instable → mean weathering intensity	→ rather acid → regosol & acidic cambisol	only in small-areas & often folded in the Doldenhorn-nappe at the base of the Eiger, Mättenberg & Wetterhorn	pasture, meadow, pasture with shrubs
Tertiary -coalic limestones -limestone breccia	→ massive chalks → coarse grained fraction → tough → badly weathering	→ neutral-basic → lime cambisol, regosol and immature soils (e.g. rendzina, humic soils)	steep north-facing walls of Eiger, Mättenberg & Wetterhorn	rock, sand, scree alternating with pasture, meadow
Mesozoic -iron sandstones	→ quarz-rich sand stone → fraction with mean grain size (e.g. sand & gravel) → mean weathering intensity	→ sour → regosols & cambisols, partly also podsols	smooth slopes between Grindelwald and Kleine Scheidegg	forest, open forest, pasture with shrubs
Mesozoic -Aalenian schists	→ mixed schistous & quarz material → fine grained fraction (clay & silt) → easy weathering	→ rather sour → cambisols & podsols	smooth slopes between Grosse and Kleine Scheidegg	forest, open forest, pasture with shrubs, pasture, meadow

Source: Geological features: Collet et al. 1938; soil and land cover type: Arealstatistik 1992/97, © BFS GEOSTAT; soil nomenclature and identities: Scheffer et al. 2010

Table A 42 Grain type and grain diameter (equivalent diameter) for substrates and components of the bedrock

	fine grained		intermediate	coarse grained	
grain type	clay	silt	sand	gravel	block
grain diameter (equivalent diameter)	63 nm-2 µm	2-63 µm	63 µm-2 mm	2 mm-63 mm	2 dm-6.3 dm

Source: Scheffer et al. 2010

Table A 43 Most important plant communities at the timber-line ecotone of the study region in relation to climate, soil and land use intensity

plant communities \ factors	climate	soil	vegetation	cultivation	location
Subalpine Norway spruce forest communities (e.g. Homogyno-Piceetum typicum)	→ mean humidity	→ acid → profoundity dependent to parent material	→ trees, shrubs & herbs → acid indicators (e.g. *Vaccinium myrtillus*)	minor influence, e.g. pasturing	dominant throughout the whole study region, smooth mean steep slopes from Grindelwald towards 1500-1600 m elevation
Subalpine dwarf shrub heath (e.g. Rhododendro-Vaccinietum)	→ humid	→ acid → rich in humus → oligotroph	→ shrubs, herbs & mosses → acid indicators (e.g. *Rhododenron ferrugineum*) → the upper boundary of *Rhododendron ferrugineum* gives rise about the potential forest limit	extensive pasturing without maintenance	dominant at the timber-line in depressions with large & long-lasting snow cover → Rhododendro hirsuti-mugetum (on limestone rich slopes, e.g. Eiger, Mettenberg, Wetterhorn, Schwarzmönch)
Subalpine dwarf shrub heath (e.g. Loiseleurio-Vaccinion)	→ windy → extremely low temperatures (max. -40 °C) → short snow cover duration (max. 3 month)	→ very acid → immature soils with shallow layer	→ short growing plant species, i.e. herbs & mosses –highly adapted to strong winds & desiccation –acid indicators (e.g. *Loiseleuria procumbens*)	no land use	occurs seldom as continous layer, forms at peaks or ridges, e.g. Männlichen, local mosaics with adjacent vegetation types
Subalpine green alder shrubs (e.g. Alnetum viridis adenostyletosum)	humid	→ profound → eutrophic clay-rich & immature soils	→ pattern dominated by *Alnus viridis* shrubs → highly adapted to erosion, avalanches & capable to bind nutrients → opulent herb layer with nutrient indicator plants (e.g. *Adenostyles alliariae*)	unmanaged pastures	dominant on steep slopes prone to landslides & surface processes in the subalpine belt (1500 m a.s.l.) towards the timber-line
Subalpine and alpine mega forbs (e.g. Adenostylo-Cicerbitetum)	humid	→ profound → humid → ventilated → nutrient rich & alkaline soils	→ tall growing perennial herbs & mosses → nutrient indicator plants (e.g. *Adenostyles alliariae*) → form mosaics with adjacent plant species of forests or Alnetum viridis	not regularly mowed or grazed	scattered occurence in: → depressions with long-lasting snow cover → areas with forest openenings, north-facing shaded slopes, prone to avalanche activity
Subalpine and alpine meadows (e.g. Poetum alpinae)	mesophilous	→ humid → nutrient rich → alkaline soils	→ dense herbal cover → nutrient indicator plants (e.g. *Poa alpina*) → forms mosaics with adjacent vegetation of Geo montani-Nardetum	occationally fertilized	not frequent & dominant on lightly inclined slopes with long-lasting snow cover at Busalp, between First & Grosse Scheidegg, Alpiglen

Source: Käsermann 2007; nomenclature plant communities: Braun-Blanquet 1948/1949, Schweingruber 1972, Hegg & Schneiter 1988 and Delarz & Gonseth 2008

Table A 43 (continued)

plant communities \ factors	climate	soil	vegetation	cultivation	location
Subalpine and alpine meadows (e.g. Geo montani-Nardetum)	mesophilous	acid & meager soils	→ tufted herbal cover → meagerness indicator plants (e.g. *Nardus stricta*) → forms mosaics with adjacent vegetation of dwarf shrub heath, Poetum alpinae or Caricetum curvulae	non-fertilized, extensive used	widely spread along smooth slopes in the subalpine and alpine belt on strongly acidifying clay-slate & iron sandstones
Subalpine and alpine pastures (e.g. Caricion ferrugineae)	mesophilous	→ moistened → nutrient rich & alkaline soils	→ tall growing meadows → humid indicator plants (e.g. *Carex ferruginea*)	extensively used pastures & hay crop	dominant on N-facing, steep slopes (1600-2300 m a.s.l.) towards Wetterhorn, Eiger north-wall on clay-rich & skelletous substratum
Peat bogs and swamps (e.g. Caricetum fuscae)	moist & high precipitation amount	moistened, acid, nutrient-poor soils	nutrient-poor indicator plant species (e.g. *Eriophorum vaginatum*)	no land use	occurs in scattered areas east of Männlichen, near Kleine and Grosse Scheidegg on water-impermeable clay-slate, iron sandstones, Flysch
Rock and debris vegetation on limestone (e.g. Thlaspietum rotundifolii)	short vegetation period, approx. 4-5 month	→ immature soils → high skellet content → nutrient-poor	→ low vegetation cover (< 10 %) → pioneer-vegetation, highly adapted to continuous changes by debris movements → rich plant species diversity	no land use	frequent in scattered areas along debris slopes on Malm limestones & Oehrli limestones between 1900 & 2500 m a.s.l.

Table A 44 The altitudes of former timber line for 1861, current timber line for 2007 and expected timber line for 2107 are displayed as interpolated average values.
Note: Results show in all cases an altitude of the actual timber line located far below the potential altitude of timber line for the Northern Swiss Alps.

year	1861	2007	2107
timber line altitude [m a.s.l.]	1612	1643	1639

Source: Digitales Geländemodell 2m © swisstopo, VECTOR25 © swisstopo, DUFOUR © swisstopo, Lawinenkataster des Kantons Bern © Abteilung Naturgefahren des Kantons Bern, Ereigniskataster NGKAT © Abteilung Naturgefahren, Amt für Wald des Kantons Bern, Collet et al. 1938, Landolt 2003, Holtmeier 2009

The altitudes of the timber line shown, for 1861 and 2007 are interpolated average values and have been calculated with ESRI ArcGIS algorithms out of all highest reached areas of forest for each year. The expected altitude of the timber line for 2107 has been calculated with ESRI ArcGIS algorithms and represents a calculated average value out of the expected future extent of the forest limit. The resulting value is somewhat below the forest limit recorded in 2007, and its altitudinal limit is expected to be determined by local site conditions (surface topography and substrate).
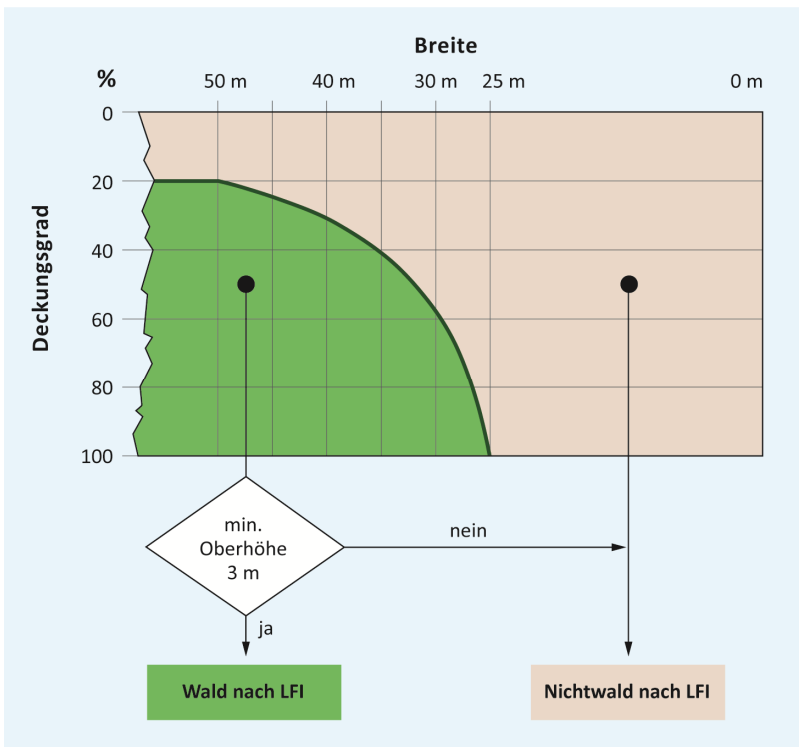
Figure A 5 Definition of forest according to the Swiss National Forest Inventory (LFI)
Source: Modified according to Brändli (2010)

The Swiss National Forest Inventory (LFI) records the main basic data on forests. The LFI publishes a sample inventory, carried out by the Swiss Federal Office of Forest, Snow and Landscape, that reports the conditions of forests in Switzerland. Areas are defined according to the LFI into: forest, shrubby forest and non-forest. The forest definition is based on the area of forest stands, forest width and the height of timber. The minimum requirement for a surface to be defined as forest is illustrated by the curve, which shows the relation between forest width and the area of canopy cover. For example, a surface is defined as forest, when the canopy area covers at least 20% of the ground area for forest stands ≥ 50 m wide, whereas smaller forest stands (e.g. 25-50 m wide) cover at least 60% of ground area.

A.8 Vegetation records from master thesis

Table A 45 GPS coordinates and habitat properties for vegetation relevés recorded in the Geo montani-Nardetum grassland

sample ID	plot size [m²]	coordinates		altitude [m a.s.l.]	slope [%]	exposition	geology & substrate	defined category of vegetation unit
		x	y					
1	4	639525	159242	2130	25	SW	Mesozoicum Aalenian schists	Geo montani-Nardetum transition form with ericaceous dwarf shrubs
2	4	639054	159003	2146	15	SW	Mesozoicum Aalenian schists	disturbed Geo montani-Nardetum
3	4	638502	158856	2130	25	SW	Mesozoicum Aalenian schists	non-disturbed Geo montani-Nardetum
4	4	634460	157088	1933	15	NE	Mesozoicum Aalenian schists	disturbed Geo montani-Nardetum
5	4	634465	157097	1933	20	NE	Mesozoicum Aalenian schists	Geo montani-Nardetum transition form with ericaceous dwarf shrubs
6	4	639545	159222	2134	20	SW	Mesozoicum Aalenian schists	Geo montani-Nardetum transition form with ericaceous dwarf shrubs
7	4	639430	159100	2154	20	SW	Mesozoicum Aalenian schists	Geo montani-Nardetum transition form with ericaceous dwarf shrubs
8	4	639418	159102	2139	45	SW	Mesozoicum Aalenian schists	Geo montani-Nardetum transition form with ericaceous dwarf shrubs
9	4	639122	158977	2152	5	SW	Mesozoicum Aalenian schists	Geo montani-Nardetum transition form with ericaceous dwarf shrubs
10	4	639052	159021	2148	2-3	SW	Mesozoicum Aalenian schists	disturbed Geo montani-Nardetum
11	4	639041	159011	2150	2	SW	Mesozoicum Aalenian schists	non-disturbed Geo montani-Nardetum
12	4	639009	159016	2142	3	SW	Mesozoicum Aalenian schists	disturbed Geo montani-Nardetum
13	4	639016	159033	2150	2	SW	Mesozoicum Aalenian schists	disturbed Geo montani-Nardetum
14	4	638522	158849	2149	5	SW	Mesozoicum Aalenian schists	Geo montani-Nardetum transition form with ericaceous dwarf shrubs
15	4	638502	158856	1916	5	SW	Mesozoicum Aalenian schists	disturbed Geo montani-Nardetum
16	4	638463	158856	1932	5-6	SW	Mesozoicum Aalenian schists	Geo montani-Nardetum transition form with ericaceous dwarf shrubs

Table A 45 (continued)

sample ID	plot size [m²]	coordinates		altitude [m a.s.l.]	slope [%]	exposition	geology & substrate	defined category of vegetation unit
		x	y					
17	4	638224	158579	1896	5	SW	Mesozoicum Aalenian schists	Geo montani-Nardetum transition form with ericaceous dwarf shrubs
18	4	634454	157067	1930	5	NE	Mesozoicum Aalenian schists	non-disturbed Geo montani-Nardetum
19	4	634397	157088	1915	5	SW	Mesozoicum Aalenian schists	Geo montani-Nardetum transition form with ericaceous dwarf shrubs
20	4	634349	157113	1920	3-4	NE	Mesozoicum Aalenian schists	Geo montani-Nardetum transition form with ericaceous dwarf shrubs
21	4	634499	157560	1902	4-5	SE	Mesozoicum Aalenian schists	Geo montani-Nardetum transition form with ericaceous dwarf shrubs
22	4	634344	157124	1913	5	NE	Mesozoicum Aalenian schists	disturbed Geo montani-Nardetum
23	4	639052	159021	1905	5	NE	Mesozoicum Aalenian schists	Geo montani-Nardetum transition form with ericaceous dwarf shrubs
24	4	634348	157136	1903	3	NE	Mesozoicum Aalenian schists	disturbed Geo montani-Nardetum
25	4	634463	157069	1942	6	SE	Mesozoicum Aalenian schists	Geo montani-Nardetum transition form with ericaceous dwarf shrubs
26	4	634905	157497	1893	3	SE	Mesozoicum Aalenian schists	disturbed Geo montani-Nardetum
27	4	634497	157065	1880	6	SE	Mesozoicum Aalenian schists	non-disturbed Geo montani-Nardetum
28	4	634450	157060	1942	8	SE	Mesozoicum Aalenian schists	non-disturbed Geo montani-Nardetum
29	4	634580	157645	1901	2-3	SE	Mesozoicum Aalenian schists	Geo montani-Nardetum transition form with ericaceous dwarf shrubs
30	4	634675	157302	1873	3	SE	Mesozoicum Aalenian schists	Geo montani-Nardetum transition form with ericaceous dwarf shrubs

Table A 46 Field data for vegetation relevés recorded in the Geo montani-Nardetum grassland

sample ID	Poaceae [%]	Cyperaceae, Juncaceae [%]	Liliaceae, Orchidaceae [%]	Fabaceae [%]	Dicotyledonae [%]	Pteridophyta [%]	mosses & lichens [%]	woody plants [%]	total number of flowering plants, ferns, mosses & lichens
1	45	5	1	5	20		< 1	25	26
2	70	< 1	1	< 1	30			< 1	14
3	60	7	2	10	18		< 1	< 1	27
4	60	10	< 1	5	30				20
5	50	5-6	2	5	30			7-8	24
6	30	10	5	5	25			23	22
7	40	20	4	5	20			10	22
8	40	15	3	5	25			10	19
9	45	5	5		35		< 1	9-10	24
10	70	5	< 1		30				19
11	65	5	1		28			< 1	26
12	70	10	3		25				17
13	60	3-4	2		30				18
14	65	15	4-5	2-3	20			10	32
15	50	5	< 1	5	42		< 1	< 1	27
16	40	5	1	1	30		1-2	10	27

Table A 46 (continued)

sample ID	Poaceae [%]	Cyperaceae, Juncaceae [%]	Liliaceae, Orchidaceae [%]	Fabaceae [%]	Dicotyledonae [%]	Pteridophyta [%]	mosses & lichens [%]	woody plants [%]	total number of flowering plants, ferns, mosses & lichens
17	70	5	2	< 1	30		< 1	10	25
18	60	5	1-2	5-6	40			< 1	30
19	50	5	2		40			10	26
20	65	3-4	< 1	3-4	30		< 1	8	20
21	30	3	< 1	3-4	30		< 1	30	25
22	50	5		3-4	40		2-3		19
23	70	5		3-4	25		1-2	8	17
24	65	5	< 1		25		< 1		18
25	50	5	1	4-5	37		1	10	35
26	70	5		4-5	30			< 1	16
27	50	2-3	1-2	5	45			< 1	31
28	40	4-5	1-2	5	45			< 1	32
29	30	2		1-2	15		1-2	40	26
30	30	1		1-2	15		2	45	23

Table A 47 GPS coordinates and habitat properties for vegetation relevés recorded in the subalpine dwarf shrub heath (Alnetum viridis and Rhododendro ferruginei-Vaccinietum)

sample ID	plot size [m²]	coordinates		altitude [m a.s.l.]	slope [%]	exposition	substrate	defined category of vegetation unit
		x	y					
1	100	634185	157142	1886	45	NW	Mesozoicum Aalenian schists	disturbed Alnetum viridis
2	100	634125	157199	1885	45	NE	Mesozoicum Aalenian schists	non-disturbed Alnetum viridis
3	100	634258	157348	1816	10	NE	Mesozoicum Aalenian schists	disturbed Rhododendro ferruginei-Vaccinietum
4	100	634667	157652	1877	25	NE	Mesozoicum Aalenian schists	non-disturbed Rhododendro ferruginei-Vaccinietum
5	100	638001	158486	1820	15	NW	Mesozoicum Aalenian schists	disturbed Alnetum viridis
6	100	638001	158802	1832	45	SW	Mesozoicum Aalenian schists	non-disturbed Alnetum viridis
7	100	637815	162557	1846	30	SW	Mesozoicum Aalenian schists	disturbed Alnetum viridis
8	100	637930	161720	1507	45	NW	Mesozoicum Aalenian schists	disturbed Alnetum viridis
9	100	634815	158121	1825	35	NE	Mesozoicum Aalenian schists	non-disturbed Rhododendro ferruginei-Vaccinietum
10	100	638038	159815	1734	25	NW	Mesozoicum Aalenian schists	non-disturbed Alnetum viridis

Table A 48 Field data for vegetation relevés recorded in the subalpine dwarf shrub heath (Alnetum viridis and Rhododendro ferruginei-Vaccinietum)

sample ID	trees[%]	shrubs [%]	herbs [%]	pteridophytes[%]	mosses & lichens[%]	total number of flowering plants, ferns, mosses & lichens
1		70	30	5	< 1	38
2		60	30	5	1	44
3	2	65	25	1	5-6	38
4	1-2	70	25		5	28
5		60	30	3-4	2-3	37
6		70	25	3	1-2	41
7	2	70	35	1-2	1-2	34
8	3	60	40	5	1-2	36
9		70	25		2-3	36
10	1-2	70	20	5	1-2	44

Table A 49 Changes in the positions of forest, tree and dwarf shrub limits. Comparison between Lüdi (1921) and our own records of 2005. The largest changes are marked in bold.

		forest limit		
location	exposure	1920 [m a.s.l.]	2005 [m a.s.l.]	difference 1920-2005 [m a.s.l.]
right valley side of Stechelberg				
Grindegg near Wengen	S & SW	2020	2030	+ 10
Grindegg near Wengen	N	1830	1850	+ 20
Männlichen below Hotel	W	2030	2035	+ 5
Männlichen below Tschuggen	W	1850	1880	+ 30
Girmschbiel	N	1820	1850	+ 30
Girmschbiel	S	1895	1913	+ 18
Steineggwald	S	1950	1965	+ 15
left valley side of Stechelberg				
Pletschenalp	E	1900	1923	+ 23
Pletschenalp	SE	1920	1925	+ 5
Dorrenhubel	N	1830	1830	0
Dorrenhubel	S	1895	1896	+ 1
Allmihubel-Hartwänge	E	1920	1955	**+ 35**
Mürrenbach-Blumental	E	1810	1826	+ 16
		tree limit		
location	exposure	1920 [m a.s.l.]	2005 [m a.s.l.]	difference 1920-2005 [m a.s.l.]
right valley side of Stechelberg				
Grindegg near Wengen	S & SW	2020	2030	+ 10
Grindegg near Wengen	N	1910	1923	+ 13
Männlichen below Hotel	W	2080	2136	**+ 56**
Männlichen below Tschuggen	W	2030	2120	**+ 90**
Steineggwald	N	1920	1962	**+ 42**
Steineggwald	S	2000	2000	0
left valley side of Stechelberg				
Pletschenalp	SE	1990	2001	+ 11
Allmihubel-Hartwänge	SE	2060	2080	+ 20
Mürrenbach-Blumental	E	1860	1899	**+ 39**
		dwarf shrub limit		
location	exposure	1920 [m a.s.l.]	2005 [m a.s.l.]	difference 1920-2005 [m a.s.l.]
right valley side until Stechelberg				
Männlichen below Hotel	W	2050	2070	+ 20
Wengernalp	S & SE	2170	2200	**+ 30**
left valley side until Stechelberg				
Pletschenalp	E	2100	2120	+ 20
Allmihubel-Hartwänge	NE & SE	2120	2126	+ 6