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„Changes in plant community composition along a successional gradient in the
forefields of the Blaueis, Northern Limestone Alps“

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Abstract

Since the last glacier advance at the end of the Little Ice Age, the glaciers in the Alps have retreated strongly. This creates more and more ice-free areas, the glacier forefields, which are colonized by vegetation, i.e., primary succession. For the Northern Limestone Alps there are not yet sufficient studies on plant community composition and associated trait changes. In this study, community weighted means of trait values (i.e., the traits of plants interacting with the environment along a gradient) were examined to determine general trends in succession in the glacier forefield. Sixteen sample plots in the forefield of the Blaueis were studied following the chronosequence of glacier retreat. Characteristics of the vegetation related to the succession over age classes was analyzed by using species richness, cover, and the specific leaf area (SLA). Both species richness and species cover increased significantly along the successional gradient, SLA decreased, but only marginally significantly. At the beginning of succession, these are stress-tolerant pioneer species with high SLA values. The slightly negative SLA trend in the late succession plots indicates more stable, well-developed vegetation with increasing stress tolerance and competitive species.

Since the measurement of traits is time-consuming, plant traits from databases are increasingly used for trait-based approaches of vegetation analysis. However, it has not been adequately tested how reliable these databased values are for extreme locations such as high mountains. This is necessary because of intraspecific variability of plant traits in response to specific environmental conditions. This study tested for differences between values for the functional trait SLA at the species and plot levels for trait values measured in the field and database trait values (TRY database). The results show that the differences seem to be rather species-specific. A large part of the species studied occurs only in alpine areas; here it is likely that the SLA values retrieved from the TRY database are also from comparable habitats to those measured in the field, in contrast to species where some specimens also occur at lower elevations. Despite species-specific differences, SLA is not consistently over- or underestimated by the values obtained from TRY database. So, there is no systematic bias at the community level of the SLA values from Blaueis forefields.

Keywords: climate change; glacier forefield succession; SLA - specific leaf area; Try database; vegetation dynamics

Zusammenfassung

Seit dem letzten Gletschervorstoß am Ende der kleinen Eiszeit, bilden sich die Gletscher der Alpen deutlich zurück. So entstehen immer mehr eisfreie Flächen, die Gletschervorfelder, die durch primäre Sukzession von der Vegetation besiedelt werden. Für die Nördlichen Kalkalpen gibt es jedoch noch nicht genügend Studien über die Zusammensetzung von Pflanzengemeinschaften und die damit verbundenen Veränderung von Merkmalen. In dieser Studie wurden gemeinschaftsgewichtete Mittelwerte der Merkmale untersucht, um allgemeine Sukzessionstrends im Gletschervorland zu ermitteln. Sechzehn Vegetationsaufnahmen im Vorfeld des Blaueis in den Berchtesgadener Alpen wurden entlang der Chronosequenz des Gletscherrückgangs untersucht. Die Reaktion auf die Sukzession wurde anhand der Artenzahl, der Deckung und der spezifischen Blattfläche (SLA) analysiert. Sowohl die Artenzahl als auch die Artenbedeckung nahmen entlang des Sukzessionsgradienten signifikant zu, die SLA nahm ab, jedoch nur marginal signifikant. Zu Beginn der Sukzession handelt es sich um stresstolerante Pionierarten mit hohen SLA-Werten. Der leicht negative SLA-Trend in den späten Sukzessionsparzellen deutet auf eine stabilere, gut entwickelte Vegetation mit zunehmender Stresstoleranz und konkurrenzfähigen Arten hin.

Da die Messung von Merkmalen zeitaufwändig ist, werden Pflanzenmerkmalswerte aus Datenbanken zunehmend für merkmalsbasierte Ansätze der Vegetationsanalyse verwendet. Es ist jedoch nicht fraglich, wie zuverlässig diese Datenbankwerte für extrem Standorte wie die der Gletschervorfelder sind. Dies ist aufgrund der intraspezifischen Variabilität von Pflanzenmerkmalen als Reaktion auf spezifische Umweltbedingungen notwendig. In dieser Studie wurde evaluiert, wie sich die mittleren Merkmalszusammensetzungen unterscheiden, wenn die Merkmale aus Datenbanken (in diesem Fall die TRY-Datenbank) gewonnen oder *in-situ* ermittelt werden. Die Ergebnisse zeigen, dass die Unterschiede eher artspezifisch zu sein scheinen. Ein großer Teil der untersuchten Arten kommt nur in alpinen Gebieten vor; hier ist es wahrscheinlich, dass die aus der TRY-Datenbank abgerufenen SLA-Werte auch aus vergleichbaren Lebensräumen stammen wie die im Feld gemessenen, im Gegensatz zu Arten, bei denen einige Exemplare auch in niedrigeren Höhenlagen vorkommen. Trotz artspezifischer Unterschiede wird die SLA durch die aus der TRY-Datenbank gewonnenen Werte nicht durchgängig über- oder unterschätzt. Es gibt also keine systematische Verzerrung der SLA-Werte aus den Blaueis Vorfeldern auf Gemeinschaftsebene.

Introduction

Worldwide, most glaciers are retreating. This is because high-altitude and high-mountain regions are particularly affected by global warming, which has greatly accelerated both the extent and speed of glacier melt (Lee et al., 2017). Thus, many glaciers will disappear completely in the next few decades. Since the end of the Little Ice Age (LIA) about 150 to 220 years ago (Munn, 2002), a large part of global glaciers has been shrinking; the last major glacier advance was around 1850 (Zemp et al., 2019). Only around 1920 there was again a small glacier advance (Gosterxeier et al., 2002; Heuberger, 1977; Nagl & Erschbamer, 2010).

Both naturally and anthropogenically driven changes in climate are responsible for the retreat of glaciers since 1850. However, the importance of human influence compared to natural factors has increased significantly in recent years (Marzeion et al., 2014). Compared to the global average, the temperature increase in the European Alps has been twice as high over the last 50 years (Cannone et al., 2008). The temperature increase affects both the biotic component (plants and vegetation) and the abiotic component (glacial retreat) in high mountains. The number of alpine and nival plant species at higher elevations is increasing, with an upward migration rate of 8-10 m per decade (Walther et al., 2005). According to Steinbauer et al. (2018), the rate of upward plants movement was five times larger from 2007 to 2016 compared to 1957 and 1966; this acceleration is synchronous with accelerated global warming. In addition, community composition is also changing (Keller et al., 2000; Steinbauer et al., 2018). Due to faster temperature rise, glaciers in the Alps are retreating 200-300 % faster than 20 years ago (Smiraglia et al., 2015; Sommer et al., 2020). Zekollari et al. (2019) predicted that Alpine glaciers will lose 94 % of their current ice mass by 2100. They become "*smaller, thinner, more perforated, and slower, decaying and disappearing*" (Kuhn et al., 2015, p.138).

Glacier melt has many consequences. One-tenth of the Earth's land area is covered by glaciers. When these glaciers recede, it often leads threats to water resources on the one hand (Cauvy-Fraunié & Dangles, 2019; Oerlemans & Fortuin, 1992) and on the other hand to a rise in sea level due to the large amounts of meltwater. In addition, landslides can occur in the mountains because the permafrost soils thaw (Orlove, 2009). The retreat of ice frees up new, previously unoccupied areas for vegetation colonization, called glacier forefields. The glacier forefield extends between the glacier front and the moraine deposited by the last glacier retreat i.e., the LIA (Anderson et al., 2017; Matthews, 1992).

Since glacier forefields are newly exposed areas, which are untouched and hardly disturbed by human activity, they are considered ideal study areas of succession, as Ellenberg (2010, p.633) stated "*nowhere can succession be studied better than in the forelands of large glaciers*". Ecological succession is a gradual change in species composition and ecosystem structure over an extended period of time at a particular site – usually following a disturbance event or a change in environmental conditions (Dierschke, 1994; Matthews, 1992). Vegetation succession means that plant communities with different species composition follow each other during the succession process in a defined space (Tansley, 1920). After a disturbance event, pioneer communities are followed by a series of successional stages and end in a stable climax community. A distinction is made between primary and secondary successions, depending on the degree of "biological inheritance", e.g., when seeds or plant fragments remain (Walker & del Moral, 2003). If plants or animals colonize an area '*in statu nascendi*', i.e., an area that was not previously colonized due to volcanic activity or glaciation, this is called primary succession. On the other hand, secondary succession is when the area already has an existing species composition and other biotic characteristics that regenerate or form a new replacement community after a disturbance (e.g., fire, erosion or flood) (Dalling, 2008). Vegetation succession in glacier forefields is primary succession as previously glaciated areas expose bare ground devoid of biological material or diaspore bank (Matthews, 1992; but see also: Gobbi et al., 2021; Hodson et al., 2008; Hotaling et al., 2017).

Another advantage of using glacial forefields as study sites for primary succession is the possibility to infer the timing of deglaciation of recently deglaciated zones (Vreeken, 1975). This allows the extraction of temporal trends from a series of samples of different ages (space-for-time substitution) (Pickett, 1989). This approach can be used to study a chronosequence (Jenny, 1941), which describes in this study a series of ecological sites that have similar characteristics, but are of different ages (Johnson & Miyanishi, 2007). Glacial chronosequences are widely used in the European Alps to assess successional dynamics of plant communities as a function of site age (Johnson & Miyanishi, 2008). The study by Foster and Tilman (2000) confirmed the validity of the chronosequence approach. Two assumptions are made in the chronosequence approach. First, all sites studied were exposed to the same environmental conditions. Second, no variable other than age has changed between sites since the triggering disturbance, such as various abiotic and biotic components. Successional change was autogenously controlled (Walker et al., 2010). In this way, the recolonization of the newly

exposed areas can be analyzed by defined "age classes" (Johnson & Miyanishi, 2008). Recently, it has been increasingly discussed that allogenic factors may influence the age of the terrain and that these assumptions may not always hold true (Walker et al., 2010; Wojcik et al., 2021).

At the beginning of vegetation colonization, pioneer species establish, which are adapted to the dominant abiotic processes by their dispersal mechanisms (Chapin et al., 1994), seed size and growth rate (Stöcklin & Bäumler, 1996), and physiognomy (Schröter et al., 1926). Dispersal of many small seeds by wind from sources outside glacier forefields or from older successional stages has been shown to be an effective dispersal mechanism (Makoto & Wilson, 2019). The abiotic influences (Raab et al., 2012) that shape the onset of primary succession can be divided into two groups. First, there are sediment properties and active geomorphic processes, and second, topographic and hydrologic influences (such as duration of snow cover, meltwater discharge, exposure, slope, moisture) (Matthews & Whittaker, 1987; Raffl et al., 2006). Glacial forefields are challenged for organisms to colonize due to their harsh site conditions (Erschbamer et al., 2008). In the later stages of succession, biotic processes such as competition (Clements, 1928) take on a greater role (Raab et al., 2012; Walker & del Moral, 2003). This temporal alternation of abiotic and biotic drivers leads to gradients in species composition. From this, conclusions about successional trends and phases can be derived (Matthews, 1992). According to several studies (Gobbi et al., 2010; Matthews, 1992; Raffl et al., 2006), e.g. it can be shown that both species number and vegetation cover increase with increasing site age until an equilibrium is achieved. After peaking in the mid-successional stage (site age 40-80 years), species numbers decrease in the late successional stage (Nagl & Erschbamer, 2010; Raffl et al., 2006). In addition, species composition also changes at all ages, and communities at early and late successional stages are very different (Eichel, 2019; Ficetola et al., 2021; Fickert et al., 2017). A variety of successional pathways exist, but a general theory is complicated by differences in species composition, site characteristics, and climate (Glenn-Lewin et al., 1992).

To date, several studies (Caccianiga & Andreis, 2004; Eichel, 2019; Raffl et al., 2006) have described changes in vegetation development along the primary succession of glacier forefields in the European Alps, but not in the Northern Limestone Alps. This has important ramifications as different parts of the Alps are made up of different bedrock. Limestone is very soluble in water compared to other types of rock in the Alps and soil formation on limestone is protracted (Zepp, 2014). Most glaciers where such studies have been carried out are "valley glaciers", i.e., those where the glacier tongues extend down into the valleys of the subalpine region (e.g.,

Morteratsch glacier in the Swiss Engadine or Forni glacier in the Italian Ortles-Cevedale mountain group) (Burga et al., 2010; Smiraglia et al., 2015); alpine grass vegetation (or sometimes even woody plants) often grows above these glaciers. Less well studied are the glacier types "cirque glacier" (e.g., Watzmann glacier and Blaueis) and "hanging glacier" (e.g., Dachstein glacier). There, the ice fields extend down the slope and there is no glacier tongue (Hagg, 2020). As these glaciers are restricted to the (sub)nival zone, there is no closed alpine vegetation above the glacier, and scree slopes predominate in the area. In a glacier valley, colonization of species can occur both from more distant areas (spread of diaspores by wind) and from the immediate vicinity (from adjacent valley slopes) by the intrusion of diaspores or plant fragments from above by snow avalanches or landslides into the glacier forefield (Nagl & Erschbamer, 2010; Raffl et al., 2006).

In contrast to studies on species number and cover, there are few results on functional leaf traits in the high mountains and especially not in the Northern Limestone Alps. In this work, the focus lies on analyzing functional leaf traits to determine general responses to succession versus analyzing succession represented by species replacement over time. Functional traits of plants are any traits that indirectly influence fitness through their effects on growth, reproduction, and survival (Violle et al., 2007). Weiher et al. (1999) and Westoby (1998) suggest specific leaf area, canopy height, and seed mass as the most basic functional plant traits that can be identified. Furthermore, leaf traits were among the most important ones defining the global spectrum of plant, form and function (Díaz et al., 2016). Specific leaf area (SLA) was selected as study object, because it is one of the leaf traits that represent the broad range of leaf investment strategies (Wright et al., 2004) and, by linking them to abiotic conditions, allow the study of species and plant community responses to the environment (Lavorel & Garnier, 2002). SLA is the ratio of leaf surface area or light-absorbing surface area to invested dry matter (mm^2/mg). It is quick to acquire, resource-efficient, and easy to measure (Díaz et al., 2004; Shipley, 2006). Weiher et al. (1999) assigned the SLA to the common list of core plant traits (core traits to predict vegetation responses to disturbance). Studies show that there is a high correlation between SLA and relative growth rate (RGR, biomass increment per unit biomass present per unit of time), photosynthetic capacity, leaf life span (Shipley, 2006; Wright et al., 2004), mass-based leaf N, and water-holding capacity (Wellstein et al., 2017). In addition, SLA is positively related to resource abundance (Wilson et al., 1999). Through these correlations, a single trait can be used to assess the functional capabilities of species. In many studies, it has

been observed that during the course of a succession, plant species with high SLA become established at the beginning (Garnier, 1992) and are replaced by species with low SLA (Shipley et al., 2005). However, little is known about the patterns and processes in the high mountains. For species growing on alpine glacial forefields, competition is secondary at the outset; adaptation to harsh environmental conditions such as extreme cold, wind, water availability, disturbance potential, intense sunlight, and snow cover duration is more important (Caccianiga et al., 2006; Cornwell & Ackerly, 2009).

Nowadays, thanks to increasingly large trait databases (e.g. Aakala & Makela, 2020), trait data can be retrieved and applied to large vegetation datasets (Bruehlheide et al., 2018). Because data are collected per species across multiple habitats and populations, it is often assumed that most of the trait variation is captured. What is often not accounted for is intraspecific trait variability among sites within a region (Aakala & Makela, 2020) that can result from genotypic diversity (Whitlock et al., 2010) or phenotypic plastic responses to environmental conditions (Garnier et al., 2001; Mokany & Ash, 2008).

The accuracy of information from databases as a substitute for field measurements has been tested rarely. Cordlandwehr et al. (2013) found that the accuracy of features depends on the level of aggregation, the trait, and the habitat type. The accuracy of traits from databases is lower for extreme habitats. One reason for this is that the database request does not allow filtering by the location of the record. However, plant functional traits are biological traits that respond to prevailing ecosystem processes (Lavorel et al., 1997), so they can vary from site to site. The individuals recorded in the database come from a much broader range of habitats. Therefore, there may be biased results when using trait database values (Cordlandwehr et al., 2013). Because this work is a case study at an extreme habitat where accuracy has not been previously studied, it is important to compare whether there are differences between trait values from databases compared to *in-situ* measured values.

Specifically, the following research questions have been addressed:

Q1: How do plant community properties change during succession in the glacial forefield, especially with respect to species number, cover, and specific leaf area (SLA)?

Q2: How do mean trait compositions differ based on records from databases or measured *in-situ*?

Methods

Study area

The Blaueis is one of five glaciers in Germany and - as the Watzmann glacier - it is located in the Berchtesgaden National Park, with the Blaueis being the northernmost glacier in the Alps (Mayer et al., 2021).

With a slope of up to 40 degrees, the Blaueis is the steepest of the German glaciers. The icefield is located in a cirque below the north face of the Hochkalter (2607 m asl) and is surrounded by the steep rock faces of the Blaueisspitze (2481 m asl) and the Kleinkalter (2453 m asl). Because of this location, the glacier is protected from sunlight most of the year. The steep rock terrain ensures that a lot of avalanche snow can accumulate (Mayer et al., 2021).

With an altitude of about 2165 m asl (lowest point without dead ice, which lies at an altitude of 1931 m asl; measured in 2018) the Blaueis is the lowest glacier of the Alps (Hagg, 2021) and therefore even more affected by glacier retreat (Bayerisches Landesamt für Umwelt, 2022). In 1820 (the peak of the LIA; Munn, 2002), the first maps from historical records showed a glacier area of 25 hectares (Mayer et al., 2021).

Whilst an ice area of 19.6 hectares was surveyed in 1889, by 1959 the area had shrunk by half since the end of the LIA to 13.1 hectares (Hagg, 2021). The decline of the ice mass in the lower field is particularly serious because it is cut off from the upper part, without further replenishment from above. This is because rock bars have been exposed into the middle of the Blaueis since the mid-1980s, now completely separating the upper part of the glacier from the lower dead ice field, which was once the glacier tongue (Mayer et al., 2021). The steeper upper part now consists of two separate ice surfaces, while the flatter lower part has broken into three separate parts. The lowest part of the glacier has been covered with debris for years (Mayer et al., 2021).

Recent surveys in 2018 revealed a remaining area of 5.2 ha. This is only one fifth of its former area. However, this value is valid only if the dead ice part covered by debris is included. It is very likely that the blue ice will soon be completely melted (Mayer et al., 2021).

The Blaueis in the Nationalpark Berchtesgaden

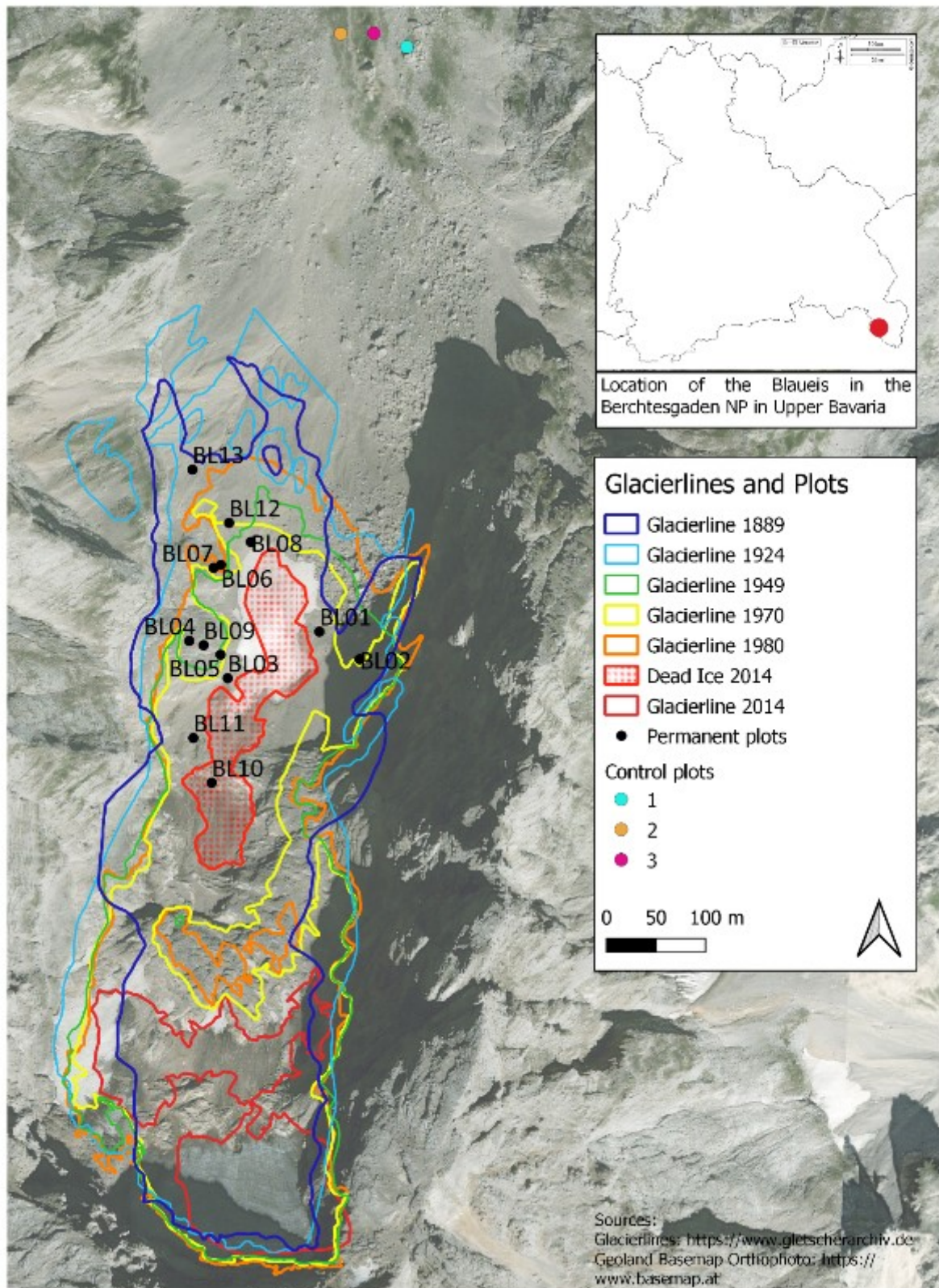


Figure 1: Map of the forefield of the Blaueis (Berchtesgaden). Points present the geographic location of the sampling plots (Blaueis and Control) in relation to the chronosequence of glacier retreat (colored lines). Please note that the GPS accuracy of the plot locations may be low due to the shadowing effects of the tall walls of the cirque.

Survey design

This master thesis is embedded in a long-term monitoring of glacier forefield succession in the Northern Limestone Alps. A total of 13 already established plots (4 in ca. 10-year-old vegetation, i.e., time since glacial retreat, 3 - 40 years, 3 - 80 years and 3 in 120 years since glacial retreat) served as basis to select the plants of the respective age classes, plants were sampled in the vicinity of these 13 plots (Figure 1). Table 1 shows that the proglacial areas (BL01 - BL13) range from 1914 to 2040 m asl. In addition to the permanent plots, three areas were also investigated that were presumably not affected by Holocene glacial advance. These are located between 1784 and 1803 m asl and are called control plots (C1, C2, C3). In selecting the three control plots, care was taken to ensure that the plots were at comparable elevations but had not been covered by glaciers in the last few thousand years. Since the exact date of glacier retreat is not known, the three control plots are defined as 250 years old. However, they may be ice-free for several thousand years. Adding this information about the age of the plots was necessary for statistical analyses (see chapter Statistical analyses) and needs to be kept in mind for discussion.

Table 1: *Blau eis glacier forefield sampling plots (BL01-BL13) and control plots (C1-C3).*

Study site	Altitude (m a.s.l.)	Estimated year of deglaciation	Age class (time since deglaciation)
<i>BL01</i>	1966	2010	10
<i>BL02</i>	1977	1980	40
<i>BL03</i>	1992	2010	10
<i>BL04</i>	2007	1950	70
<i>BL05</i>	1994	1980	40
<i>BL06</i>	1960	2010	10
<i>BL07</i>	1959	1920	100
<i>BL08</i>	1931	2010	10
<i>BL09</i>	2019	1920	100
<i>BL10</i>	2040	1950	70
<i>BL11</i>	2025	1950	70
<i>BL12</i>	1927	1980	40
<i>BL13</i>	1914	1920	100
<i>C1</i>	1803	1770	250
<i>C2</i>	1784	1770	250
<i>C3</i>	1797	1770	250

Locations of sites were located using GPS (Garmin Oregon 650t). Metal pins in the ground mark the corners of the permanent plots (area = 1 m²). Sampling of vascular plants was performed at each plot. Figure 2 shows examples of differently aged plots.

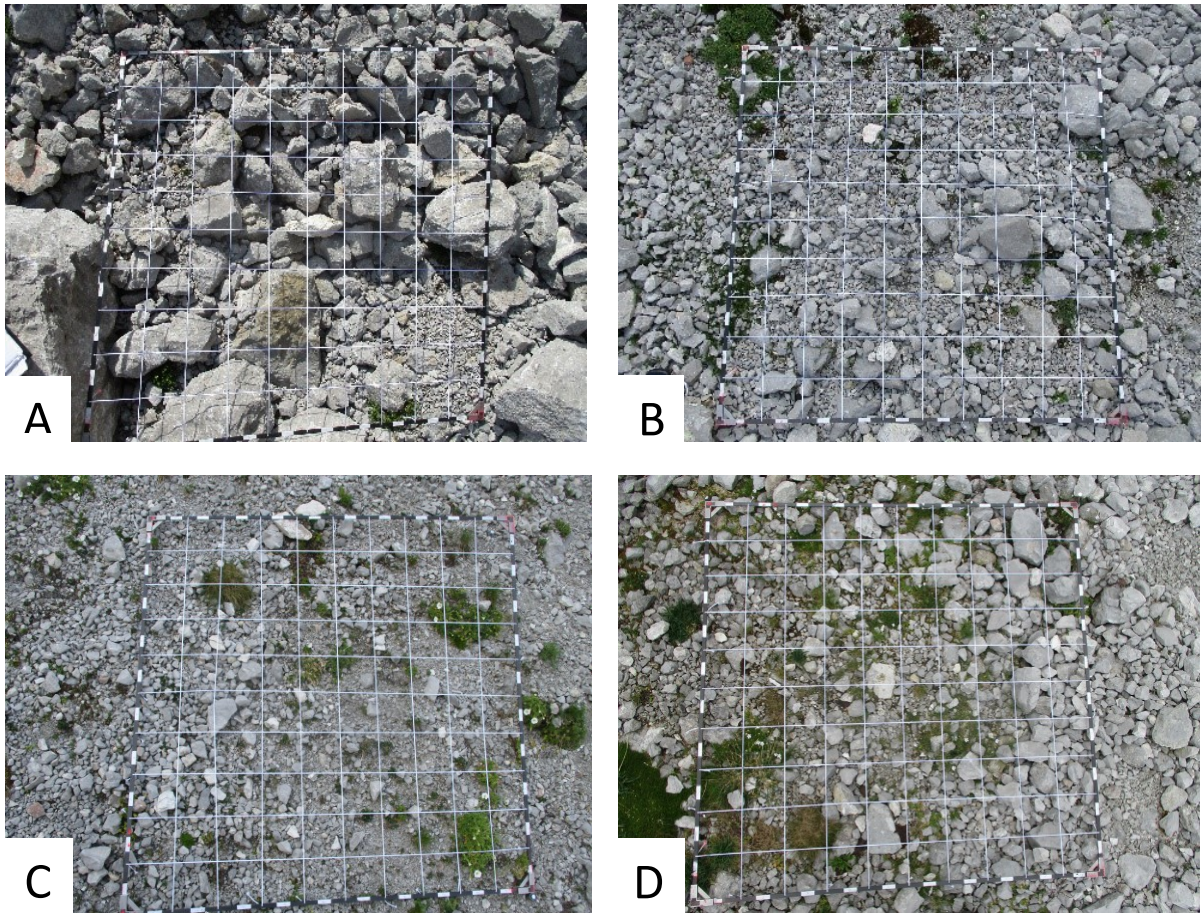


Figure 2: Examples of different age plots of the vegetation survey. A = 10-year-old plot (BL01), B = 40-year-old plot (BL02), C = 70-year-old plot (BL04), D = 100-year-old plot (BL09).

Vegetation Sampling

All vegetation survey data for the glacier forefield plots (BL01-BL13) were collected in July and August 2020 by Ingolf Kühn and Christian Hecht, and data for the control plots were collected in July and August 2021.

For the estimation of vegetation cover of glacier forefields and control plots the modified scale of Reichelt & Wilmans (1973) was used (after Braun-Blanquet 1964). Since there was only one herb layer, differentiation between tree, shrub, and herb layers was not necessary. Mosses were not recorded at species level. All plant species present in the plots were listed and their

respective cover was estimated. Cover is the ground area covered by the leaves. The estimation scale for species richness (Reichelt & Wilmanns, 1973) is explained below:

- $r = < 1\%$ covered, usually only very isolated, small individuals.
- $+$ = 2-5 individuals, up to 1 % cover.
- 1 = 6-50 individuals to 5% cover; or < 10 individuals and $> 5\%$ cover.
- 2m = $< 5\%$ covered, > 50 individuals.
- 2a = 5-15% covered, any number of individuals
- 2b = 16-25% covered, any number of individuals
- 3 = 25-50% covered, any number of individuals.
- 4 = 50-75% covered, any number of individuals.
- 5 = 75-100% covered, any number of individuals.

All vascular plants were named and determined according to the nomenclature of Fischer et al. (2008). Lichens and mosses were not determined.

Trait sampling in the field

To not disturb the permanent plots, species occurring in the plots were identified and then sampled outside the plots in close vicinity. All trait measurements were performed following to the standard LEDA protocol (Knevel et al., 2003):

Sampling consisted of collecting ten leaves per species, taken from ten individuals if possible. The whole leaf including the petiole was collected. Both herbaceous and small woody plants were collected. For example, if it was not possible to collect ten leaves from different individuals due to the rarity of the species or plant herbivory, two leaves were collected from the same individual or only 5-9 individuals were collected in total. If the leaves of a species were too small (< 2 mm length) or there were fewer than five individuals of species, no trait data were sampled. The same leaves samples were used to measure leaf size and dry weight.

The collected leaf samples were transported in closed plastic zip bags with a small piece of wet paper tissue to minimize water losses due to evapotranspiration. The leaf surfaces were determined the same day via cell phone (Apple I Phone 6s plus, 12 MP, image size 3024 x 4032) using the LeafByte app (version 1.3.0) (Getman-Pickering et al., 2020). Getman-Pickering et al. (2020) compared the use of different programs for recording leaf surface (e.g., the software ImageJ (Abràmoff et al., 2004) or mobile apps such as BioLeaf (Machado et al., 2016)), including

the open-source mobile app LeafByte. LeafByte saves the results with date, time and GPS coordinates to GoogleDrive (if internet access was available) or to a spreadsheet program on the cell phone. To avoid shrinkage of the leaf surface, measurements should be taken as soon as possible after collection. By using a glass cover, the leaves were positioned as flat as possible for accurate measuring. The basis for the size calibration is a scale by four black dots that form a square and surround the leaf (1 x 1 cm and 10 x 10 cm), background is a white sheet of paper. The scale mark and the leaf are marked by the app as foreground due to the darker color, the rest as background. This is done using an algorithm called the Otsu method (Otsu, 1979), which looks at a histogram of the lumens in the image. A luma value is used to separate the high luminance mode (leaf and scale mark) from the low luminance mode (background). This is an automatically determined threshold that can be manually adjusted. Each pixel of the image is identified individually, this process is called "tresholding" (Otsu, 1979). The distance between each scale mark can be chosen by the user to allow LeafByte to convert the number of pixels into real units. With LeafByte it is only possible to take one picture per leaf.

After measuring, leaves per species and plot were stored in paper bag. After field work was finished, leaf samples were oven-dried (BINDER GmbH) at 70 °C for 48 hours in September 2021 to determine their dry mass (= leaf mass). Using a balance (Mettler AE 260 Delta Range), the leaves of one species per plot are weighed together as if they were one unit, which improves accuracy (Cornelissen et al., 2003).

After leaf size and mass were determined, the Specific Leaf Area (SLA) was calculated, a ratio of fresh leaf area (all ten leaves summed up) to leaf dry mass (of the jointly weighed leaves), expressed in mm²/mg (Cornelissen et al., 2003).

Traits from the TRY database

The TRY Plant Trait Database (Aakala & Makela, 2020; www.try-db.org) was used for the database comparison. This global database of curated plant traits offers more than 400 datasets covering a wide range of plant traits worldwide. There are original datasets with unpublished and published data but also collective databases (e.g. LEDA, GlopNet, BiolFlor, SID, EcoFlora, FRED) (Aakala & Makela, 2020).

For this study, public and unpublished data were requested from TRY. A selection of species and traits (TraitID 3115, 3116, 3117) was made. Depending on the recording method, the TRY database distinguishes three different types of SLA measured:

- a) Leaf area per leaf dry mass (SLA): petiole excluded
- b) Leaf area per leaf dry mass (SLA): petiole included
- c) Leaf area per leaf dry mass (SLA): undefined if petiole is in- or excluded

After receiving data, the raw table was processed using Microsoft Excel (version 2206) as follows: First, all data were sorted by observation ID so that all associated contextual information of a sample are grouped. Second, the data were sorted by region and location, so that data from Europe (Alpine region) were identified. Third, the trait ID column was used to filter for SLA. Fourth, sorting was done by species name, in some cases there were multiple names for the same species as synonyms were also searched and harmonized with their valid name. Finally, the data per species were divided into SLA groups a), b) and c) (see above).

Because some species were missing from the TRY database (e.g., *Hornungia alpina* or *Carex firma*) and too few *in-situ* values were measured for some species (e.g., *Ranunculus montanus* or *Veronica aphylla*), 14 species were compared to determine if the distribution of SLA values observed in the field differed from those in the TRY database for groups a and b, and 10 species were compared for group c.

Occasionally, there were several measured values of the SLA behind one data set. Therefore, a weighted mean value was calculated per species and SLA group. The mean was calculated using the standard value, weighted by the number of replicates. It was calculated with the `weighted.mean()` function by `dplyr` package (Wickham et al., 2021), which was used in the following, too.

Community weighted mean

For plot-level comparison between the *in-situ* values and TRY database values, the community weighted mean (CWM) was calculated per plot, which is the average of SLA at each plot weighted by species abundance (Miller et al., 2019). According to the "mass ratio hypothesis", more abundant species have a stronger influence on ecosystem functions (Grime, 1998), which is why CWM is often used in ecological studies (Lavorel et al., 2007). CWMs per plot were calculated for the:

- i. *in-situ* measured values,
- ii. TRY database values (a, b, c) and
- iii. *in-situ* values excluding those species which are missing in the TRY database (a, b, c).

Statistical analyses

Data of the experimental series were stored and manipulated in Microsoft Excel (version 2206). Statistical analysis was performed using R 4.1.2 with RStudio 2021.9.1.372 (R Core Team, 2021). The following R packages have been used, in addition to those specifically mentioned: ggplot2 (Wickham, 2016), gridExtra (Auguie, 2017), here (Müller, 2020), readxl (Wickham & Bryan, 2019).

Linear (mixed effects) models

Regression analyses were performed to determine the extent to which plant community traits differ during succession in the glacial forefield in terms of species number, cover, and average leaf trait composition.

Univariate linear regression (linear model) analysis was used to test for a relationship between a dependent variable (response) and an independent variable (predictor). This is a fixed effects model. Species number and cover were chosen as response, age class as predictor, respectively. To fit linear regression the lm function by stats package (R Core Team, 2021) was used.

SLA was tested for differences among plot' age classes, and species cover was included. Here the mixed effects model (GLMM) was used, with the lmer() function in the lmerTest package (Kuznetsova et al., 2017). This model includes both fixed and mixed effects and provides a better way to analyze data that violate the IID assumption (iid = independent and identically distributed) (Zuur et al., 2009). Following is the model notation:

$$SLA \sim \text{ageclass} + (1|\text{Plot}), w = \text{cover}$$

where SLA is the dependent variable, age classes are the fixed effects, plots are the random effects, w is weighted by cover.

The significance level $\alpha = 0.05$ was used ($p \leq 0.05$).

The four age classes of glacier forefields are a numerical (cardinal) variable. For the linear model, the control plots were arbitrarily assigned to the age classes 250 years for pragmatic reasons.

t-Test

To detect systematic differences in mean trait composition per species between TRY database values and the *in-situ* measured data, a one sample t-test was performed. The distribution (SLA values measured *in-situ*) was tested against the expected value (sample size). A precondition

for a t-test is a demonstration of normal distribution. This can be inspected using a histogram, the values were transformed by their natural logarithms.

To compare at plot level, a paired two sample t-test was used. If there are systematic differences between *in-situ* and TRY database values, it is important to test whether the differences are due to either systematically biased entries in the TRY databases or systematic gaps in the databases of the listed species due to missing species. To test for this difference, species that were not present in the plant trait databases were filtered out of the *in-situ* measurements (see below).

The following possible combinations were tested:

Table 2: Matrix of parameter combinations (CWMs and SLA groups) which were tested using a paired two sample t-Test. i = CWM for the in-situ measured values; ii = CWM for the database values; iii = CWM for the in-situ values excluding those species which are missing in the database; a = SLA: petiole excluded; b = SLA: petiole included, c = SLA: undefined if petiole is in- or excluded.

i is compared with ii	ii is compared with iii
i ~ iia	iia ~ iiia
i ~ iib	iib ~ iiib
i ~ iic	iic ~ iiic

Table 3: Species occurrence (x) at plot-level at the Blaueis forefield, sorted by age classes (10 = BL01, BL03, BL06, BL08; 40 = BL02, BL05, BL12; 70 = BL04, BL10, BL11; 100 = BL07, BL09, BL13; 250 = C1-C3).

Species	BL 01	BL 03	BL 06	BL 08	BL 02	BL 05	BL 12	BL 04	BL 10	BL 11	BL 07	BL 09	BL 13	C 1	C 2	C 3
<i>Achillea atrata</i>														x	x	x
<i>Arabis alpina</i>		x			x	x	x	x	X	x	x	x				
<i>Arabis bellidifolia</i>								x	X	x	x		x	x		
<i>Bellidiastrum michelii</i>														x	x	x
<i>Biscutella laevigata</i>														x		x
<i>Bistorta vivipara</i>														x	x	x
<i>Campanula cochleariifolia</i>								x				x	x			
<i>Campanula scheuchzeri</i>														x	x	x
<i>Carex feruginea</i>															x	x
<i>Carex firma</i>												x	x	x	x	x
<i>Carex sempervirens</i>														x	x	x
<i>Cerastium uniflorum</i>		x		x	x	x		x	X	x	x	x	x			
<i>Crepsis terglouensis</i>													x			
<i>Euphrasia minima</i>								x								x
<i>Festuca alpina</i>			x		x		x	x		x	x	x	x	x		x
<i>Galium anisophyllum</i>															x	x
<i>Galium megalospermum</i>											x		x	x		
<i>Heliosperma pusillum</i>					x		x	x	X		x	x	x			
<i>Hornungia alpina</i>	x	x	x	x	x	x	x	x	X	x	x	x	x	x		x
<i>Juncus monanthos</i>														x		x
<i>Linaria alpina</i>							x				x					
<i>Minuartia gerardii</i>											x	x				
<i>Moehringia ciliata</i>	x				x										x	
<i>Mutellina adonidifolia</i>																x
<i>Papaver alpinum</i>					x		x	x	X	x						
<i>Parnassia palustris</i>															x	x
<i>Pedicularis rostratospicata</i>															x	x
<i>Poa alpina</i>		x		x	x	x	x	x	X	x	x	x	x			
<i>Ranunculus alpestris</i>											x		x	x	x	x
<i>Ranunculus montanus</i>																x
<i>Salix serpyllifolia</i>														x	x	x
<i>Saxifraga azoides</i>											x					
<i>Saxifraga moschata</i>		x			x	x			X	x	x	x				
<i>Saxifraga stellaris</i>			x		x						x	x	x			
<i>Scorzoneroideis montana</i>								x			x					
<i>Sesleria caerulea</i>								x				x		x	x	x
<i>Silene acaulis</i>								x		x		x	x	x		
<i>Soldanella alpina</i>														x	x	x
<i>Taraxacum alpinum</i>											x					
<i>Thlaspi rotundifolia</i>		x	x				x	x		x	x	x	x			
<i>Tofieldia pusilla</i>														x		
<i>Valeriana saxatilis</i>														x		
<i>Veronica aphylla</i>												x				
<i>Viola biflora</i>											x	x	x	x	x	

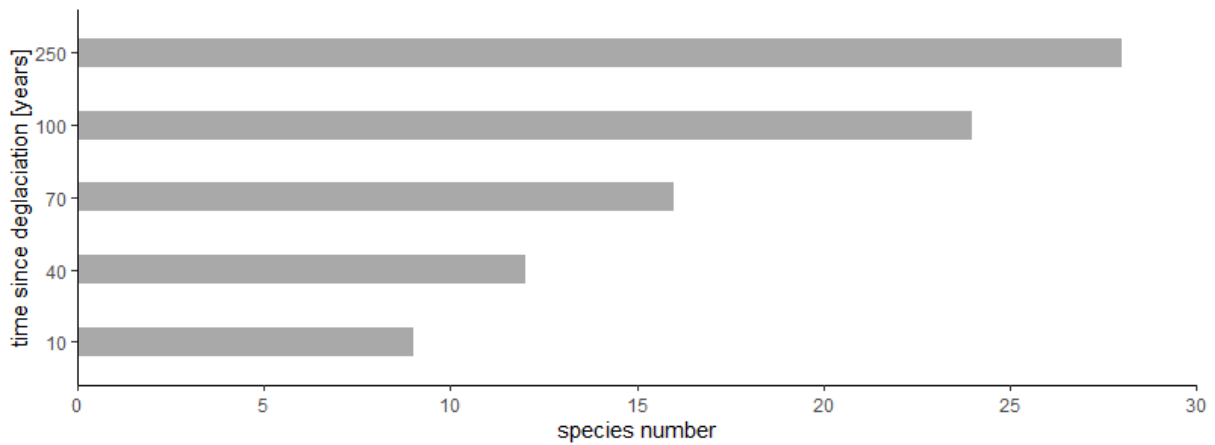


Figure 4: Total plant species number of plots per age class

A total of nine species occurred in the 10-year-old plots: *Arabis alpina*, *Cerastium uniflorum*, *Festuca alpina*, *Hornungia alpina*, *Moehringia ciliata*, *Poa alpina*, *Saxifraga moschata*, *Saxifraga stellaris* and *Thlaspi rotundifolium*. Most of the species initially encountered were found over all age classes, only *Euphrasia minima*, *Moehringia ciliata*, and *Papaver alpinum* did not occur in the 100-year-old plots. There were no species that occurred only in age class 10 or 40 years. There is a total of twenty-four species in age class 100. Newly recorded species that were not present in the younger age classes were *Carex firma*, *Crepis terglouensis*, *Galium megalospermum*, *Ranunculus alpestris*, *Veronica aphylla* and *Viola biflora*. Species that occurred only in the control plots are shown in Figure 3.

A total of twenty-six species of vascular plants were recorded on the Blaueis forefield (excluding control plots), but only nine species had cover values > 5%, and only half of the species (16) had cover values of 2.5%. Most of the time, many species cover is $\leq 1\%$ (Table S3, Appendix 1).

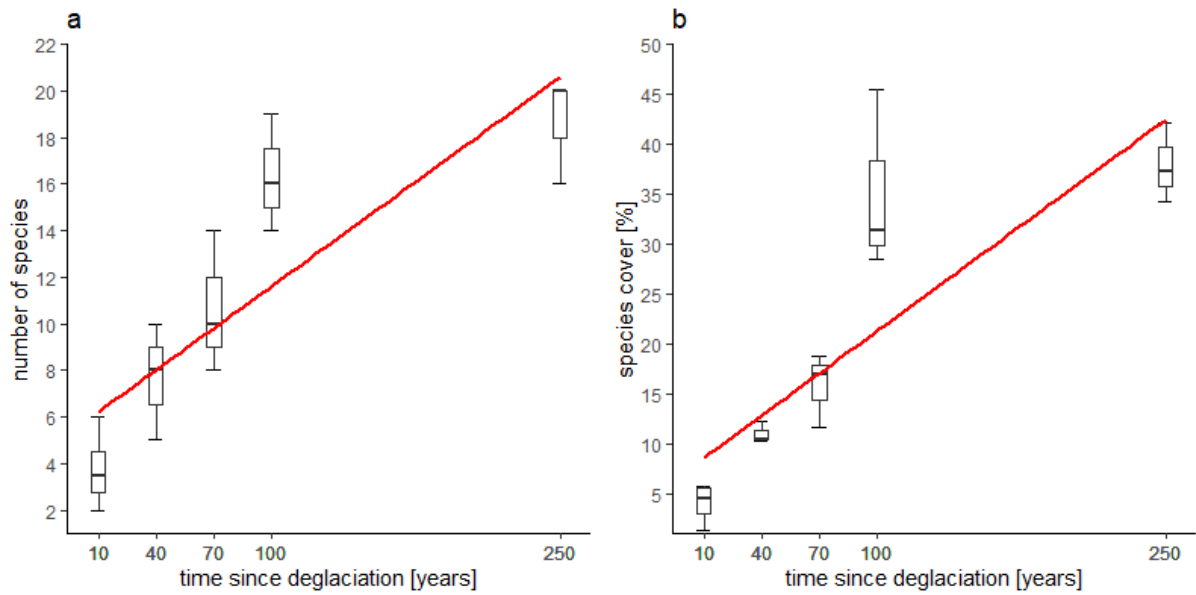


Figure 5: Number of species per plot (m²) along age classes (a) ($R^2 = 70.4$, $a = 5.62$, $b = 0.06$); vegetation cover in % per plot (m²) at the Blaueis forefield (b) ($R^2 = 0.67$, $a = 7.14$, $b = 0.14$). (Coverage values were converted from Braun-Blanquet (1964) scale). Boxes represent the interquartile range; the median is the horizontal line in the box. Linear regression slope is shown in red.

There is a significant increase in species number and cover along the age classes (Figure 5): For species richness, the median for age classes 10 is 3.5 species per plot, for age class 40 it is 8, for age class 70 is 10 and for the 100-year-old plots is 16. For the control plots, the median is 20. For species cover the median for age classes 10 is 4.5, for age class 40 is 10.4, for age class 70 is 17 and for age class 100 is 31.4. For the control plots, the median is 37.2.

The explained variance is remarkably high for both regressions (see figure caption Figure 5).

Vegetation cover is increasing due to both increasing numbers of species and increasing cover values for individual species (Table 2, e.g., *Cerastium uniflorum*).

Specific leaf area

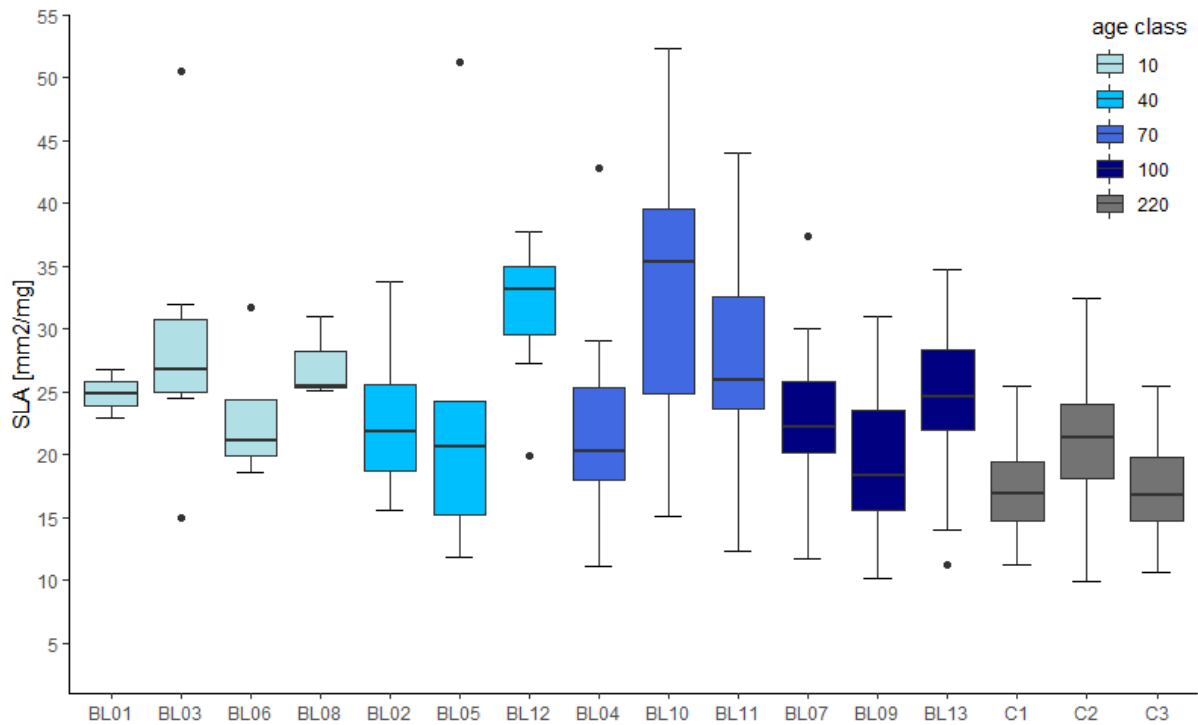


Figure 6: Boxplots of specific leaf area of vascular plants along the studied plots sorted by age classes representing the successional gradients (different shades of blue) at the Blaueis forefield. Boxes represent interquartile range; median is horizontal line in box; dots represent outliers.

The values of specific leaf area (SLA) vary within and between plots, e.g., the ranges within plot BL10 or plot BL05 are very large (Figure 6). For comparison, the ranges within plot BL01 or plot BL08 are much smaller. Within age classes, the plots also vary widely, e.g., within age class 40, where plots BL05 (median = 20.6) and BL12 (median = 33.2) are very different. The same is true for age classes 70, where plots BL04 (median = 20.2) and BL10 (median = 35.3) are very different.

The median of the control plots is in most cases lower than that of the Blaueis plots. To study for possible trends along the successional gradient, the plots were aggregated (Figure 7).

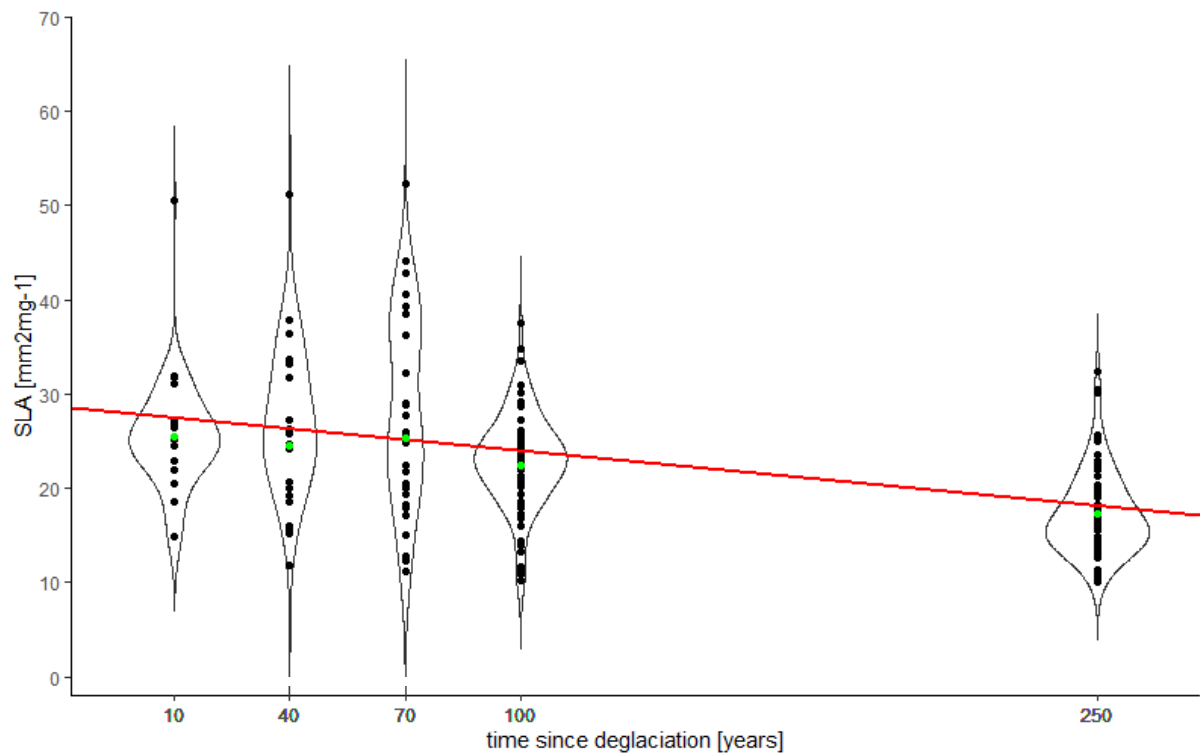


Figure 7: Violin plots of the specific leaf area of vascular plants against time since deglaciation at the Blaueis forefield. The distribution of SLA values is shown as black dots. Median is shown as a green dot. Linear regression is shown in red (fixed effect $R^2 = 0.31$, $a = 27.9$, $b = -0.04$, $p = 0.052$). The width of the plots reflects the weighting by cover.

A marginally significant relationship is observed between the SLA and the time since deglaciation, with moderate amount of variance explained (see figure caption Figure 7).

Comparison of database SLA values with in-situ measurements

Of the fourteen species tested, seven species show a significant difference between the distribution of SLA values observed in the field compared to those of the TRY database group “petiole included” (Table 4). *In-situ* measured values were significant larger for four species and smaller for three species. In contrast to the comparison of the TRY database values with the *in-situ* values of the Try database trait “Petiole excluded” and “undefined if petiole is in- or excluded” (Table S1, Table S2, Appendix 1). Here in both cases the SLA of five species is significant underestimated and only one overestimated by the TRY database values.

Poa alpina, *Carex sempervirens* and *Sesleria caerulea* show larger *in-situ* measured values than TRY database values over all three SLA metrics (“petiole included”, “petiole excluded”, “undefined if petiole is in- or excluded”); conversely, *Viola biflora* shows lower *in-situ* measured values across all 3 groups.

The results of the paired t-test show that there is no significant difference between the tested CWM groups, neither for the comparison between the database values of all three groups and the *in-situ* measured values (Figure 5) or the comparison between the TRY database values of all three groups and the *in-situ* measured values, but without species having values missing in the TRY database (Table 6).

Table 4: Comparison of database values with *in-situ* measured values per species for the SLA trait “Petiole included”. μ = expected value (mean of database values); $M (\pm \sigma)$ = mean of *in-situ* values with standard deviation; t = size of the difference between groups relative to the variation in the sample data; df = degrees of freedom; p -value = error probability (* $0.01 < p \leq 0.05$, ** $0.001 < p \leq 0.01$, *** $p \leq 0.001$).

Species name	μ	$M (\pm \sigma)$	t	df	p -value
<i>Bellidiastrum michelii</i>	3.35	2.98 ± 0.07	-7.03	2	0.02*
<i>Biscutella laevigata</i>	2.97	2.64 ± 0.06	-5.68	1	0.11
<i>Bistorta vivipara</i>	2.79	2.87 ± 0.07	1.82	2	0.21
<i>Campanula scheuchzeri</i>	3.40	3.14 ± 0.05	-6.99	2	0.02*
<i>Carex sempervirens</i>	2.37	2.90 ± 0.11	6.66	2	0.02*
<i>Cerastium uniflorum</i>	3.63	3.37 ± 0.18	-4.17	9	0.002**
<i>Euphrasia minima</i>	3.28	3.23 ± 0.14	-0.33	1	0.79
<i>Juncus monanthos</i>	2.82	2.84 ± 0.03	0.69	1	0.61
<i>Poa alpina</i>	2.83	3.26 ± 0.22	6.40	10	<0.001***
<i>Salix serpyllifolia</i>	2.57	2.66 ± 0.00	26.31	2	0.001*
<i>Saxifraga stellaris</i>	3.15	2.96 ± 0.27	-1.39	4	0.24
<i>Sesleria caerulea</i>	2.88	2.92 ± 0.03	2.34	4	0.88

<i>Silene acaulis</i>	3.17	2.78 ±0.37	-1.82	3	0.17
<i>Viola biflora</i>	3.94	3.22 ±0.02	-59.76	4	<0.001***

Table 5: Comparison of community weighted means (CWM) of SLA based on database values vs. in-situ measured values. *t* = *t*-test statistic value; *df* = degrees of freedom; *p*-value = significance level (* = $p \leq 0.05$).

Try database group	<i>t</i>	<i>df</i>	<i>p</i> -value
SLA: Petiole excluded	-0.67	14	0.515
SLA: Petiole included	-1.80	13	0.094
SLA: undefined if petiole is in- or excluded	0.56	13	0.586

Table 6: Comparison of community weighted means (CWM) of SLA based on database values vs. in-situ values excluding those species which are missing in database. *t* = *t*-test statistic value; *df*= degrees of freedom; *p*-value = significance level (* = $p \leq 0.05$).

Try database group	<i>t</i>	<i>df</i>	<i>p</i> -value
SLA: Petiole excluded	0.16	14	0.877
SLA: Petiole included	-1.14	13	0.274
SLA: undefined if petiole is in- or excluded	1.31	13	0.213

Discussion

Species numbers and cover along the glacier forefield chronosequence

At the Blaueis forefield, both species numbers and cover increased significantly with increasing age of the glacier forefield. The number of species increased from 3.5 species (median) in the age class 10 to 16 species (median) in age class 100 compared to 20 species (median) in the control plots. Cover increased from 4.5% (median) in age class 10 to 31.4% (median) in age class 100 compared to 37.2% (median) in the control plots. Similar to the patterns in Blaueis. This finding corresponds well with Gobbi et al. (2010) who showed that vegetation cover and the number of species increased until 150 years after deglaciation and Late Glacial, but with a steeper increase between 40 and 150 years.

Other studies differ greatly from the results of my study. According to Nagl & Erschbamer (2010), it can be observed that the vegetation cover at the glacier forefield of the Rootmoosferner in the Austrian Ötztal is already between 30-50% after 15-40 years. Subsequently, between 40 and 80 years after deglaciation, a peak in species numbers is reached by a cover of 60-70%. The first shrub species (e.g., *Salix* spp.) appear or initial alpine grasslands develop. In the late successional stage, first tree species such as *Larix decidua* appear and the number of species decreases (Nagl & Erschbamer, 2010; Raffl et al., 2006). Raffl et al. (2006) and Prach & Rachlewicz (2012) have found similar results; species numbers and cover gradually increase up to 50 years after deglaciation and then peak. The species composition and cover of the latest succession stages, i.e., those on the LIA moraine, resembles that of the nearby areas outside the glacier forefields. Schumann et al. (2016) observed a plateau of species richness in the mid to late successional stage in the Eastern Alps, while species richness continued to increase in the Western Alps. At the Blaueis forefield, species numbers and cover increase at a lower rate, species of later succession do not occur.

The differences between the patterns observed on Blaueis forefield compared to others are striking, but I can only speculate about the reasons. The location of the glaciers in the Alps is very different. While the glacier forefield of this study is located in the northern limestone Alps, the glacier forefields of most studies are located in the Central Alps (Burga, 1999; Ficetola et al., 2021; Raffl et al., 2006). There are geochemical and gross morphological differences between regions that influence rock weathering and soil development (Walker et al., 2010). Limestone is highly water soluble compared to other typical rocks of the Alps and weathers

mainly chemically. Karstified (Limestone) plateaus have largely subsurface water drainage and almost no surface water. Soil formation on limestone is protracted, as is the accumulation of nutrients and the time it takes for the water balance to stabilize (Zepp, 2014). In general, increasing age is related to higher surface stability, due to soil development and organic matter accumulation in the Central Alps (Erschbamer et al., 2008; Raffl et al., 2006). This change in abiotic features affects the rate and species of colonization (Raffl et al., 2006). A positive feedback loop occurs between sediment, soils, vegetation and fauna (Khedim et al., 2021).

One fundamental process for primary succession in glacier forefields is the colonization reaching the bare ground (Bradshaw, 1993). Here, the type of glacier and the location of the glacier terminus are essential (Fickert et al., 2017), which in turn influence the abiotic conditions. Plant colonization in the forefields of large glaciers that reach alpine or subalpine areas is more rapid and species-rich than in the forefields of smaller glaciers at upper alpine or subnival elevations (Burga, 1999; Burga et al., 2010). An important driver of initial colonization of glacier forefields is landslides or erosion (H. R. Miller & Lane, 2019), which can set back the development of vegetation by years or decades (Rehberger, 2002). Disturbance is a dynamic factor that creates often stress to plants but can also have positive effects. Stawska (2017) observed that in areas with sediment erosion and deposition, fine material is deposited that promotes moisture retention and soil development (Whittaker, 1991). Vegetation developed much more in these areas (Stawska, 2017). In addition, increased input of plant fragments or seeds from outside the glacier forefield by snow avalanches, debris flows on slopes and landslides, or simply the force of gravity, into the forefield is likely, facilitating the onset of succession (Nagl & Erschbamer, 2010; Raffl et al., 2006). This is much more likely in valley glaciers, for example on the Morteratsch glacier in the Swiss Engadine (Burga et al., 2010). Site conditions also change with elevation (e.g., higher temperature shifts, duration of snow cover, less wind, higher nutrient inputs). Eichel (2019) stated improved environmental conditions (e.g., higher temperatures and more advanced soil development) after 15-40 years after deglaciation.

The Blaueis, at about 2165 m a.s.l., is the lowest glacier in the Alps (Hagg, 2021), but it lies in the cirque below Hochkalter with steep side walls without vegetation above the glacier, so that seed input from above is likely rare. Fickert et al. (2017) observed that low elevation and a rich source pool alone were not sufficient to promote rapid plant colonization at the onset of succession. Distance from the source pool of successful colonizers (scree slope species rather

than, e.g., alpine heath species) is critical. Climate change-induced glacier melt leads to a shift of the glacier terminus and thus to a shift of the new glacier forefields to higher elevations. In some cases, this means an increasing distance to alpine vegetation, even for glaciers that terminated in alpine heath or within the treeline ecotone during the LIA. Hence, the deglaciated Blaueis forefield need to be colonized largely from below, rather than above (as in Central Alpine valley glaciers).

The newly exposed ice-free areas are colonized by vascular plants after one or two years (Cannone et al., 2008; Erschbamer et al., 1999). Species like *Arabis alpina*, *Cerastium uniflorum* and *Poa alpina* are pioneer species (Caccianiga et al., 2006) that are successful colonizers. They tolerate high solar radiation (Robbins & Matthews, 2014), produce small seeds that are dispersed by wind (Nagl & Erschbamer, 2010), and germinate even in cold conditions. As the Blaueis forefield ages, the number of "new" species also increases. Even the species that became established at the beginning remain. The age classes of Blaueis are quite mixed in their species composition, with virtually no species specifically occurring only in a particular age class. Only some species occur exclusively in the older age classes (e.g., *Carex firma* or *Veronica aphylla*). This indicates an stochastic species composition at the beginning of the colonization of the glacier forefield. Hanusch et al. (2022) examined five groups of organisms along an ecological gradient of primary succession in a glacier forefield. The results suggest that stochastic processes (likely dispersal-dominated) are replaced by more deterministic processes (such as environmental filtering and biotic interactions) after about 60 years of succession. This threshold also describes a change in community composition before and after the threshold. Initially, pioneer species dominate, reaching their abundance optimum early in the succession. This is followed by taxa that have no clear preference. Subsequently, the specialists of the later successional stages displace the specialists of the earlier successional stages. I assume that on the Blaueis forefield, the stochastic processes persist longer than described by Hanusch et al. (2022). Which species establish first depends in part on site conditions (i.e., environmental filters) and species traits (e.g., dispersal ability) but is primarily stochastic. In the case of Blaueis, no seed entry from above is possible, but predominantly by wind (or animals and humans). Since it is difficult for the species and their diaspores to reach the forefield, the species that were there first remain because they are not displaced by more competitive species. Because there is only minimal competition for nutrients, water, and space comparable to the forefields in other studies (Schumann et al., 2016), the increase in species numbers and cover is not

stagnating. Rather, stochastic processes are the limiting factors here for cover and species numbers to be generally lower, even if they are not stagnant.

There are not only different site conditions between plots of different terrain age, but also differences even on a small spatial scale. Sites can have microtopographic security due to depressions and protection by larger rocks (Nagl & Erschbamer, 2010; Raffl et al., 2006). This may cause differences between the plots within an age class. For example, plot BL13 is located next to a rock face. Compared to the other plots in the age classes 100, the number of species occurring is the largest with fourteen species (Table 3). This may be related to more favorable conditions such as lower wind speeds, less erosion, and higher moisture availability (Jumpponen et al., 1999). We also noticed that BL13, unlike the other plots, has a good water supply due to a small rivulet and its location below a slope. Pauli et al. (2012) have shown that improved water availability can contribute to an increase in species numbers.

Loher et al. (2013) found that while species numbers and cover increased with time since deglaciation, the same trend was observed in combination with the elevation factor. Since the investigated plots are at similar elevations (Table 1), I conclude that the trend in species number and cover can be explained by the time since deglaciation rather than elevation.

Specific leaf area

SLA increased marginally significant along the chronosequence of deglaciation. Previous studies have identified SLA responses to processes such as abandonment of cropland and grassland (Kahmen & Poschlod, 2004), landuse (Díaz et al., 2001) or disturbance (McIntyre et al., 1995, Lavorel et al., 1999). In addition, there are some studies examining the effects of drought on intraspecific SLA variation (Apple et al., 2022). According to Diaz et al. (2004), pioneer species often have a higher SLA typical of fast-growing ruderal species. Species with tender leaves are replaced during succession by species with dense leaves that have a low SLA, invest more dry mass per leaf, have low relative growth rates, and whose leaves have a longer life span (Shipley et al., 2005). This is typical of "conservative/restrained" species (Diaz et al., 2004). However, these results apply more to successional processes in lowlands and are less well studied in the high mountains.

Due to the fact that plants are exposed to different abiotic and biotic environmental factors (Weiher et al., 1999), there are different adaption types. Grime (1977) defines three basic adaptation types of plant life. The c-type (competitor) is in competition with other plant

species. The s-type (stress) is able to thrive under extreme site conditions that inherently limit plant production (light, water, and mineral deficiencies). The r-type (ruderal) is more susceptible to disturbance factors that can lead to destruction of plant biomass (e.g., intensification factors such as grazing or extreme climatic events such as frost, wind, and soil erosion). The r-species are generally short-lived but widely distributed. There are also mixed and transitional types. For species growing on alpine glacial forefields, competition at the beginning is secondary; adaptation to harsh environmental conditions such as extreme cold, wind, limited resources, intense sunlight, disturbance and snow cover duration is more important (Cornwell & Ackerly, 2009). The early pioneer phase species (e.g., *Arabis alpina*, *Cerastium uniflorum* and *Hornungia alpina*) show high SLA values and are characterized by a short leaf life, low leaf dry mass and rapid growth (Shipley et al., 2005; Wright & Westoby, 2000). At the beginning of succession in glacier forefields, these are stress-tolerant pioneer species with ruderal strategies that can handle the harsh conditions and strong stress gradient.

Since the number of species and vegetation cover increased, but the average SLA against age did decrease only slightly, an overall increase in biomass at the community level seems more likely than a fundamental change in plant function, as it has already been stated by Gobbi et al. (2010). In the northern Alpine glacier forefields, no phase of "stabilization" is reached where biotic interactions and competition become important (except in the control plots). Therefore, I can explain the little declines in SLA by the strongly retarded succession. The stochastic factors act longer than the deterministic ones compared to other (central Alpine) glacier forefields.

The slight negative SLA trend indicates more stable, well-developed vegetation in the late successional plots with increasing stress tolerance and competitive of species. These results are in agreement with the results of Caccianiga (2006), who mentioned species turnover along a gradient of the glacier forefield from ruderal and stress tolerant species to more stress tolerant competitive species. Fickert et al. (2017) recorded a total of 29 vascular plant species in areas that have been deglaciated for about 50 years, more than half of which are both competitive and stress tolerant; about one-third of the species also show ruderal characteristics in Grime's scheme (1977). This indicates a faster change in dominance from stochastic processes during initial stages of primary succession to deterministic processes in later stages than in the Blaueis forefield.

Gobbi (2010) also indicated a negative trend of SLA along the age gradient of the glacier forefields, with a significant difference between last step of the succession (age class >150) and younger succession stages. The plots > 150 years are dominated by slow-growing species with a low SLA (Gobbi et al., 2010).

The observed variation of SLA within plots is due to interspecific variability in SLA values. A difference in SLA values between plots in an age class may be due to both intra- and interspecific variability in SLA values. A cause of variability independent of the age of the plots may be either the stochasticity dominating at the beginning of succession or different site conditions (see chapter Species numbers and cover). Dwyer et al. (2014) also noted that SLA varied intra- and interspecifically, influenced by local environmental conditions. A positive correlation of SLA with factors such as shade, nutrient enrichment, and increased water availability was observed (Apple et al., 2022; Galmes et al., 2005). Apple et al. (2022) found significantly lower SLA values with increasing distance from the water-rich snowfield edge. Reduction in SLA in response to drought or water stress can be considered a phenotypic adjustment for improved water-use efficiency (Wellstein et al., 2017).

Several studies have shown that in addition to time since glaciation other factors (e.g., topography, solar radiation, soil moisture) also have an influence (Burga et al., 2010; Raffl et al., 2006). A combination of the time factor with environmental and stochastic factors (especially stochastic disturbances such as avalanches, rockfall, landslides ect.) leads to heterogeneous vegetation patterns on glacier forefields (Matthews & Whittaker, 1987; Raffl et al., 2006).

Comparison between TRY database and *in-situ* values

For the fourteen species studied, I found no significant difference between the TRY database values and the *in-situ* values across plot levels, while at the species levels there are significant differences for some species.

By comparing two sites (mesic wet meadow and salt marsh), Cordlandwehr's (2013) study showed that the accuracy of traits retrieved from a database depends on habitat type and that this accuracy is lower for extreme habitats. One reason for this is that database requests cannot be filtered by location of record. When traits are retrieved from the database, database records by species identity often include an averaged value, which includes values for different populations and habitats distributed over different elevations and longitudes. This can be both

an advantage and a disadvantage, as aggregating trait data by species captures much of the trait variation. However, if the data are already provided as aggregated values, the variation in the original data is lost, and the site specificity due to intraspecific variability is consequently lost. As mentioned earlier, different environmental conditions affect the functional traits (Lavorel et al., 1997) that make species better adapted to the conditions. Therefore, database values derived from individuals sampled in a wide range of habitats are sometimes too inaccurate for predicting the distribution of trait values at extreme and therefore very specific sites.

Because glacier forefield areas are habitats with extreme abiotic conditions, I hypothesized that traits retrieved from the TRY database would have a rather low agreement with the *in-situ* measured values, similar to the findings of Cordlandwehr (2013). However, it has been shown that while the alpine-nival sites in this study are extreme habitats, the environmental filtering also results in a small species pool with specialized species adapted to these conditions. A large part of the species occurs only in alpine areas, e.g., *Cerastium uniflorum* or *Euphrasia minima* (Table S4, Appendix 1). Therefore, it is likely that the values retrieved from the TRY database are also from comparable habitats. Thus, by implication, filtering by location (inside the Alps) would likely barely influence the analyses, as putatively also data from TRY were sampled in such locations. However, for species such as *Viola biflora* SLA is greatly overestimated by the TRY database values. This can be due to the fact that *Viola biflora* does not only occur at high elevations, but also in updwelling-wet valley locations (Schmeil et al., 2016) (Table S4, Appendix 1). Therefore, it is possible that the majority of specimen recorded in the TRY database was sampled in moister lower elevations, which can lead to significantly higher database values for SLA (Apple et al., 2022).

In the case of *Salix serpyllifolia*, it is noticeable that the trait values from TRY differ significantly from *in-situ* measurements. I suspect that it may be because *Salix serpyllifolia* is a late successional species and young specimens are more likely to show up in my measurements, while the measurements in TRY database are probably measured from large stands composed of old specimens. It is well-known that older specimens have lower SLA values for most species due to the increasing cuticle thickness (England & Attiwill, 2006; Marron et al., 2008).

It should also be noted that the degrees of freedom (df) in this study are very low. This is the consequence of a small sample size, and consequently, it is difficult to come up with significant

results. For species such as *Campanula scheuchzeri* or *Euphrasia minima*, it is noticeable that the results would be significantly different if the sample size was larger (given their t-values). For some species, the required sample size for the paired t-test was even not available, so a comparison between TRY database values and *in-situ* values was not possible in the first place, e.g., for *Ranunculus montanus* or *Veronica aphylla*. The sample size can be a maximum of 16 (i.e. the number of plots), but most species are much rarer, so degrees of freedom are < 10 for all species tested. For some species, such as *Moehringia ciliate* or *Hornungia alpina*, several traits such as plant height are stored in the TRY database, but SLA is not, so no comparison could be made.

Comparing the CWM of the TRY database values and the *in-situ* values, I have found that despite species-specific differences, SLA is not consistently over- or underestimated by the values obtained from TRY, in contrast to the findings of Cordlandwehr et al. (2013). So, there is no systematic bias at the community level of the SLA values from Blaueis glacier forefields. When comparing the CWM of the TRY database values with the *in-situ* measured values and the *in-situ* values without the species missing from the TRY database, there were no significant differences, but it was noticeable that the differences were even smaller when comparing the CWM between *in-situ* excluding those species which are missing in the TRY database and database values. Because some species are missing, CWM SLA values could not be calculated for some plots (e.g., plot BL01), which reduces the power of the analyses for all three groups. In the future, more species or traits need to be added to the TRY database.

Methodological considerations

There are some assumptions that were made prior to the start of the vegetation surveys that need to be taken into consideration. The selection of sample sites was consistent with the two assumptions (1. all sites were exposed to the same initial environmental conditions, 2. underwent the same sequence of changes) for the chronosequence approach. However, allogenic factors (changes caused by factors other than time) also influence the rate or progression of successional sequences in heterogeneous ways. These include initial environmental conditions (e.g., substrate properties and microtopography) and geomorphological disturbances (Walker et al., 2010; Wojcik et al., 2021). There may also be differences in environmental history during succession. Matthews & Vater (2015) found in their study that there were environmental differences between plots due to variations in the rate of glacier retreat. Newly deglaciated areas that were at the terminus of the glacier at the time of

slower glacier retreat rate were exposed to factors such as glacial winds longer than areas with faster glacier retreat. Another factor affecting the environmental history is the global warming of about 0.6 °C in the 20th century (Jones & Moberg, 2003). This temperature increase has accelerated significantly in recent years. The consequences are, for example, a shorter duration of snow cover (ZAMG, 2022) or a faster initial colonization of surface-active invertebrates (Kaufmann, 2001). Still, when selecting the sampling sites, care was taken to minimize those effects, specifically those related to disturbance regimes, as much as possible.

Another fact that needs to be discussed is that for the scaling of the age classes, the control plots were arbitrarily dated to 250 years. The exact date of glacial retreat is not known, so they may be deglaciated even for much longer. When using ordinal classes though, the numerical character of the "true" age classes would be lost. In addition, the result versus age classes is calculated as orthogonal polynomial contrasts that are difficult to interpret. In addition, this would distort the results because the control plots are much older than the age classes 10-100, hence the "age" was scaled metrically (except for the arbitrarily assigned age of the control plots).

Using a trait-based approach also yielded some difficulties: First, not for all species present SLA could be measure *in-situ*. For *Linaria alpina* (abundance <0.1), only cover and number were recorded on all plots, but not SLA. For *Arabis bellidifolia* or *Silene acaulis*, only a few individuals occurred (abundance <1) on or around respective plots, so they were not recorded. But since this relates to usually rare species, the impact on community weighted means should be negligible.

Second, variations in SLA may also be due to measurement errors. In particular, the determination of the leaf surface may also have been subject to errors. Leaf morphology and light conditions partly prevented a precise measurement. The used app LeafByte is sensitive to shadow due to poor light management. In addition, curled leaves can cause shadows and overlaps can lead to an underestimation of the leaf surface (Getman-Pickering et al., 2020). In addition, it should be noted that there was likely an inaccuracy in the SLA due to an inaccuracy in establishing the basis for the size calibration. Four black dots forming a square (e.g., 10 x 10 cm) were plotted on a white sheet of paper. However, the scale mark is recognized by the app as foreground only if the dots are thick enough. If the dots are drawn too thinly, they are recognized as background and need to be set manually on the screen, which again involves a

probability of error. The larger points can cause the center of the point and thus the reference surface to be determined more inaccurately, which has a greater effect on smaller leaves in particular. However, the error is not systematic, but varies in different directions depending on the location and size of the points. A systematic over- or underestimation of the SLA can therefore not be assumed, only the error noise is increased.

Conclusion

The initial conditions for successional vegetation are ideosyncratic for each glacier forefield and are strongly influenced by the location of the glacier within the Alps, which is reflected in different patterns and processes of vegetation succession. I showed that species cover and number at the Blaueis glacier forefield increase at a slower and lower rate compared to succession in the Central Alps, and species of later succession like tree or shrub species are not present in the Blaueis forefield plots. Most species of glacial forefields are pioneer species that have a comparably high SLA. They are characterized by short leaf life, low leaf dry mass and rapid growth. My results suggest that the pattern of vegetation succession at the Blaueis differs from other studies because stochastic processes that are usually most important in the early stages of primary succession (Cutler et al., 2008) persist longer at the Blaueis forefield and become less important much later (i.e., beyond the age extent of the current succession). Colonization appears to be a combination of the chance of seed arrival and suitable establishment conditions. Different initial morphological and geochemical conditions play a major role. Deterministic processes only become more dominant in later succession stages. Consequently, only the lower SLA in the control plots indicates more stable, well-developed vegetation with competitive stress-tolerance species (Shipley et al., 2005). The comparison between studies from the Central Alps and the Northern Limestone Alps shows that a uniform development of successional vegetation in the Alps cannot be assumed.

My study suggests that SLA values from databases can be used as a surrogate for field measurements at alpine glacier forefields. Comparing TRY database values with the *in-situ* measured ones, I conclude that there are no systematic differences between the TRY database values and the *in-situ* values. In general, the differences appear to be more species-specific. However, this over- or underestimation of species-level values did not have a significant impact on community level trait composition in my study. Cordlandwehr et al. (2013) suggested that intraspecific variability that may arise in response to specific environmental conditions of the population in which they were measured (Lavorel et al., 1997) when using trait values from databases. If the species occur only at comparable sites (such as strict alpine species), database values seem to agree with those *in-situ* measured values.

Outlook

Vegetation characteristics were examined for trends in plots along a chronosequence of glacier retreat. In summary, chronosequences can be used to draw conclusions about changes in species numbers and cover on ice-free plots over varying lengths of time. Since the plots are part of a series of long-term studies, the chronosequences will be combined with ongoing permanent observations. In this way, it can be assessed in subsequent years whether the developments now evident in the chronosequences are mirrored in the permanent observation plots at the corresponding age of succession.

My findings further support the relevance of taking the different patterns and processes of vegetation succession depending on the location and morphology of the glacier forefields. To confirm these presumed processes and to formulate more general statements, further studies including other glacier forefields of the Northern Limestone Alps would be necessary. In addition, there is the question of how other functional traits behave and what the resulting differences in community composition would be. Other traits include canopy height, seed mass or leaf dry matter content (LDMC). LDMC is the ratio of leaf dry matter to leaf fresh matter and is negatively correlated with potential relative growth rate and positively correlated with leaf longevity. LDMC can be determined independently of leaf area (Cornelissen et al. 2003).

With rising temperatures, the location of glacier termini will be in different environmental conditions (i.e., higher altitude and associated climatic, geological and edaphic conditions), in contrast to the location after the end of the LIA. Thus, it must be expected in the future that this will not only change the distance to potential seed sources, but also the course of the succession. Future studies should take this into account.

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Appendix 1

Table S1: Comparison of database values with in-situ measured values per species for the SLA trait “Petiole excluded”. μ = expected value (mean of database values); $M (\pm \sigma)$ = mean of in-situ values with standard deviation; t = size of the difference between groups relative to the variation in the sample data.; df = degrees of freedom; p -value = error probability (* $0.01 < p \leq 0.05$, ** $0.001 < p \leq 0.01$, *** $p \leq 0.001$).

Species name	μ	$M (\pm \sigma)$	t	df	p -value
<i>Arabis alpina</i>	3.192	3.23 \pm 0.32	0.33	8	0.75
<i>Bistorta vivipara</i>	2.766	2.88 \pm 0.09	-2.52	2	0.13
<i>Campanula cochleariifolia</i>	3.295	3.17 \pm 0.07	-2.52	2	0.13
<i>Campanula scheuchzeri</i>	2.762	3.14 \pm 0.05	10.35	2	0.13
<i>Carex sempervirens</i>	2.565	2.90 \pm 0.11	4.22	2	0.05*
<i>Cerastium uniflorum</i>	3.455	3.37 \pm 0.18	-1.34	9	0.21
<i>Euphrasia minima</i>	2.555	3.23 \pm 0.14	4.9	1	0.12
<i>Pedicularis rostratospicata</i>	2.662	2.81 \pm 0.19	0.82	1	0.56
<i>Poa alpina</i>	3.209	3.26 \pm 0.22	0.8	10	<0.001***
<i>Salix serpyllifolia</i>	2.289	2.65 \pm 0.00	106.69	2	<0.001***
<i>Saxifraga stellaris</i>	2.866	2.96 \pm 0.27	0.72	4	0.51
<i>Sesleria caerulea</i>	2.630	2.92 \pm 0.03	19.25	4	<0.001***
<i>Silene acaulis</i>	2.177	2.78 \pm 0.37	2.8	3	0.05*
<i>Viola biflora</i>	3.948	3.22 \pm 0.02	-60.46	4	<0.001***

Table S2: Comparison of database values with in-situ measured values per species for the SLA trait “undefined if petiole is in- or excluded”. μ = expected value (mean of database values); $M (\pm \sigma)$ = mean of in-situ values with standard deviation; t = size of the difference between groups relative to the variation in the sample data.; df = degrees of freedom; p -value = error probability (* $0.01 < p \leq 0.05$, ** $0.001 < p \leq 0.01$, *** $p \leq 0.001$).

Species name	μ	$M (\pm \sigma)$	t	df	p -value
<i>Arabis alpina</i>	3.270	3.23 \pm 0.32	-0.36	8	0.73
<i>Bistorta vivipara</i>	2.670	2.87 \pm 0.07	4.3	2	0.05*
<i>Campanula scheuchzeri</i>	2.607	3.14 \pm 0.05	14.55	2	0.01*
<i>Carex sempervirens</i>	2.504	2.90 \pm 0.11	4.97	2	0.04*
<i>Cerastium uniflorum</i>	3.318	3.37 \pm 0.18	0.89	9	0.39
<i>Euphrasia minima</i>	3.003	3.23 \pm 0.14	1.66	1	0.34
<i>Poa alpina</i>	2.772	3.26 \pm 0.22	7.2	10	<0.001***
<i>Sesleria caerulea</i>	2.578	2.92 \pm 0.03	22.75	4	<0.001***
<i>Silene acaulis</i>	2.645	2.78 \pm 0.37	0.61	3	0.59
<i>Viola biflora</i>	3.940	3.22 \pm 0.02	-59.78	4	<0.001***

Table S3: Species occurrence with SLA and cover at plot-level.

Plot	Age classes	Species name	SLA (mm ² mg ⁻¹)	Species cover (in %)
BL01	10	<i>Hornungia alpina</i>	22.887	2.5
		<i>Moehringia ciliata</i>	26.814	1
BL02	40	<i>Arabis alpina</i>	19.174	0.1
		<i>Cerastium uniflorum</i>	25.872	1
		<i>Festuca alpina</i>	19.150	1
		<i>Heliosperma pusillum</i>	26.234	1
		<i>Hornungia alpina</i>	24.409	2.5
		<i>Moehringia ciliata</i>	18.509	2.5
		<i>Papaver alpinum</i>	24.668	1
		<i>Poa alpina</i>	15.570	1
		<i>Saxifraga moschata</i>	33.718	0.1
		<i>Saxifraga stellaris</i>	15.932	0.1
BL03	10	<i>Arabis alpina</i>	26.402	1
		<i>Cerastium uniflorum</i>	31.933	0.1
		<i>Hornungia alpina</i>	24.530	2.5
		<i>Poa alpina</i>	27.213	1
		<i>Saxifraga moschata</i>	50.560	0.1
		<i>Thlaspi rotundifolium</i>	14.929	1
BL04	70	<i>Arabis alpina</i>	20.550	0.1
		<i>Arabis bellidifolia</i>	12.838	0.1
		<i>Campanula chochleriifolia</i>	21.852	1
		<i>Cerastium uniflorum</i>	25.256	2.5
		<i>Euphrasia minima</i>	29.061	0.1
		<i>Festuca alpina</i>	19.361	2.5
		<i>Heliosperma pusillum</i>	27.771	1
		<i>Hornungia alpina</i>	17.890	2.5
		<i>Papaver alpinum</i>	19.941	1
		<i>Poa alpina</i>	25.415	1
		<i>Saxifraga moschata</i>	42.757	2.5
		<i>Sesleria caerulea</i>	18.174	0.1
		<i>Silene acaulis</i>	17.049	0.1
		<i>Thlaspi rotundifolia</i>	11.173	2.5
BL05	40	<i>Arabis alpina</i>	51.200	0.1
		<i>Cerastium uniflorum</i>	24.200	10
		<i>Hornungia alpina</i>	15.200	0.1
		<i>Poa alpina</i>	20.600	0.1
		<i>Saxifraga moschata</i>	11.800	0.1
BL06	10	<i>Festuca alpina</i>	20.441	0.1
		<i>Hornungia alpina</i>	31.696	0.1
		<i>Saxifraga stellaris</i>	21.889	0.1
		<i>Thlaspi rotundifolium</i>	18.537	1

BL07	100	<i>Arabis alpina</i>	20.711	1
		<i>Arabis bellidifolia</i>	-	0.1
		<i>Campanula cochleariifolia</i>	26.060	2.5
		<i>Cerastium uniflorum</i>	23.400	1
		<i>Festuca alpina</i>	22.190	10
		<i>Galium megalospermum</i>	26.189	1
		<i>Heliosperma pusillum</i>	22.776	0.1
		<i>Hornungia alpina</i>	19.327	2.5
		<i>Linaria alpina</i>	-	0.1
		<i>Minuartia gerardii</i>	20.929	1
		<i>Poa alpina</i>	30.087	1
		<i>Ranunculus alpestris</i>	16.739	1
		<i>Saxifraga aizoides</i>	17.311	0.1
		<i>Saxifraga moschata</i>	37.443	1
		<i>Saxifraga stellaris</i>	20.139	0.1
		<i>Scorzoneroides montana</i>	20.948	2.5
		<i>Taraxacum alpina</i>	25.123	1
		<i>Thlaspi rotundifolium</i>	11.733	2.5
		<i>Viola biflora</i>	25.826	0.1
BL08	10	<i>Cerastium uniflorum</i>	25.471	1
		<i>Hornungia alpina</i>	25.137	1
		<i>Poa alpina</i>	31.047	2.5
BL09	100	<i>Arabis alpina</i>	17.007	1
		<i>Campanula cochleariifolia</i>	23.441	0.1
		<i>Carex firma</i>	14.312	0.1
		<i>Cerastium uniflorum</i>	28.905	10
		<i>Festuca alpina</i>	19.358	10
		<i>Heliosperma pusillum</i>	23.800	10
		<i>Hornungia alpina</i>	18.571	2.5
		<i>Minuartia gerardii</i>	15.969	1
		<i>Poa alpina</i>	22.495	1
		<i>Saxifraga moschata</i>	31.000	2.5
		<i>Saxifraga stellaris</i>	13.337	0.1
		<i>Sesleria caerulea</i>	17.927	2.5
		<i>Silene acaulis</i>	10.889	1
		<i>Thlaspi rotundifolium</i>	10.168	1
		<i>Veronica aphylla</i>	18.143	0.1
		<i>Viola biflora</i>	24.413	2.5
BL10	70	<i>Arabis alpina</i>	25.942	2.5
		<i>Arabis bellidifolia</i>	15.038	1
		<i>Cerastium uniflorum</i>	40.620	2.5
		<i>Heliosperma pusillum</i>	38.439	1
		<i>Hornungia alpina</i>	21.748	2.5
		<i>Papaver alpinum ssp. Sendtneri</i>	39.262	1
		<i>Poa alpina</i>	32.176	1
		<i>Saxifraga moschata</i>	52.341	0.1
BL11	70	<i>Arabis alpina</i>	25.907	1

		<i>Arabis bellidifolia</i>	-	0.1
		<i>Cerastium uniflorum</i>	36.288	10
		<i>Festuca alpina</i>	22.485	1
		<i>Hornungia alpina</i>	24.870	2.5
		<i>Papaver alpinum</i>	-	1
		<i>Poa alpina</i>	28.864	1
		<i>Saxifraga moschata</i>	44.056	1
		<i>Silene acaulis</i>	-	0.1
		<i>Thlaspi rotundifolium</i>	12.337	1
BL12	40	<i>Arabis alpina</i>	33.452	2.5
		<i>Festuca alpina</i>	27.261	1
		<i>Heliosperma pusillum</i>	31.760	2.5
		<i>Hornungia alpina</i>	36.443	1
		<i>Papaver alpinum ssp. Sendtneri</i>	37.786	2.5
		<i>Poa alpina</i>	33.199	2.5
		<i>Thlaspi rotundifolium</i>	19.972	0.1
BL13	100	<i>Arabis bellidifolia</i>	13.954	0.1
		<i>Carex firma</i>	11.210	1
		<i>Cerastium uniflorum</i>	34.750	0.1
		<i>Crepis terglouensis</i>	22.341	0.1
		<i>Festuca alpina</i>	24.807	2.5
		<i>Galium megalospermum</i>	25.588	1
		<i>Heliosperma pusillum</i>	21.875	2.5
		<i>Hornungia alpina</i>	33.532	1
		<i>Poa alpina</i>	27.257	1
		<i>Ranunculus alpestris</i>	23.156	10
		<i>Saxifraga stellaris</i>	29.229	1
		<i>Silene acaulis</i>	28.759	0.1
		<i>Thlaspi rotundifolium</i>	21.325	1
		<i>Viola biflora</i>	24.422	10
C1	250	<i>Achillea atrata</i>	22.847	1
		<i>Arabis bellidifolia</i>	16.576	0.1
		<i>Bellidiastrum michelii</i>	20.288	2.5
		<i>Biscutella laevigata</i>	13.220	2.5
		<i>Bistorta vivipara</i>	16.898	2.5
		<i>Campanula scheuchzeri</i>	22.791	1
		<i>Carex firma</i>	13.130	2.5
		<i>Carex sempervirens</i>	17.238	2.5
		<i>Festuca alpina</i>	14.893	2.5
		<i>Galium megalospermum</i>	25.442	1
		<i>Hornungia alpina</i>	18.179	0.1
		<i>Juncus monanthos</i>	17.589	2.5
		<i>Ranunculus alpestris</i>	15.565	2.5
		<i>Salix serpyllifolia</i>	14.163	2.5
		<i>Sesleria caerulea</i>	19.100	1
		<i>Silene acaulis</i>	12.579	2
		<i>Soldanella alpina</i>	11.260	2.5
		<i>Tofieldia pusilla</i>	16.139	2.5

		<i>Valeriana saxatilis</i>	16.807	2.5
		<i>Viola biflora</i>	25.373	1
C2	250	<i>Achillea atrata</i>	30.152	1
		<i>Bellidiastrum michelii</i>	21.339	2.5
		<i>Bistorta vivipara</i>	19.506	2.5
		<i>Campanula scheuchzeri</i>	22.003	1
		<i>Carex feruginea</i>	22.328	2.5
		<i>Carex firma</i>	14.072	1
		<i>Carex sempavirens</i>	21.298	2.5
		<i>Galium anisophyllum</i>	32.417	1
		<i>Moehringia ciliata</i>	30.474	1
		<i>Parnassia palustris</i>	23.536	0.1
		<i>Pedicularis rostratocapitata</i>	20.090	2.5
		<i>Ranunculus alpestris</i>	14.883	10
		<i>Salix serpyllifolia</i>	14.236	10
		<i>Sesleria albicans</i>	19.246	2.5
		<i>Soldanella alpina</i>	9.972	1
		<i>Viola biflora</i>	25.625	1
C3	250	<i>Achillea atrata</i>	22.716	1
		<i>Bellidiastrum michelii</i>	17.918	2.5
		<i>Biscutella laevigata</i>	14.846	2.5
		<i>Bistorta vivipara</i>	16.913	2.5
		<i>Campanula scheuchzeri</i>	24.910	1
		<i>Carex ferruginea</i>	19.782	2.5
		<i>Carex firma</i>	10.917	1
		<i>Carex sempavirens</i>	16.423	2.5
		<i>Euphrasia minima</i>	22.081	1
		<i>Festuca alpina</i>	16.387	1
		<i>Galium anisophyllum</i>	25.516	1
		<i>Hornungia alpina</i>	16.135	0.1
		<i>Juncus monanthos</i>	16.588	2.5
		<i>Mutellina adonidifolia</i>	15.651	1
		<i>Parnassia palustris</i>	20.024	0.1
		<i>Pedicularis rostratocapitata</i>	13.859	1
		<i>Ranunculus alpestris</i>	13.545	2.5
		<i>Ranunculus montanus</i>	16.871	1
		<i>Salix serpyllifolia</i>	14.333	2.5
		<i>Sesleria caerulea</i>	18.067	2.5
		<i>Soldanella alpina</i>	10.581	2.5

Table S4: Species occurrence at the Blaueis forefield with lower and upper range limits and main area of distribution. subniv = subnivale zone: Scree slopes and snow floors above 2500 - 2800m; alp = Alpine zone: stage of patchy grassland from about 2200m to 2800m; subalp = Subalpine zone: stage of alpine meadows, shrubs and dwarfed trees from about 1400 to 2200 m; mont = Montane zone: stage between mid-elevation forests at 500 m to the tree line at about 1700 m, unterteilt in obermontan und untermontan; submont = Submontane zone: Hill country, low mountain ranges up to approx. 500; coll = Foothills, colline lowlands, lowest section of mountains (Fischer et al., 2008; Oberdorfer & Müller, 1979).

Species	lower range limits (m a.s.l.)	upper range limits (m a.s.l.)	Main area of distribution
<i>Achillea atrata</i>	1300	2630	alp
<i>Arabis alpina</i>		2620	coll-alp
<i>Arabis bellidifolia</i>			(mont)suba - alp
<i>Bellidiastrum michelii</i>		2420	coll-alp
<i>Biscutella laevigata</i>		2375	(coll)mont - alp
<i>Bistorta vivipara</i>			omont - alp
<i>Campanula cochleariifolia</i>			(submont) mont - alp
		2590	
<i>Campanula scheuchzeri</i>	1300	2420	omont - alp
<i>Carex feruginea</i>		2020	omont - alp
<i>Carex firma</i>		2580	(mont)alp
<i>Carex sempervirens</i>	1500	2420	subalp - alp
<i>Cerastium uniflorum</i>	1800	3400	alp - subniv
<i>Crepsis terglouensis</i>	1800	2620	alp
<i>Euphrasia minima</i>	1600	2500	omont - alp
<i>Festuca alpina</i>	1500	1600	alp
<i>Galium anisophyllum</i>	1500	2560	alp
<i>Galium megalospermum</i>		2610	(mont) alp
<i>Heliosperma pusillum</i>	1350	2300	subalp - alp
<i>Hornungia alpina</i>		2950	(mont) subalp - alp
<i>Juncus monanthos</i>	1600	2000	oalp
<i>Linaria alpina</i>	1700	2600	alp - subniv
<i>Minuartia gerardii</i>	1590	2600	subalp - alp
<i>Moehringia ciliata</i>	1250	2590	subalp - alp
<i>Mutellina adonidifolia</i>			subalp - alp
<i>Papaver alpinum</i>	1850	2670	alp
<i>Parnassia palustris</i>		2320	coll - alp
<i>Pedicularis rostratospicata</i>	1800	2100	subalp - alp
<i>Poa alpina</i>		2600	subalp - alp
<i>Ranunculus alpestris</i>	1600	2590	subalp - alp
<i>Ranunculus montanus</i>			omont - alp
<i>Salix serpyllifolia</i>			alp
<i>Saxifraga azoides</i>		2470	mont - alp
<i>Saxifraga moschata</i>	1750	2760	subalp - alp
<i>Saxifraga stellaris</i>	1100	2460	subalp - alp
<i>Scorzoneroideis montana</i>	1400	2500	alp

<i>Sesleria caerulea</i>		2560	mont - alp
<i>Silene acaulis</i>	1150	2570	alp
<i>Soldanella alpina</i>	1000	2880	alp
<i>Taraxacum alpinum</i>	1800	2270	alp
<i>Thlaspi rotundifolia</i>	1600	2700	subalp - alp
<i>Tofieldia pusilla</i>	1630	2350	subalp - alp
<i>Valeriana saxatilis</i>	1100	2420	(mont) subalp- alp
<i>Veronica aphylla</i>	1300	2580	(subalp) alp
<i>Viola biflora</i>	1300	2630	coll - alp
