Vegetation changes at the timberline ecotone of the Lauterbrunnen valley, Bernese Oberland, Switzerland

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This case study explores vegetation dynamics to understand whether changes at the timberline ecotone have been caused by land-use changes or by a warmer atmosphere. The Lauterbrunnen valley (northern Swiss Alps) has been chosen for this study, because existing vegetation data goes back to 1920, allowing the detection of changes over a baseline of 85 years. Vegetation mapping and plant relevés were used to analyze the vegetation dynamics of selected areas and to distinguish changes that are a probable response to global warming from those caused by changes in land-use activity. In July and August 2005, vegetation surveys were made in subalpine and alpine grassland (Geo montani-Nardetum) at sites which had already been studied by Lüdi in 1920. The results showed a significant surface increase in spruce forest and an advance of the tree limit to higher elevation at several sites, with highest values of +90 m near the Männlichen Mountain (2343 m a.s.l.). Because most plotted Geo montani-Nardetum sites (53 %) have been attributed to heath facies, we propose, in agreement with other studies, that these vegetation dynamics are driven mostly by reduction in land-use activity rather than by climate warming.

Vegetationsänderungen am Waldgrenzökoton des Lauterbrunnentales (Berner Oberland, Schweiz). **Die Fallstudie untersucht die Vegetationsdynamik des Waldgrenzökotons, um abzuklären, inwieweit Veränderungen durch veränderte Landnutzung oder durch Klimaerwärmung verursacht worden sind. Das Lauterbrunnental (nördliche Schweizer Alpen) ist für diese Studie gewählt worden, weil Vegetationsdaten bis zurück zum Jahr 1920 vorhanden sind, was eine Analyse über einen Zeitraum von 85 Jahren hinweg erlaubte. Methodisch wurden Vegetationskartierung und Vegetationsaufnahmen angewandt, um die Vegetationsdynamik an ausgewählten Untersuchungsgebieten zu analysieren und dadurch Veränderungen bedingt durch die Klimaerwärmung, von denjenigen, bedingt durch die Änderungen in der Landnutzung unterscheiden zu können. Im Juli und August 2005 wurden Vegetationserhebungen in den subalpinen und alpinen Weiden (Geo montani-Nardetum) an Standorten durchgeführt, die bereits von Lüdi 1920 studiert worden waren. Die Ergebnisse haben gezeigt, dass der subalpine Fichtenwald bedeutend an Fläche zugenommen hat und dass sich die Baumgrenze an mehreren Standorten nach oben verschoben hat, mit höchsten Werten von +90 m in der Nähe des Männlichen (2343 m ü. M.). Weil die meisten kartierten Flächen von Geo montani-Nardetum (53 %) der Variante mit Zwergsträuchern zugeordnet werden mussten, schlagen wir in Übereinstimmung mit anderen Studien vor, dass diese Vegetationsveränderungen grösstenteils durch nachlassende Landnutzung und weniger durch die globale Klimaerwärmung gesteuert werden.**

Keywords
Alpenrose dwarf shrub heath, anthropo-zoogenic impacts, Braun-Blanquet (1964) vegetation mappings, alpine timberline ecotone, forest vegetation succession

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Over the past 100 years global warming (+0.6 °C) has strongly affected landscape and vegetation in many regions of the Earth (IPCC 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 2006). In particular, 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 that provide a rich source of data reaching far back into the last century (Lüdi 1921; Ozenda 1988; Burga & Perret 1998; Kullmann 2000; Walther et al. 2005; Aeschimann et al. 2011, 2013). The study of plant species migrations to higher elevations has been shown to be relevant to understanding the effect of global climate warming, because plant growth is strongly dependent on temperature (Körner 2003). Previous studies have shown that the effect of plant species migration to higher elevation is 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: an increase in species diversity on high summits, a process of thermophilization of the vegetation at high elevation, and a change in the phytodiversity and ecological behavior of a habitat (Braun-Blanquet 1957; Hofer 1992; Burga & Perret 1998; Carraro et al. 2001; Grabherr et al. 2001; Theurillat & Guisan 2001; Burga et al. 2003; 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. 2005; Burga et al. 2007). In addition, other studies have shown that timberlines have shifted in direct response to the global warming effect in several mountain regions during the last 100 years (Tranquillini 1979; Burga & Perret 1998; Körner 1998; Kullmann 2000; Perret 2005; Hoch & Körner 2009; Körner 2012). In the Russian Polar-Ural, for example, where human impact is low, the timberline has climbed by 60–80 m (Moiseev & Shiyatov 2003). In the Alps, however, large areas have been affected by anthropo-zoogenic impacts, such as wood clearings and pasture activity. As a result, the timberline has been lowered from its potential value by about 300–400 m to a current elevation of 1800–2000 m a.s.l. (northern Swiss Alps) (Hegg 1984 a, b; Burga 1988; Burga & Perret 1998; Perret 2005; Holtmeier 2009).

Existing studies have mostly focused on monitoring mountain flora at several mountain peaks by comparing old with new vegetation records. None of these studies has yet considered historical vegetation maps, which show vegetation change as a dynamic process and can distinguish between changes attributable to land use and those in response to climate change.

Study purpose and working hypothesis

The aim of this study was to show the importance of vegetation as a dynamic process by assessing the effects of current vegetation dynamics at the Alpine timberline of the Lauterbrunnen valley. We studied the effect of global warming and changes in land-use activity by comparing: **a** the vegetation pattern of subalpine and alpine vegetation and **b** the occurrence of single spruce trees within the timberline ecotone of selected areas of the Lauterbrunnen valley with Lüdi's mapping of the 1920s (Lüdi 1921). Thanks to Lüdi's detailed vegetation study of the

1920s, the dynamics of vegetation boundaries in the Lauterbrunnen valley can be studied over the last 85 years, a period when global climate warming has taken effect. This study seeks to answer the question: To what extent is the vegetation pattern of the timberline ecotone affected by non-disturbed processes, in probable response to global warming, and to what extent by disturbed processes, in response to overgrazing? To perform this study, we diagnosed the effect of anthropo-zoogenically modified timberline in the field by analyzing the amount of: **a** non-disturbed surfaces and **b** grazing overused surfaces within the dominant plant communities of the timberline ecotone, i.e. Geo montani-Nardetum grassland and subalpine Alpenrose heath. Anthropo-zoogenically produced impacts of land use, such as forest clearance and overgrazing, result in soil degradation. Hence, undemanding plant communities, especially grassland communities of the alpine belt, are favored to invade the area 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. Furthermore, subalpine and alpine grassland communities are well suited to studying the driving factor of vegetation dynamics, since their habitat-forming capacity is lower than forest communities. Therefore, grassland communities often show a relationship to shrub communities like green alder and ericaceous scrub heath. Geo montani-Nardetum invaded by ericaceous dwarf shrubs (e.g., *Calluna vulgaris, Rhododendron ferrugineum* and *Vaccinium myrtillus)* is frequent in areas of the timberline ecotone that show reduction in pasture activity and a transition to the potential climax coniferous forest. Cattle manure promotes the grass species *Nardus stricta,* while a decrease in anthropo-zoogenic land-use benefits the development of dwarf shrub species (Hegg et al. 1993).

Study region

The Lauterbrunnen valley (46°36′0″ N, 7°54′32″ E) is situated in the northern Swiss Alps and belongs to the world heritage site Jungfrau Region (Fig. 1). Its climate is subalpine-humid and the region's microclimate is affected by different wind systems. The mean annual temperature is 5.95 °C in Lauterbrunnen (795 m a.s.l.) and −7.6 °C at the Jungfraujoch (3580 m a.s.l.), the mean annual precipitation ranges between 1164 mm (Lauterbrunnen) and 1800–2000 mm (Kleine Scheidegg: 2061 m a.s.l.).

The landscape features in the study region are a result of complex-ancient geological and tectonic structures (i.e., granitic Aar massif, autochthonic crystalline sediments, and limestone covers of Diablerets, Wildhorn and Doldenhorn nappe), and glaciological history (moraines and alluvial deposits), but also recent processes of landscape evolution (rock-fall and landslide activity), which gives rise to a wide distribution of different soil and vegetation types (Lüdi 1921; Nabholz 1967).

The studied vegetation types are: ericaceous dwarf shrub heath (Rhododendro-Vaccinietum), subalpine green alder shrubs (Alnetum viridis) and subalpine and alpine meadows (Geo montani-Nardetum) (Lüdi 1948; Braun-Blanquet 1948/1949; Schweingruber 1972; Delarze & Gonseth 2008).

Material and Methods

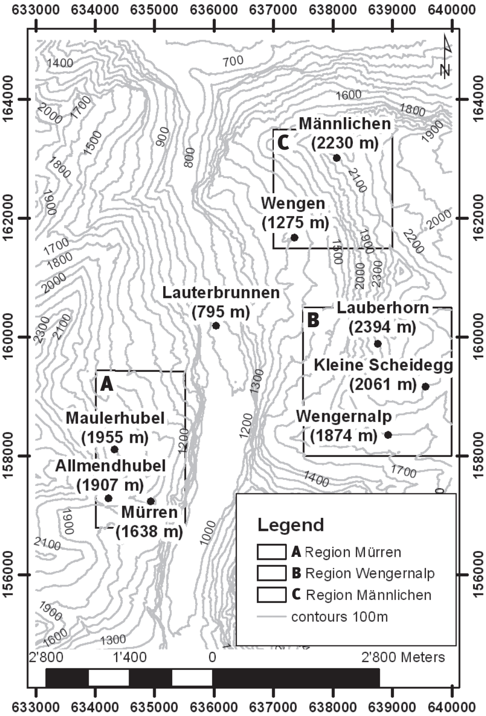
Our study is based on the work by Lüdi that was published in 1921. Lüdi was one of the first scientists to describe an Alpine valley according to the genetic-dynamic principle, publishing the following maps of the vegetation for the Lauterbrunnen valley in 1921: **1** Economic vegetation map and **2** Genetic-dynamic vegetation map.

1 Economic vegetation map

The first vegetation map of the Upper Rhine valley that was published by Hager in 1916 served as an important basis for establishing further economic vegetation maps, because it could illustrate the relationship between human and climatic-edaphic impacts on subalpine forest. In Lüdi's economic vegetation map forest vegetation is classified according to the type of surface cultivation. The vegetation for the year 1920 is given by the intensity of cultivated area with demand for agricultural use, which correlates with climate and landscape morphology. The potential natural vegetation of these land-use maps can be approximated with the help of plant ecological knowledge.

2 Genetic-dynamic vegetation map

Lüdi's genetic-dynamic vegetation map of plant communities is an early study of plant sociology in the Alps. He introduced plant succession as a genetic-dynamic principle to illustrate changes taking place in the ecosystem over a certain time period. Plant succession processes are important for studying changes in plant communities that take place at the level of associations. The term "association" was defined by Braun-Blanquet (1921) as a basic unit of a plant community that expresses a habitat in which the environmental conditions are uniform. When plant species move from a certain location, as occurs when the timberline advances or recedes, the ecology of the invaded habitat is transformed. Initial changes in the biotic/abiotic conditions of a habitat can be well identified by the distribution of character species in plant communities. To analyze initial changes in the elevation of the timberline, Lüdi studied the effect of invasive plant species in several plant communities by vegetation mapping in the Lauterbrunnen valley, for example the invasion of ericaceous dwarf shrub communities (Rhododendro-Vaccinion) into grassland communities of the Geo montani-Nardetum. Elevation measurements of the upper occurrence of single trees, krummholz and ericaceous dwarf shrubs were carried out with an aneroid barometer (Lüdi 1921). Geo montani-Nardetum is a



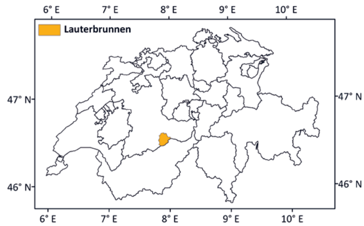


Fig. 1: Geographic location and map of the research areas:
A region Mürren: Grid 634 000/156 750 to 635 450/159 450
B region Wengernalp: Grid 637 500/158 000 to 640 500/160 500
C region Männlichen: Grid 637 000/161 500 to 639 000/163 500

Source/Quelle: Amt für Geoinformation (Bau-, Verkehrs- und Energiedirektion des Kantons Bern). Digitale geographische Daten zum Ausschnitt Grid 633 500/156 000 bis 641 000/164 500.

Abb. 1: Geografische Lage und Karte der Untersuchungsflächen:
A Gebiet Mürren: Grid 634 000/156 750 bis 635 450/159 450
B Gebiet Wengernalp: Grid 637 500/158 000 bis 640 500/160 500
C Gebiet Männlichen: Grid 637 000/161 500 bis 639 000/163 500

dominant grassland community of the subalpine and alpine belt on acid soils and is the most frequent subalpine and alpine grassland type in the Lauterbrunnen valley. It is therefore well suited to analyzing the effect of non-disturbed and overgrazed surfaces in the timberline ecotone. Furthermore its extent is well documented in the genetic-dynamic vegetation map by Lüdi (1921).

Here, we compare the subalpine and alpine vegetation of the timberline ecotone of selected areas **A** Mürren, **B** Wengernalp, and **C** Männlichen (Fig. 1) in the year 2005 with Lüdi's data from 1920. Especially changes that could be attributed to land use or climate warming have been taken into account. The following methods were used: **1** Mapping of the current dominant vegetation and vegetation relevés, **2** establishment of GIS-maps of the current dominant plant communities and **3** pairwise comparison (t-test) of the differences between the 1920 data and the 2005 data.

The vegetation mapping and vegetation relevés in three selected areas (Mürren, Wengernalp, Männlichen) were carried out according to the modified Braun-Blanquet method in the Geo montani-Nardetum. Since forest encroachment related to recession in pasture activity is explained by the invasion of dwarf shrub species and a certain spread of green alder into pasture (Holtmeier 2009), we also mapped areas of sub-alpine dwarf shrub heath and green alder scrub to complete this study. The Braun-Blanquet method has been applied by many botanists to characterize plant communities and vegetation patterns (Braun-

Blanquet 1957, 1964; Dierschke 1994; Ellenberg 1996). In the present study, we modify the combined cover-abundance index defined by Braun-Blanquet because his cover-abundance index values consider only a certain scale range (e.g., index 2: 5–25 %) and are 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. Therefore, we split Braun-Blanquet's cover-abundance index 2 (5–25 %) into four sub-cover-abundance index steps, each of 5 %. We selected each plot size according to the concept of minimum area size (Braun-Blanquet 1921); 4 m^2 for Geo montani-Nardetum and 100 m^2 for ericaceous dwarf heath and green alder scrub. The vegetation mapping of the three areas was based on the topographical map scale 1:25000 (Office of Geoinformation 2002). Vegetation mapping was carried out in 20 sites near Mürren and 20 sites near Wengernalp during several field campaigns in July and August 2005 (Fig. 1). Within each area, 15 sites of Geo montani-Nardetum and 5 sites of ericaceous dwarf heath and green alder scrub were sampled. In the third study area, Männlichen, no vegetation relevés were carried out, but the current occurrence of the uppermost growing single trees of Norway spruce *(Picea abies)* forest was recorded to compare their distribution with Lüdi's 1920 results. The 40 sites were selected within areas that were most intensively studied by Lüdi in 1920 and therefore well documented in Lüdi's genetic-dynamic vegetation map. Some of these were affected by anthropo-zoogenic impacts like grazing. Each site was located and identified with GPS in x- and y-coordinates that were given by the Geographic Coordinate System GCS_CH1903 in Swiss Grid. Plant species were first recorded according to the identification key by Landolt (2003); the present plant species nomenclature follows that of Lauber et al. (2012). For each site we differentiated between non-disturbed and overgrazed surfaces by defining vegetation units according to three categories: **1** Non-disturbed areas of Geo montani-Nardetum showing a high presence of character species, such as *Pseudorchis albida, Geum montanum, Gentiana acaulis, Ajuga pyramidalis, Campanula barbata, Arnica montana;* **2** Geo montani-Nardetum areas invaded by *Calluna vulgaris* dwarf heath (transition form with ericaceous dwarf shrubs) and **3** overgrazed alpine pastures of the Geo montani-Nardetum with a high presence of trivial flora, e.g. *Poa alpina, Deschampsia cespitosa, Leontodon helveticus* (Braun-Blanquet 1948/1949; Delarze & Gonseth 2008). Sites in the subalpine dwarf shrub heath were chosen in areas most strongly affected by anthropo-zoogenic impact and well documented in the genetic-dynamic vegetation map by Lüdi (1921), and were studied according to the same procedure as was used to study the sites of Geo montani-Nardetum. At selected sites already surveyed in 1920, we used GPS to measure the current position of the forest, tree and dwarf shrub limits and compared them with those on the older maps published by Lüdi (1921). In addition, changes in the surface of subalpine spruce forest (particularly Vaccinio-Piceion) and subalpine dwarf shrub heath (particularly Rhododendro-Vaccinion), but also the number of single Norway spruce forest trees, were considered to show the intensity of human impact at the timberline ecotone over the past 85 years. Each detailed vegetation map is based on standard ESRI-ArcGIS (ArcGIS 9) algorithms. Subsequently, a pairwise comparison (t-test) using SPSS was applied for testing significant differences in the response variables between the years 1920 and 2005, for: **a** the position of vegetation boundaries and **b** changes in the surface of important plant communities.

Results

Current vegetation dynamics at the timberline ecotone

The current subalpine and alpine surface of Geo montani-Nardetum are given in percent of the surface of both slopes of the Lauterbrunnen valley until Stechelberg (region of Mürren, region of Wengernalp). Results showed for both sites a high density of Geo montani-Nardetum (53 %) invaded by *Calluna vulgaris*, 17 % non-disturbed, and 30 % overgrazed areas. Overgrazed pastures of the Geo montani-Nardetum were more frequent in the region of Wengernalp (33 %) than in the region of Mürren (27 %). In contrast, the density of non-disturbed Geo montani-Nardetum, with high presence of character species, was higher (20 %) in the region of Mürren than in the Wengernalp region (13 %). The same was true for the Alnetum viridis and the Rhododendro-Vaccinion dwarf shrub heath, where disturbed surfaces were more frequent in the region of Wengernalp (60 %) than in the region of Mürren (40 %).

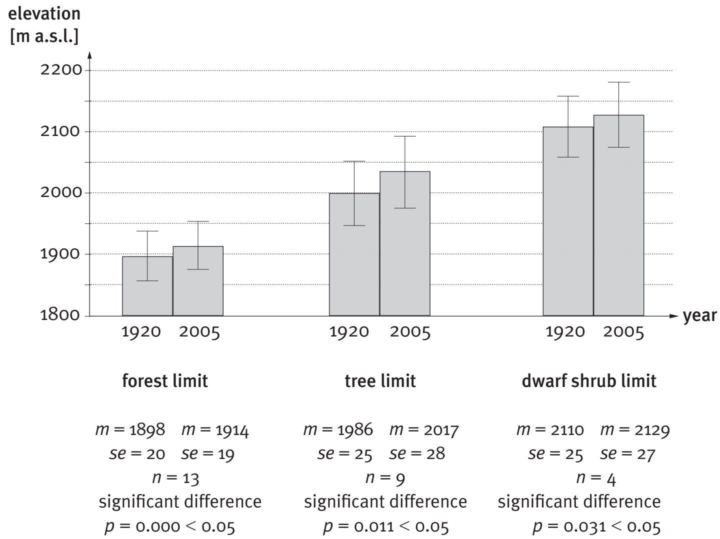
Changes in vegetation dynamics at the timberline ecotone

Alpenrose dwarf shrub heath showed major changes in the timberline ecotone among all recorded vegetation mapping units (Fig. 2 and 4). Although *Rhododendron ferrugineum* showed the greatest altitudinal increase, 30 m at Wengernalp (Table 1), it decreased in surface area, on average by 40 %, in all studied regions (Fig. 4). Changes in the surface of subalpine spruce forest and Geo montani-Nardetum were smaller. Single spruce groups showed the largest increases, particularly in the study region of Mürren with an increase in single spruce groups from 16 to 30 (47 %) (Fig. 3 and 4). In all recorded vegetation mapping units the changes in area between 1920 and 2005 were not significant (Fig. 4).

At all sites, the upper limit of the subalpine spruce forest in 2005 was at a higher elevation than recorded in 1920 by Lüdi (Fig. 2). Only the north-facing slope at Dorrenhubel showed a similar altitudinal position of the timberline. The largest shift of the timberline (35 m) was found at Allmihubel-Hartwänge (Table 1). Like the timberline, the tree limit increased in elevation at all sites between 1920 and 2005, except for the south-facing slope of Steineggwald where recorded values were similar to those measured in 1920. The largest changes in elevation were

Fig. 2: Changes in the elevation of the upper forest limit, the tree limit, and the dwarf shrub limit between 1920 and 2005 in the study area (Mürren, Wengernalp, Männlichen). The bar height displays the elevation in m (+/- 2 se). The significance of the change was tested with a pairwise comparison *(t-test)*.

Abb. 2: Veränderung der Waldgrenze, der Baumgrenze und der Obergrenze der Zwergstrauchheide im Untersuchungsgebiet (Mürren, Wengernalp, Männlichen) zwischen 1920 und 2005.
Die Balkenhöhe zeigt die Höhe in m (+/- 2 se). Die Signifikanz der Änderung wurde mit einem paarweise Vergleich *(T-Test)* geprüft.



found at Männlichen below Tschuggen (+90 m) and Männlichen below the hotel (+ 56 m), at Steineggwald (+42 m) and Mürrenbach-Blumental (+39 m) (Fig. 5; Table 1). In contrast to the data for the area of recorded vegetation mapping units, changes in the elevational limit for forest, tree and Alpenrose dwarf shrub heath between 1920 and 2005 were significant (Fig. 2 and 4).

Discussion

This study has shown the value of Lüdi's work for studies in vegetation dynamics and for understanding whether changes at the timberline ecotone can be attributed to land use or climate warming.

During the past 85 years, the timberline of the Lauterbrunnen valley has been partly influenced by anthropo-zoological practices. However, these influences are not as severe as expected, because the Federal Office of Nature introduced conservation measures in 1947, such as the support of sustainable managed land use at Alp Untersteinberg at the rear of the Lauterbrunnen valley, which have helped to maintain areas of non-disturbed vegetation (Graf 1989). Our results showed that the effect of overgrazing was more pronounced in the region of Wengernalp than in the region of Mürren. This is probably because Wengen has larger areas of suitable land for agriculture and is more easily accessible (Graf 1989). Human impact in the Lauterbrunnen valley is noticeable, mainly in the relevés of the Geo montani-Nardetum. Because of overgrazing, several surfaces have become impoverished due to soil exhaustion (Lüdi 1948; Hegg 1984 a, b; Hegg et al. 1992; Spielberger et al. 2006). In addition, mechanical effects, such as trampling caused either by cattle or browsing livestock, but also selective feeding, for

Table 1: 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.**

Tabelle 1: Verschiebung der Wald-, Baum- und Zwergstrauchheidengrenze. Vergleich zwischen Lüdi (1921) und unseren eigenen Aufzeichnungen von 2005. Die grössten Änderungen sind **fett** gekennzeichnet.

Forest limit

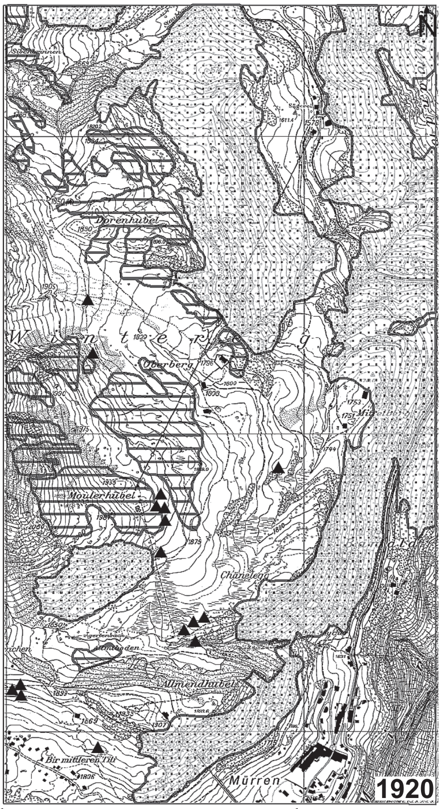
location	exposure	1920 (m a. s. l.)	2005 (m a. s. l.)	difference 1920–2005 (m a. s. l.)
right valley side of Stechelberg				
Grindegg near Wengen	S & SW	2020	2030	+ 10
Grindegg near Wengen	N	1830	1850	+ 20
Männlichen below Hotel	W	2030	2035	+ 5
Männlichen below Tschuggen	W	1850	1880	+ 30
Girmschbiel	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



0 500 m 1 km

Fig. 3: Map of the region of **A** Mürren showing survey results for subalpine Norway spruce forest (spotted and checkered), *Rhododendron ferrugineum* (horizontally and vertically striped) and single trees of spruce (triangle and tree symbol) for 1920 (**left**, LÜDI 1921) and 2005 (**right**, STRÄHL 2006).

Abb. 3: Karte des Gebiets **A** Mürren. Subalpiner Fichtenwald (gepunktet und kariert), *Rhododendron ferrugineum* (waagrecht und senkrecht gestreift) und Einzelfichten (Dreiecke und Baumsymbole).
Links: 1920 (LÜDI 1921). **Rechts:** 2005 (STRÄHL 2006).

1920
Subalpine spruce forest
Subalpiner Fichtenwald

1920
Alpenrose dwarf shrub heath
Alpenrosen-Zwergstrauchheide

▲ 1920
Single spruce
Einzelfichte

1920 & 2005
Geo montani-Nardetum grassland / Geo montani-Nardetum-Weide

The occurrence of green alder has been mapped separately. / Das Vorkommen der Grünerle ist getrennt kartographisch dargestellt worden.

2005
Subalpine spruce forest
Subalpiner Fichtenwald

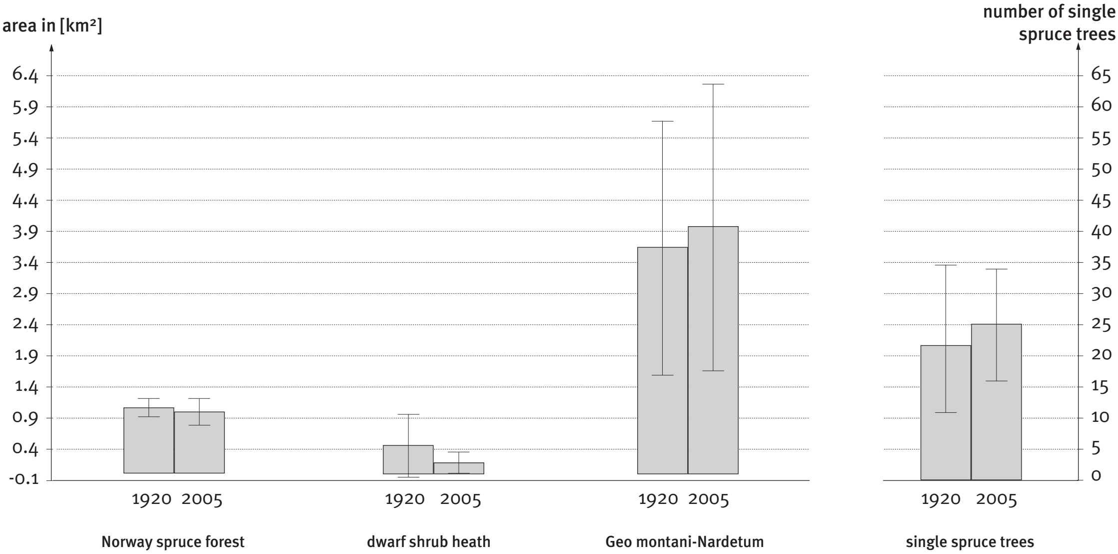
2005
Alpenrose dwarf shrub heath
Alpenrosen-Zwergstrauchheide

2005
Single spruce
Einzelfichten

Source/Quelle: Amt für Geoinformation (Bau-, Verkehrs- und Energiedirektion des Kantons Bern). Digitaler Übersichtsplan des Kantons Bern 1:10 000 zum Ausschnitt Grid 634 000/156 750 bis 635 450/ 159 450. Genetisch-dynamische Vegetationskarte von LÜDI (1921).

example avoiding *Nardus stricta,* which has low nutrient values and is avoided as a pasture weed, account for a similar effect of overgrazing (Hegg et al. 1993). Important plant species, mainly orchids like *Gymnadenia conopsea, Nigritella rhellicani* and *Pseudorchis albida* that grow on non-disturbed Geo montani-Nardeum, are missing in overused areas, whereas undemanding trivial vegetation with plant species of rich meadow communities like *Poa alpina* and *Deschampsia cespitosa* become dominant. The Geo montani-Nardetum surveyed in the Lauterbrunnen valley therefore harboured, beside the common plant species *Arnica montana, Geum montanum* and *Nardus stricta,* a high number of rich meadow plant species like *Leontodon helveticus.* In most cases, a transition of a poor Geo montani-Nardetum to a Poion alpinae can be recorded. Also Hegg (1984 a, b) studied the effect of fertilization on Geo montani-Nardetum surfaces located on the Schynige Platte near Interlaken and re-sampled sites that Lüdi sampled from 1931 to 1942 and 1946 to 1954 on the same plots. Hegg (1984 a, b) showed that natural ecosystems recover slowly after interventions and the effects of manuring were still noticeable, even more than 25 years after the last fertilization of the test surfaces took place. According to the three defined categories of surveyed Geo montani-Nardetum, results show that non-disturbed areas of Geo montani-Nardetum affected by hay crop are less frequent (17 % of the investigated surface) in the Lauterbrunnen valley than impoverished areas affected by overgrazing (30 % of the investigated surface). Most plots (53 %) show a dominance of Geo montani-Nardetum, invaded by *Calluna vulgaris.* Invasion of dwarf shrub heath into subalpine grassland has caused heath-formation on abandoned pastures at the timberline ecotone between 1800 and 2200 m a.s.l. The density of dwarf shrub heath increases as soon as pasture activity is reduced. Also single Norway spruces are connected to pasture activity and their number increases mainly in areas where pasture activity is reduced (Bischof 1984). The greatest changes in the coverage of single Norway spruce trees occurred in the study area of Mürren (Fig. 3). Between 1920 and 2005, however, the area of *Rhododendron ferrugineum* dwarf shrub communities decreased and became fragmented (Fig. 3). This was probably due to overgrazing as well as ski tourism, as skiing causes damage that can kill Alpenrose. The same applies to other dwarf shrubs like *Vaccinium gaultherioides* or *Loiseleuria procumbens.* In addition, the fertilization effect of artificial snow may have had a greater impact, because of higher input of water and harmful additives (Rixen et al. 2003).

An anthropo-zoological impact was evidenced by the invaders into the dwarf shrub heath. Overgrazing in the herb layer of dwarf shrub heath contributes to the development of richly manured alpine pasture (Rumicetum alpini), which is dominated by *Rumex alpinus* or *Senecio alpinus.* At the same time overgrazing contributes to an increase in density of *Nardus stricta*



Norway spruce forest	dwarf shrub heath	Geo montani-Nardetum	single spruce trees
m = 10 45800 *m* = 984 327	*m* = 440 250 *m* = 173 963	*m* = 3 639 319 *m* = 3 967 079	*m* = 21 *m* = 25
se = 72 526 se = 108 062	se = 251 304 se = 86 238	se = 1 018 885 se = 1 151 533	se = 6 se = 4
n = 3	n = 3	n = 3	n = 3
non-significant difference	non-significant difference	non-significant difference	non-significant difference
$p = 0.329 \geq 0.05$	$p = 0.253 \geq 0.05$	$p = 0.143 \geq 0.05$	$p = 0.624 \geq 0.05$

Fig. 4: Changes in the cover of Norway spruce forest, dwarf shrub heath, Geo montani-Nardetum, and single spruce forest trees between 1920 and 2005. The bar height displays the area in km² (+/- 2 *se)*, for single spruce forest trees the number of trees. The significance of change was tested with a pairwise comparison *(t-test)*.

Abb. 4: Flächenveränderung zwischen 1920 und 2005 des subalpinen Fichtenwaldes, der subalpinen Zwergstrauchheide und des Geo montani-Nardetum sowie einzeln stehenden Fichten. Die Balkenhöhe zeigt die Ausdehnung in km² (+/- 2 *se)*, bei Einzelfichten die Stückzahlen. Die Signifikanz der Änderung wurde mit einem paarweise Vergleich *(T-Test)* geprüft.

(Hegg et al. 1993). The Alnetum viridis showed a large invasion of *Rumex alpestris* species in the herb layer, growing together with *Nardus stricta*. In large areas in the Alps, studies showed that the invasion of *Alnus viridis* into areas that were formerly pastured contributed to high input of reactive nitrogen release, which reduced biodiversity and constrained forest succession (Bühlmann et al. 2014). This was, however, not observed in the Lauterbrunnen valley.

Less pronounced are the effects on a probable response of the vegetation to global warming. We found a significant increase in the elevation of the upper limits of Norway spruce forest, tree occurrence and dwarf shrub heath between 1920 and 2005, although the surface area of spruce forest and Alpenrose dwarf shrub heath was reduced. We found a tendency of a vertical migration of the potential limit of the timberline by 30 to 50 m between 1920 and 2005 (Fig. 4; Table 1). This tendency to an altitudinal increase in the forest and tree limit is consistent with the expected influence of global warming. For example, the decadal increase of 0.9 °C in mean air temperature recorded by the climate stations of Jungfraujoch (3580 m a.s.l.) and Meiringen (595 m a.s.l.), both near the Lauterbrunnen valley, indicate the influence of global warming over the past 100 years (Federal Institute for Meteorology 2011). This observation is also supported by the observed changes in the number of single spruce groups. The largest increases of single spruce groups were

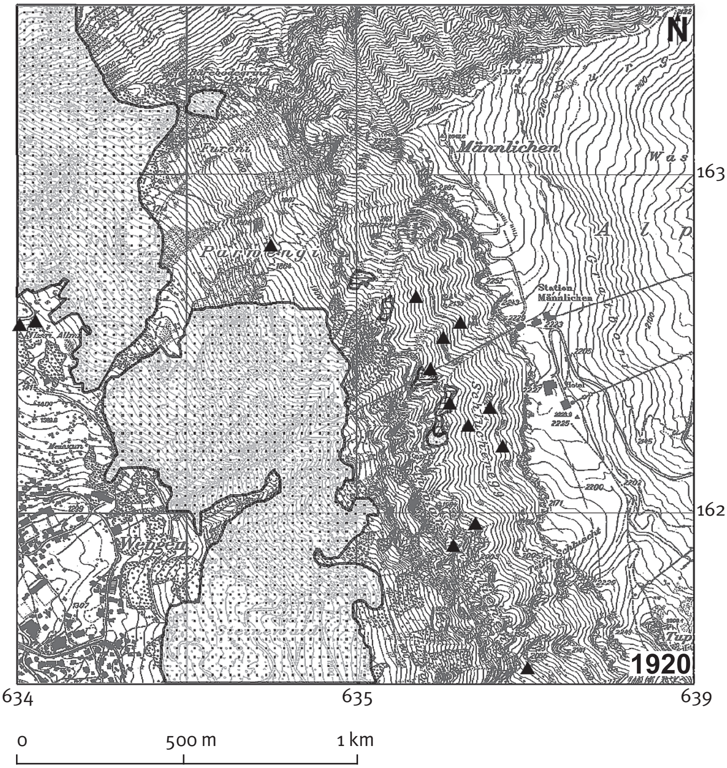
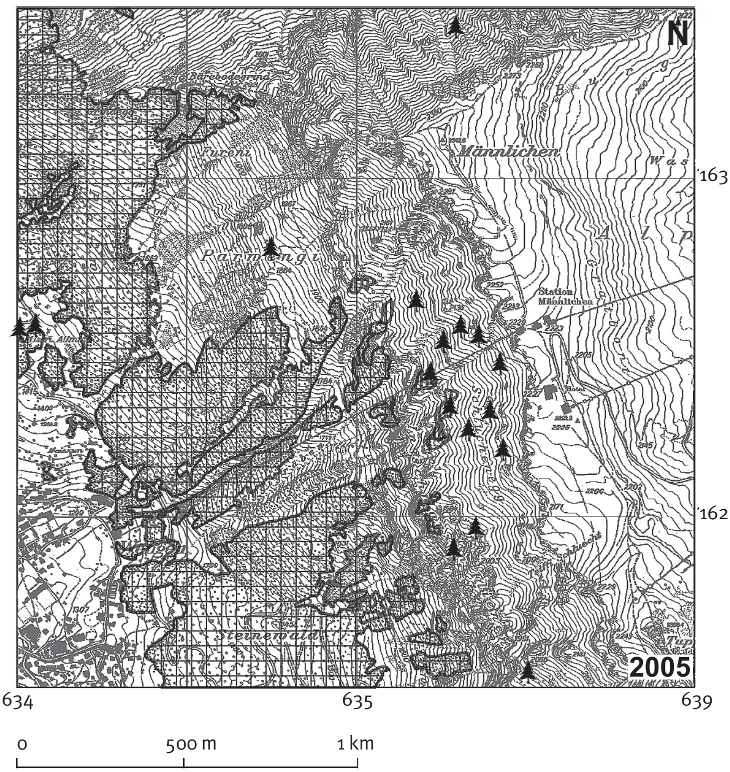


Fig. 5: Map of the region of **C** Männlichen showing survey results for the subalpine Norway spruce forest (spotted and checkered), *Rhododendron ferrugineum* (horizontally and vertically striped) and the number of single trees of spruce (triangle and tree symbol).
Top: 1920 (LÜDI 1921).
Below: 2005 (STRÄHL 2006).
Key to symbols: see Fig. 3.

Abb. 5: Karte des Gebiets **C** Männlichen. Subalpiner Fichtenwald (gepunktet und kariert), *Rhododendron ferrugineum* (waagrecht und senkrecht gestreift) und Einzelfichten (Dreiecke und Baumsymbole).
Oben: 1920 (LÜDI 1921).
Unten: 2005 (STRÄHL 2006).
Symbole siehe Abb. 3.



Source/Quelle: Amt für Geoinformation (Bau-, Verkehrs- und Energiedirektion des Kantons Bern). Digitaler Übersichtsplan des Kantons Bern 1:10 000 zum Ausschnitt Grid 634 000/156 750 bis 635 450/159 450. Genetisch-dynamische Vegetationskarte von LÜDI (1921).

found in the region of Männlichen (Fig. 5). This is probably due to its topography, since the steep and isolated slope sites are not easily accessible and therefore less favorable for pasture activity.

The design of this particular study, however, has not allowed us to conclusively determine which of these processes predominantly drove changes at the alpine timberline between 1920 and 2005 and therefore the above interpretation of results remain assumptions. Moreover, Lüdi's data identifies his sample sites by location name, recorded altitude, and exposure, but gives neither exact coordinates nor plot sizes. Hence, the values provided by historical mappings might not allow exactly the same sites to be re-inventoried and may not provide a similarly accurate comparison between old and new vegetation records as when the exact GPS-position in the field is known. Nevertheless, our results reveal tendencies in the dynamics within the timberline ecotone related to impacts of possible climate warming and/or land-use changes. In agreement with similar analysis (Gehrig-Fasel et al. 2007), most areas were influenced by anthropo-zoogenic land-use practices and few areas showed signs consistent with a direct impact of climate warming. We draw this conclusion from the observation that the majority of plotted Geo montani-Nardetum surfaces show a heath facies, which is caused mainly by a *Calluna vulgaris* invasion and therefore evidences a response to a reduction in pasture activity rather than to climate warming.

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References

AESCHIMANN D, RASOLOFO N & THEURILLAT J-P (2011) Analyse de la flore des Alpes. 1: historique et biodiversité. The Conservatory and Botanical Garden of the City of Geneva 66/1: 27–55

AESCHIMANN D, RASOLOFO N & THEURILLAT J-P (2013) Analyse de la flore des Alpes. 5: milieux et phytosociologie. The Conservatory and Botanical Garden of the City of Geneva 68/1: 5–27

BENISTON M (2006) Mountain weather and climate: A general overview and a focus on climate change in the Alps. In: Lami A & Boggero A (eds), Ecology of High Elevation Aquatic Systems in the Alps. Hydrobiologia 562: 3–16

BISCHOF N (1984) Pflanzensoziologische Untersuchungen von Sukzessionen aus gemähten Magerrasen in der subalpinen Stufe der Zentralalpen. Botanisches Institut der Uni Basel. Verlag F. Flück-Wirth, Teufen AR. pp 1–2, 12–23, 92–101

BRAUN-BLANQUET J (1921) Prinzipien einer Systematik der Pflanzengesellschaften auf floristischer Grundlage. Jahresbericht der St. Gallischen Naturwissenschaftlichen Gesellschaft 57/2: 305–351

BRAUN-BLANQUET J (1948/1949) Übersicht über die Pflanzengesellschaften Rätiens. Sonderdruck aus: Vegetatio, acta geobotanica: vol 1 (1948) & vol 2 (1949). Sammelband der GEOBOT-Bibliothek. Junk Verlag Den Haag. 168 pp

BRAUN-BLANQUET J (1957) Ein Jahrhundert Florenwandel am Piz Linard (3414 m). Bulletin du Jardin botanique de l'Etat a Bruxelles 27/2: 221–232

BRAUN-BLANQUET J (1964) Pflanzensoziologie: Grundzüge der Vegetationskunde, 3. Aufl. Springer, Wien. 865 pp

BÜHLMANN T, HILTBRUNNER E & KÖRNER C (2014) *Alnus viridis* expansion contributes to excess reactive nitrogen release, reduces biodiversity and constrains forest succession in the Alps. Alp Botany 124: 187–191

BURGA CA (1988) Swiss vegetation history during the last 18000 years. New Phytology 110: 581–602

BURGA CA & PERRET R (1998) Vegetation und Klima der Schweiz seit dem jüngeren Eiszeitalter, 1. Aufl, Ott Verlag, Thun. 805 pp

BURGA CA, FREI E, REINALTER R & WALTHER G-R (2007) Neue Daten zum Monitoring alpiner Pflanzen im Engadin. Berichte der Reinhold-Tüxen-Gesellschaft 19: 37–43

BURGA CA, HAEBERLI W, KRUMMENACHER B & WALTHER G-R (2003) Abiotische und biotische Dynamik in Gebirgsräumen – Status quo und Zukunftsperspektiven, 25–37. Autorenausgabe

CARRARO G, GIANONI P, MOSSI R, KLÖTZLI F & WALTHER G-R (2001) Observed changes in vegetation in relation to climate warming. In: Burga & Kratochwil (eds) Biomonitoring – General and Applied Aspects on a Regional and Global Scale. Tasks for Vegetation Science 35: 195–205

DELARZE R & GONSETH Y (2008) Lebensräume der Schweiz: Ökologie, Gefährdung und Kennarten, 2. Aufl.. Ott Verlag, Thun. 424 pp

DIERSCHKE H (1994) Pflanzensoziologie. Grundlagen und Methoden. Eugen Ulmer, Stuttgart. 683 pp

ELLENBERG H (1996) Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht. Eugen Ulmer, Stuttgart. 1095 pp

FEDERAL OFFICE OF METEOROLOGY AND CLIMATOLOGY (2011) Climate today. Trends in Switzerland. URL: http://www.meteoschweiz.admin.ch/web/en/climate/climate_today/trends_in_switzerland. Html. Accessed 13 July 2011

GEHRIG-FASEL J, GUISAN A & ZIMMERMANN NE (2007) Tree line shifts in the Swiss Alps: Climate change or land abandonment? Journal of Vegetation Science 18/4: 571–582

GOTTFRIED M, PAULI H et al. (2012) Continent-wide response of mountain vegetation to climate change. Nature climate change 2: 111–115

GRABHERR G, GOTTFRIED M & PAULI H (2001) Long-term monitoring of mountain peaks in the Alps. In: Burga & Kratochwil (eds), Biomonitoring – General and Applied Aspects on a Regional and Global Scale. Tasks for Vegetation Science 35: 153–177

GRAF C (1989) Geschichte der Talschaft Lauterbrunnen, Neuzeit

1798 bis um 1980. Buch- und Offsetdruckerei Schlaefli AG, Interlaken. pp 108–132, 144–156, 195–324

Hager K (1916) Verbreitung der wildwachsenden Holzarten im Vorderrheintal (Kanton Graubünden): von der Oberalp bis Ilanz-Schleuis. Buchdruckerei Büchler, Bern. 331 pp

Hegg O (1984a) Langfristige Auswirkungen von Düngung auf einigen Arten des Nardetums auf der Schynigen Platte ob Interlaken. Angewandte Botanik 58: 141–146

Hegg O (1984b) 50 jähriger Wiederbesiedlungsversuch in gestörten Nardetum-Flächen auf der Schynigen Platte ob Interlaken. Dissertationes Botanicae 72: 459–479

Hegg O, Beguin C & Zoller H (1993) Atlas schutzwürdiger Vegetationstypen der Schweiz. Herausgegeben vom Bundesamt für Umwelt, Wald und Landschaft, Bern. 160 pp

Hegg O, Feller U, Dähler W & Scherrer C (1992) Long term influence of fertilization in a Nardetum. Vegetatio 103/2: 151–158

Hoch G & Körner C (2009) Growth and carbon relations of tree line forming conifers at constant vs. variable low temperatures. Journal of Ecology 97: 57–66

Hofer HR (1992) Veränderungen in der Vegetation von 14 Gipfeln des Berninagebietes zwischen 1905 und 1985. In: Berichte des geobotanischen Institutes der Eidgenössischen Technischen Hochschule 58, 39–54, Stiftung Rübel

Holtmeier F-K (2009) Mountain timberlines. Ecology, patchiness, and dynamics: advances in global research. Volume 36, Springer. 437 pp

Intergovernmental Panel on Climate Change (IPCC) (ed) (2014) Migration of Climate Change. Working Group III contribution to the fifth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge. 1435 pp

Körner C (1998) A re-assessment of high elevation treeline positions and their explanation. Oecologia (1998) 115: 445–459

Körner C (2003) Alpine plant life. Functional Plant Ecology of High Mountain Ecosystems. 2nd edition. Springer, Berlin. 344 pp

Körner C (2012) Alpine treelines: functional Ecology of the Global High Elevation Tree Limits. Springer, Basel. 220 pp

Kullmann L (2000) Tree-limit rise and recent warming: a geoecological case study from the Swedish Scandes. Norsk Geografisk Tidsskrift-Norwegian Journal of Geography 54: 49–59

Landolt E (2003) Unsere Alpenflora. Schweizer Alpen-Club SAC, 7. Aufl, SAC-Verlag, Frutigen. 341pp

Lauber W, Wagner G & Gygax A (2012) Flora Helvetica. 5. Aufl. Paul Haupt, Bern

Lüdi W (1921) Die Pflanzengesellschaften des Lauterbrunnentales und ihre Sukzession. Versuch zur Gliederung der Vegetation eines Alpentales nach genetisch-dynamischen Gesichtspunkten, Rascher & Cie, Zürich. 364 pp

Lüdi W (1948) Die Pflanzengesellschaften der Schynige Platte bei Interlaken und ihre Beziehungen zur Umwelt. Eine vergleichend ökologische Untersuchung. Veröffentlichungen des Geobotanischen Institutes Rübel in Zürich. 23. Heft, Huber, Bern. 400 pp

Moiseev PA & Shiyatov SG (2003) Vegetation Dynamics at the Treeline Ecotone in the Ural Highlands, Russia. In: Nagy et al. (ed), Alpine Biodiversity in Europe, pp 423–435. Springer, Berlin

Nabholz W (1967) Geologischer Führer der Schweiz. Heft 4, Verlag Wepf & Co. Basel

Office of Geoinformation (ed) (2002) Digitaler Übersichtsplan des Kantons Bern. Digitaler Übersichtsplan UP5. Amt für Geoinformation des Kantons Bern

Ozenda P (1988) Die Vegetation der Alpen im europäischen Gebirgsraum. Fischer, Stuttgart. 353 pp

Pauli H, Gottfried M et al. (2012) Recent Plant Diversity Changes on Europe's Mountain Summits. Science 336/6079: 353–355

Perret R (2005) Standortmerkmale, Strukturen und Dynamik des Waldgrenzökotons im Weisstannental (östliche Schweizer Voralpen, Kt. St. Gallen). Dissertation, Universität Zürich. 198 pp

RIXEN C, STÖCKLI V & AMMANN W (2003) Does artificial snow production affect soil and vegetation of ski pistes? A review. Perspectives in Plant Ecology, Evolution and Systematics, 5/4: 219–230

SCHWEINGRUBER FH (1972) Die Subalpinen Zwergstrauchgesellschaften im Einzugsgebiet der Aare (schweizerische nordwestliche Randalpen). Mitteilungen / Schweizerische Anstalt für das forstliche Versuchswesen, 48/2: 197–504

SPIELBERGER T, HEGG O, MATTHIES D, HEDLUND K & SCHAFFNER U (2006) Long-term effects of short-term perturbation in a subalpine grassland. Ecology 87/8: 1939–1944

STRÄHL SC (2006) Natürliche und anthropogene Vegetationsdynamik der letzten 85 Jahre im Lauterbrunnental, Berner Oberland. Diplomarbeit Geographisches Institut, Universität Zürich

THEURILLAT J-P & GUISAN A (2001) Potential impact of climate change on vegetation in the European Alps: a review. Climatic change 50: 77–109

TRANQUILLINI W (1979) Physiological Ecology of the Alpine Timberline. Tree existence at high elevations with special reference to the European Alps. Springer, Berlin. 137 pp

WALTHER G-R, BEISSNER S & BURGA CA (2005) Trends in the upward shift of alpine plants. Journal of Vegetation Science 16: 541–548

WIPF S, STÖCKLI V, HERZ K & RIXEN C (2013) The oldest monitoring site of the Alps revisited: accelerated increase in plant species richness on Piz Linard summit since 1835. Plant Ecology & Diversity 6/3–4: 447–455