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„ β-Diversity of vegetation along successional gradients at Blaueis and Watzmann in the Northern Limestone Alps "

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Abstract

The glacier forefields of the Northern Limestone Alps have so far only been sparsely studied with respect to their vegetation. Also, the β-diversity which is defined as „the extent of change of community composition, or degree of community differentiation, in relation to a complex-gradient of environment" (Whittaker 1960:320) is understudied on glacier forefields. It provides much information about biological diversity between sites and their successional development. Furthermore, the results can be used in many ways, for example for management plans or ecological questions. By studying β-diversity, one not only obtains information about changes in species composition, but also about the phenomena of species turnover and nestedness. In this thesis, the β-diversity of vegetation was investigated along two successional gradients in glacier forefields of the Northern Limestone Alps in the national park Berchtesgaden, Germany. The first gradient extended over different age classes of the glacier forefields at the Blaueis glacier. The second gradient extended over different succession levels at the Watzmann glacier and extended beyond the glacier forefields. It started from glacier forefields to the approximate tree line and could thus be linked to the first gradient at the Blaueis.

The aim of this work was to find out how and from when the species composition changes during succession at the selected study sites. For this, 28 vegetation surveys were conducted, in which the species as well as their coverages were recorded.

The results of the glacier forefields of Blaueis do not show major changes in species composition (β-diversity) between the different age classes. On Watzmann, however, a more significant change is observed along the gradient. Thus, to detect a change in β-diversity between plots, they must be at a certain distance from each other, or the successional stage must differ. This distance does not appear to be present in the different age classes of the glacier forefields at Blaueis, and they appear to be at the same successional stage. The causes for the change in species composition seem to be mainly successional age and the resulting variation in site conditions, such as soil and microclimatic conditions, which change during succession but also stochastic processes. It was also found that successional processes of the glacier forefields seem to be much faster in the Central Alps than in the Northern Limestone Alps. Stochastic processes last longer at the sites studied here and are also replaced by deterministic processes later.

Keywords: β-diversity; climate change; glacier forefield; Nestedness; Succession; Turnover

Zusammenfassung

Die Gletschervorfelder der Nördlichen Kalkalpen sind hinsichtlich ihrer Vegetation bisher nur spärlich untersucht worden. Aber auch die β-Diversität, die definiert ist als "das Ausmaß der Veränderung der Gemeinschaftszusammensetzung oder der Grad der Gemeinschaftsdifferenzierung im Verhältnis zu einem komplexen Umweltgradienten" (Whittaker 1960:320), ist auf Gletschervorfeldern noch wenig erforscht. Dabei bietet die β-Diversität viel Aufschluss über die biologische Vielfalt zwischen Standorten und der Sukzessionsentwicklung. Darüber hinaus können die Ergebnisse vielfältig weiterverwendet werden und zum Beispiel für Managementpläne oder ökologische Fragestellungen herangezogen werden.

Durch die Untersuchung der β-Diversität erhält man nicht nur Aufschluss über die Veränderungen der Artenzusammensetzung, sondern auch über die Phänomene des Artenturnovers (Artenaustausch) und der Nestedness (Artenverlust).

In dieser Arbeit wurde die β-Diversität der Vegetation entlang von zwei Sukzessionsgradienten auf Gletschervorfeldern in den Nördlichen Kalkalpen im Nationalpark Berchtesgaden (Deutschland) untersucht. Der erste Gradient erstreckte sich über verschiedenen Altersklassen der Gletschervorfelder am Blaueisgletscher. Der zweite Gradient erstreckte sich über verschiedene Sukzessionslevel am Watzmanngletscher und reichte über die Gletschervorfelder hinaus, bis hin zur Baumgrenze. Somit konnte der zweite Gradient mit dem ersten am Blaueis verknüpft werden.

Ziel dieser Arbeit war es herausfinden, wie und ab wann sich die Artenzusammensetzung im Laufe der Sukzession an den ausgewählten Standorten verändert. Dafür wurden 28 Vegetationsaufnahmen durchgeführt, bei denen die Arten sowie ihre Deckungen aufgenommen wurden.

Die Ergebnisse der Gletschervorfelder des Blaueises zeigen zwischen den verschiedenen Altersklassen keine großen Veränderungen in der Artenzusammensetzung (β-Diversität). Eine deutlichere Veränderung ist jedoch entlang des Gradienten am Watzmann zu beobachten. Um eine Veränderung der β-Diversität zwischen den Flächen feststellen zu können, müssen diese also eine gewisse Entfernung zueinander aufweisen bzw. die Sukzessionsstufe muss sich unterscheiden. Diese Entfernung ist bei den unterschiedlichen Altersklassen der Gletschervorfelder scheinbar nicht gegeben und sie scheinen sich auf der gleichen

Sukzessionsstufe zu befinden.

Ursachen für den Wandel der Artenzusammensetzung scheinen vor allem mit dem Sukzessionsalter und der daraus resultierenden unterschiedlichen Standortbedingungen wie Boden- und mikroklimatische Bedingungen zusammenzuhängen, welche sich im Laufe einer Sukzession verändern aber auch stochastische Prozesse. Es wurde außerdem festgestellt, dass Sukzessionsprozesse der Gletschervorfelder in den Zentralalpen sehr viel schneller ablaufen zu scheinen als in den Nördlichen Kalkalpen. Stochastische Prozesse dauern auf den hier untersuchten Flächen länger an und werden auch erst später durch deterministische Prozesse abgelöst.

Introduction

Mountains offer ideal conditions to study changes in species composition along an altitudinal gradient. These mostly directional gradients often have very different environmental conditions in a small area. According to Körner (2007) there are four atmospheric factors for organisms that change with altitude: The total pressure and partial pressure of all atmospheric gases decreases, as well as the temperature, which in turn affects the ambient humidity. With cloudless skies, solar radiation and the proportion of UV-B radiation increases with altitude. In addition, size of available land declines with altitude. Changes in the availability of moisture, wind velocity and seasonality cannot be considered an altitude effect because they are not specific to mountains, however, they can follow the altitudinal gradient (Körner 2007). These extreme and strongly changing environmental conditions shape the vegetation of the Alps.

Billings (1974) identifies four levels at which selection takes place in plants due to interactions between the alpine environment and available genetic systems, resulting in the development of adaptations to mountain life. These are the morphological level, the physiological level, the reproductive level, and the ecological level.

Most common at high altitudes are small perennial herbs with relatively large root and/or rhizome systems. This adaptation of the root systems serves to store carbohydrates over the long winters in the mountains. Since the growing season is greatly reduced in the mountains, one of the physiological adaptations is the ability of plants to have an active metabolism even at low temperatures. Nevertheless, the establishment and thus the germination of seeds of a plant can take several years.

In order not to risk a delay in flowering when environmental conditions are suddenly suitable or snowmelt begins, almost all alpine species produce flower primordia (flower buds) at least one year before flowering, which can flower directly. Pollination is then taking place mainly by wind in the case of graminoids and by insects in the case of showy flower primordia (Billings, 1974).

As a result of these environmental conditions and adaptions by plants, only rock and debris patches as well as alpine grasslands occur at the higher altitudes. However, even coarse gravel and scree material provides an initial niche for plants to grow (Körner, 2003).

Due to advancing climate change, environmental conditions will continue to change, especially in mountainous areas (Grabherr et al., 1994). Warming also has an impact on the glaciers in the mountains. These are melting more and more quickly (Sommer et al., 2020). This results in increasing new areas that are no longer covered with ice, the so-called glacier forefields. These areas are now exposed after the retreat of a glacier and extend from the glacier front to the last deposited moraine (Anderson et al., 2017; Matthews, 1992). Glacier forefields are initially characterized by primary soils and low vegetation cover, therefore succession processes play an important role. Both human influences and the vegetation that will settle there in the future are missing.

The chronosequence approach can be used to divide these forefields into different age classes. In this way, ecological, biogeochemical, and physical characteristics of autogenic successional change can be studied as a function of time. However, this approach assumes that all sites were exposed to the same environmental conditions and sequence of change, and the only difference between them is when it was last covered by glacier (age) (Wojcik et al., 2021).
Therefore, glacier forefields represent ideal study areas, because the conditions present create the optimal conditions for investigating succession processes. Succession processes occur after a disturbance and refer to changes in the species composition and structure of the ecosystem and their physical environment (Dierschke 1994; Matthews 1992).

Succession is controlled by various biotic and abiotic processes, which are dependent on the environmental conditions present there, and occurs at different succession stages. These include, for example, soil properties, topography or the respective altitude. If the geomorphic activity has decreased to a certain point on glacier forefields, species can slowly establish themselves and biogeomorphic interactions develop. The first pioneer species or ecosystem engineered species appear, leading to an increase in biomass makes the species numbers rise more and more (Raffl et al., 2006). This influences geomorphological processes, for example by stabilizing glacial sediments. This biogeomorphological feedback, in turn, facilitates the establishment of new species that follow the first ones (Eichel, 2019). There is a change in species composition, as new species are added but also old ones can disappear (Stöcklin & Bäumler, 1996).
On glacier forefields, in contrast to areas where vegetation cover has already formed and thus soil was already present, primary succession takes place. Primary succession is characterized by

organisms colonizing a place for the very first time where no ecosystem has ever been before. In this process, species cannot draw on a "biological inheritance" because there are no diaspora banks or biological material (Gobbi et al., 2010; MacDonald, 2002). Areas of secondary succession are those where a pre-existing ecosystem has been disturbed by, for example, a storm or fire. After these disturbance events, species communities can regenerate or form replacement communities, which is not the case with primary succession.

Both short-term succession processes after the retreat of glaciers and natural long-term ones along longer altitudinal gradients, allow to study the change in vegetation composition. In this study, both processes were investigated at two different sites. The former at Blaueis and the latter at Watzmann.

A method for the study of these processes is the analyses the *β-diversity*. β-diversity was first defined by Whittaker (1960:320) as „the extent of change of community composition, or degree of community differentiation, in relation to a complex-gradient of environment". It is a measure of the variation in species composition of communities in relation to an environmentally gradient and analysed to determine whether environmental changes, ecological interactions or biogeographical evolutions are taking place (Koleff et al., 2003; McKnight et al., 2007).
There are different approaches to measure β-diversity such as according to Wilson & Shmida (1984), Shi (1993) or Koleff et al. (2003), however, these do not consider the partitioning of the contributions of spatial turnover and nestedness (Baselga, 2010). This study follows the concept of Baselga (2010), as he divides β-diversity into its components of nestedness and spatial species turnover.
N*estedness* is "characterized by the poorest site being a strict subset of the richest site" (Baselga 2012: 1224). Therefore, it is the proportion of the species that occur in both sites. On the other hand, species *Turnover*, where because of environmental sorting or spatial and historical constraints species are replaced by newly added species (Qian et al., 2005). These two variables offer a way to describe differences in communities (Baselga, 2010), and thus plays a decisive role in analysing diversity patterns. This allows me to quantify how the vegetation changes along the two different (also with regard to the time scale) succession processes.

Specifically, the following research questions were addressed:

Q1: How does the species composition (β-diversity) change along a successional gradient (different age classes) on the glacier forefields at Blaueis?

Q2: And how does the species composition (β-diversity) change at Watzmann when a longer successional gradient (longer time scale) is considered, which goes beyond the glacier forefields?

Material and Methods

Study region

The data was collected in glacier forefields at two locations in the national park Berchtesgaden (founded in 1978), which is located in the Berchtesgaden Alpen in southern Bavaria, Germany. The mountain range belongs to the Northern Limestone Alps, which are part of the geological section of the Eastern Alps (Gassler, 1984).

The geological terrain is called a Lofer-Cyklothems stratigraphy (Bayerisches Landesamt für Umwelt (LfU), 2023). The summits and walls of the massifs are mostly made of Dachstein Limestone and the lower elevation bedrock of Ramsau dolomite, which easily fragments and leads to the formation of large gravel fields. Both types of rock mostly lead to shallow humus carbonate soils with low water storage capacity (Lippert et al., 1997).

The climate is characterized by high precipitation. This leads to frequent rainfall in the summers and to long-lasting snow cover in the winters (Lippert et al., 1997). At an elevation of 1500m, there can be an annual precipitation of 2800mm and a snow cover duration of 200 to 215 days. The maximum snow heights for this altitude are reached between February and March (Nationalparkverwaltung Berchtesgaden n.d.). The annual mean temperatures range between +7°C and -2°C, with the lowest temperatures usually in February (Lawinenwarndiest Bayern n.d.).

Due to the glacial and post-glacial history, different vegetation units and landscape types such as gravel fields or alpine mats occur in the national park. Besides the common alpine plants, also glacial relicts such as *Androsace hausmannli* or *Saxifraga burserana* are occuring (Lippert et al., 1997).

The first study area is located at the Hochkalter (2607 m asl), in the Blaueiskar (cirque) below the Blaueis, which is the northernmost glacier in the Alps (Mayer, Hagg, et al., 2021) (Figure 1). This mountain stock is the second highest massif in the Berchtesgaden Alps. The Blaueiskar is exposed to the north and is encircled by the Hochkalter (south), Kleinkalter and Rotpalfen (west) and Blaueisspitze and Schärtenspitze (east). This is also the core zone of the national park.

The Blaueis is still classified as a glacier, although after substantial melting in the last decades it has shrunken substantially and it is divided by a rock bar. Due to the northern slope, the steep

shady rock walls protecting it from the sun and because the lower part is covered with debris, the glacier is still preserved today (Hagg, 2022; Mayer, Weber, et al., 2021). Here, the study area extended over the chronosequence of the glacier forefields and across three reference plots that lay outside the glacier forefields.

The Watzmann (2713 m asl) represents the central massif and the highest peak of the Berchtesgaden Alps. The second study area is located in the cirque if the Watzmannkar (Figure 2). The Watzmannkar is also north exposed and encircled by the Watzmannfrau or Kleiner Watzmann (in the east), the Watzmannkinder (south) and in the Watzmann itself (west). This mountain area is in the core zone of the National Park. Human intervention and use (except for recreation) are not allowed here.

In the upper end is the glacier, whose last maximum advance was in 1888. Whether and for how long ice field can still be called a glacier is questionable, since there is hardly any ice movement and it rather consists of firn fields, snow ice or dead ice (Bayerisches Landesamt für Umwelt (LfU), 2023).

The exact study area here extended from the tree line to the glacier forefields. Since many plots of the glacier forefields were still covered by snow at the time of the investigation, the sample design had to be changed and was placed along this longer gradient.

However, given current climate warming trends, both Blaueis and Watzmann glaciers will have melted and thus disappeared in a few years (Mayer, Weber, et al., 2021).

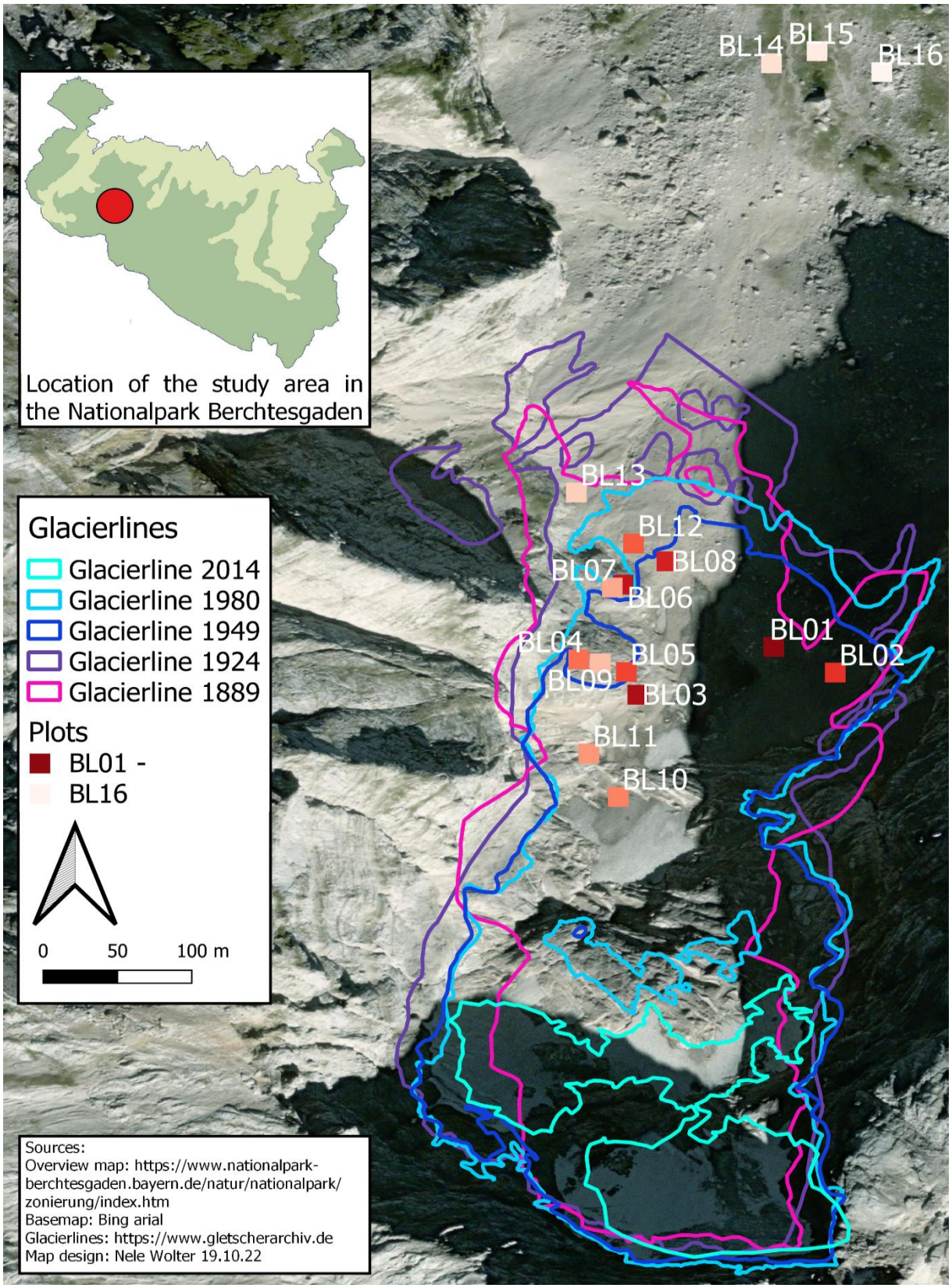

Figure 1: Overview map of the study area at the Blaueis forefields in the national park Berchtesgaden. All sampling plots (BL01-BL16 = brown-beige) and the glacier extent (lines in pink = 1889, purple = 1924, blue = 1949, light blue = 1980, turquoise = 2014) are shown, which approximately match the age classes studied.

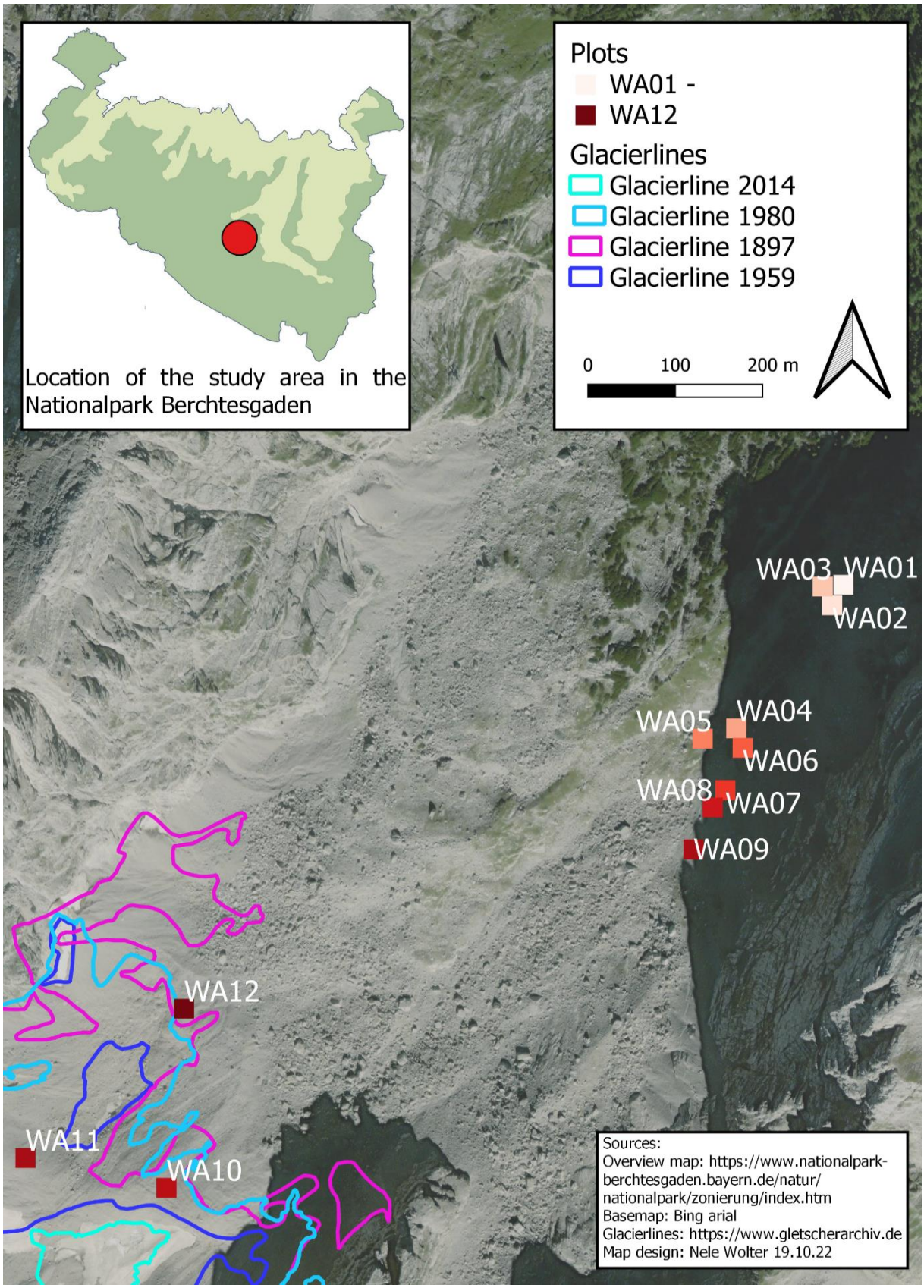

Figure 2: Overview map of the study area at the Watzmann forefields in the national park Berchtesgaden. Lines represent the glacier extent of different years: Blue = 1959, pink = 1897, light blue = 1980, turquoise = 2014. The squares represent the plots under investigation from beige to brown (WA01-WA12).

Study design

In the Blaueiskar, 16 plots were examined in five different age classes of the glacier forefield. An age class was defined as the time since the glacier retreated. Long-term monitoring of the glacier forelands at different age classes served as a basis. For this, samples were taken in the vicinity of the already 13 existing plots. In addition, three new plots were determined as reference plots. These were probably not affected by the Holocene glacier advance and are therefore not defined as a glacier foreland area.

The 16 plots were divided into four age classes. Of these, four were in locations where the glacier had retreated approximately 10-years ago and three were each in locations were the glacier had retreated 40-, 80-, 120-, and more than 250-years (reference plots) ago (Figure 1, Table 1). Glacier retreat was unknown for the last category and was therefore estimated.

In the Watzmannkar a total of 12 plots were examined along the altitude/succession gradient, extending from the treeline to, which lay under up to the glacier forefields. Due to the extensive and unusually long snow cover of most of the glacier forefields during the year under investigation, it was not possible to investigate only the glacier forefields on Watzmann. The plots now investigated are probably many hundred or a few thousand years older than of those of Blaueis.

These plots were distributed over four different succession levels (three plots per altitude level). The first was chosen last just after the treeline at about 1760 m asl and was densely covered with Alpine sward, the second third is loosely covered by sward, right below the beginning of Alpine scree at about 1824 m asl, the third in scree fields at 1843 m asl and the last and highest level at the oldest glacier forefields at 1960 m asl (Table 2).

The locations for the plots at Watzmann were chosen under the following conditions: the distance between the plots of a succession level should not be less than 30 meters, they should be representative and arbitrarily chosen and the vegetation height within a stage should also be comparable. The plots had to be quite homogeneous and not obviously disturbed by human influences such as hiking trails.

Table 1: Overview of the Age classes, altitude (m a.s.l.) and estimated year of deglaciation of the plots on the Blaueis forefields.

Plot	Age class (years)	Altidude (m a.s.l.)	Estimated year of deglaciation
BL16	>250	1797	1770
BL15	>250	1784	1770
BL14	>250	1803	1770
BL09	100	2019	1920
BL07	100	1959	1920
BL13	100	1914	1920
BL10	70	2040	1950
BL11	70	2025	1950
BL04	70	2007	1950
BL05	40	1994	1980
BL02	40	1977	1980
BL12	40	1927	1980
BL03	10	1992	2010
BL01	10	1966	2010
BL06	10	1960	2010
BL08	10	1931	2010

Table 2: Overview of the succession levels (Level 1 = I, level 2 = II, level 3 = III, level 4 = IV) and altitude (m a.s.l.) of the plots on the Watzmann forefields.

Plot	Succession level	Altidude (m a.s.l.)
WA01	I	1760
WA02	I	1760
WA03	I	1760
WA04	II	1824
WA05	II	1824
WA06	II	1824
WA07	III	1843
WA08	III	1843
WA09	III	1843
WA10	IV	1960
WA11	IV	1960
WA12	IV	1960

Vegetation Sampling

The vegetation at Watzmann was recorded during the flowering period in July and August 2021. The data of the vegetation at Blaueis came from a long-term monitoring project and were recorded in July and August 2020 by Ingolf Kühn and Christian Hecht. In each $1m^2$ plot, all species were identified, and their respective cover estimated. For estimation of cover, the modified scale of Reichelt & Wilmanns (1973) was used (after Braun-Blanquet 1964) (Table 3).

Table 3: Abundance/ Species richness scale after Reichelt & Wilmans 1973

Symbol	Covered (%)	Individuals
r	<1	usually only very isolated, small
+	<1	2-5
1	< 5	6-50
2m	< 5	>50
2a	5 - <15	any number
2b	16 - <25	any number
3	25 - <50	any number
4	50 - <75	any number
5	75 - 100	any number

A distinction between tree, shrub and herb layers was not necessary, as the plots consisted only of herbaceous layers. Lichens, mosses and algae were not determined.

Statistical Analyses

All data preparation was done with Microsoft Excel (version 2301). Writing was done with Microsoft Word (version 2301).

The maps were created with QGIS (version 3.10.10-A Coruña).

All statistical analyses were done with the program R 4.1.2 in RStudio (version 2022.02.0+443). The following R packages were used: here 1.0.1 (Müller & Bryan, 2020), dplyr 1.1.0 (Wickham, François, et al., 2023), readxl 1.4.2 (Wickham, Bryan, et al., 2023) for data preparation, ggplot2 1.0 (Wickham, 2016) to create the graphs and betapart 1.6 (Baselga et al., 2022), lmPerm 2.1.0 (Wheeler & Torchiano, 2016) and agricolae 1.3-5 (Mendiburu, 2021) for statistical analysis.

β-diversity

The β-diversity was calculated according to the method of Baselga (2017) with the Bray–Curtis index (figure eqn 1) of total dissimilarity, which is directly related to the quantitative Sørensen similarity index, but accounts for the abundance.

$$\beta_{BC} = \beta_{BC.BAL} + \beta_{BC.GRA} \equiv \frac{B_M + C_M}{2A_M + B_M + C_M} = \frac{B_M}{A_M + B_M} + \frac{C_M - B_M}{2A_M + B_M + C_M} \times \frac{A_M}{A_M + B_M} \quad \text{eqn 1}$$

A_M = The total abundance in the data set minus the sum across species of the maximum abundance of each species across sites

B_M = The sum of all the minimum complements across all pairs of sites

C_M = The sum of all the maximum complements across all pairs of sites

Further, β-diversity was partitioned into turnover ($\beta_{BC.BAL}$) and Nestedness ($\beta_{BC.GRA}$). With this index (eqn 1), all three elements were tested for each of the individual plot against each other. The complete design of tests is depicted in tables 4 (Blaueis) and 5 (Watzmann).

Table 4: Plot comparisons on the Blaueis. Plots are divided into subgroups A.01 – E.15. Each subgroup represents a comparison between different plots at different succession levels (age classes). The age classes are coloured to show which are being compared (orange = Reference plots, blue = 100 years, yellow = 70 years, light green = 40 years, purple = 10 years).

Groups/ Subgroups					
A	A.01	A.02	A.03	A.04	A.05
	BL14 – BL15	BL07 – BL09	BL04 – BL10	BL02 – BL05	BL01 – BL03
	BL14 – BL16	BL07 – BL13	BL04 – BL11	BL02 – BL12	BL01 – BL06
	BL15 – BL16	BL09 – BL13	BL10 – BL11	BL05 – BL12	BL01 – BL08
					BL03 – BL06
					BL03 – BL08
					BL06 – BL08
B	B.06	B.07	B.08	B.09	
	BL14 – BL07	BL07 – BL04	BL04 – BL02	BL02 – BL01	
	BL15 – BL07	BL09 – BL04	BL10 – BL02	BL05 – BL01	
	BL16 – BL07	BL13 – BL04	BL11 – BL02	BL12 – BL01	
	BL14 – BL09	BL07 – BL10	BL04 – BL05	BL02 – BL03	
	BL15 – BL09	BL09 – BL10	BL10 – BL05	BL05 – BL03	
	BL16 – BL09	BL13 – BL10	BL11 – BL05	BL12 – BL03	
	BL14 – BL13	BL07 – BL11	BL04 – BL12	BL02 – BL06	
	BL15 – BL13	BL09 – BL11	BL10 – BL12	BL05 – BL06	
	BL16 – BL13	BL13 – BL11	BL11 – BL12	BL12 – BL06	
				BL02 – BL08	
				BL05 – BL08	
				BL12 – BL08	
C	C.10	C.11	C.12		
	BL14 – BL04	BL07 – BL02	BL04 – BL01		
	BL15 – BL04	BL09 – BL02	BL10 – BL01		
	BL16 – BL04	BL13 – BL02	BL11 – BL01		
	BL14 – BL10	BL07 – BL05	BL04 – BL03		
	BL15 – BL10	BL09 – BL05	BL10 – BL03		
	BL16 – BL10	BL13 – BL05	BL11 – BL03		
	BL14 – BL11	BL07 – BL12	BL04 – BL06		
	BL15 – BL11	BL09 – BL12	BL10 – BL06		
	BL16 – BL11	BL13 – BL12	BL11 – BL06		
			BL04 – BL08		
			BL10 – BL08		
			BL11 – BL08		
D	D.13	D.14			
	BL14 – BL02	BL07 – BL01			
	BL15 – BL02	BL09 – BL01			
	BL16 – BL02	BL13 – BL01			
	BL14 – BL05	BL07 – BL03			
	BL15 – BL05	BL09 – BL03			
	BL16 – BL05	BL13 – BL03			
	BL14 – BL12	BL07 – BL06			
	BL15 – BL12	BL09 – BL06			
	BL16 – BL12	BL13 – BL06			
		BL07 – BL08			
		BL09 – BL08			
		BL13 – BL08			
E	E.15				
	BL14 – BL01				
	BL15 – BL01				
	BL16 – BL01				
	BL14 – BL03				
	BL15 – BL03				
	BL16 – BL03				
	BL14 – BL06				
	BL15 – BL06				
	BL16 – BL06				
	BL14 – BL08				
	BL15 – BL08				
	BL16 – BL08				

Table 5: Plot comparisons on the Watzmann. Plots are divided into subgroups A.01 - D.10. Each subgroup represents a comparison between different plots at different succession levels (age classes). The succession levels are coloured to show which are being compared (grey = level 1, red = level 2, light blue = level 3, green = level 4)

Groups/ Subgroups				
A	A.01	A.02	A.03	A.04
	WA01 – WA02	WA04 – WA05	WA07 – WA08	WA10 – WA11
	WA01 – WA03	WA04 – WA06	WA07 – WA09	WA10 – WA12
	WA02 – WA03	WA05 – WA06	WA08 – WA09	WA11 – WA12
B	B.05	B.06	B.07	
	WA01 – WA04	WA04 – WA07	WA07 – WA10	
	WA01 – WA05	WA04 – WA08	WA07 – WA11	
	WA01 – WA06	WA04 – WA09	WA07 – WA12	
	WA02 – WA04	WA05 – WA07	WA08 – WA10	
	WA02 – WA05	WA05 – WA08	WA08 – WA11	
	WA02 – WA06	WA05 – WA09	WA08 – WA12	
	WA03 – WA04	WA06 – WA07	WA09 – WA10	
	WA03 – WA05	WA06 – WA08	WA09 – WA11	
	WA03 – WA06	WA06 – WA09	WA09 – WA12	
C	C.08	C.09		
	WA01 – WA07	WA04 – WA10		
	WA01 – WA08	WA04 – WA11		
	WA01 – WA09	WA04 – WA12		
	WA02 – WA07	WA05 – WA10		
	WA02 – WA08	WA05 – WA11		
	WA02 – WA09	WA05 – WA12		
	WA03 – WA07	WA06 – WA10		
	WA03 – WA08	WA06 – WA11		
	WA03 – WA09	WA06 – WA12		
D	D.10			
	WA01 – WA10			
	WA01 – WA11			
	WA01 – WA12			
	WA02 – WA10			
	WA02 – WA11			
	WA02 – WA12			
	WA03 – WA10			
	WA03 – WA11			
	WA03 – WA12			

The function beta.pair.abund (Abundance-based pair-wise dissimilarities) from the package betapart, developed by Baselga (2017), was used to make abundance based comparisons between the different sites. Following is the model notation:

```
c <- xtabs(Ergebnisse$Braun ~ Ergebnisse$Plot + Ergebnisse$Name)
betapart::beta.pair.abund(c)
```

where $Braun is the dependent variable, $Plot is the independent variable and $Name are the names of the species to create the matrix.
With betapart::beta.pair.abund(c) the partitioning is done.

As a result, the following three different components of dissimilarity were obtained: Balanced variation in abundances, abundance gradients, and total dissimilarity (i.e. the sum of both components) (Baselga et al. 2022).

`beta.bray.bal` = balanced variation in abundances (Turnover)

`beta.bray.gra` = abundance gradients (Nestedness)

`beta.bray` = total dissimilarity (β-diversity)

Comparing components of β-diversity

To determine whether there were significant differences between the β-diversity results of the various comparisons (see tables 4 and 5), a variation of a single factor ANOVA was performed. Because the pairwise comparisons inflate the degrees of freedom in an oridinary ANOVA, and hence would result in incorrect error probabilities, the function lmp in the lmPerm package for linear models was used. This approach calculates error probabilities based on permutation tests and is hence independent of degrees of freedom.
The result is significant, at a value of $\alpha = 0.05$.

However, this analysis only provides information on whether there is a statistically significant difference within a group. To find out which elements significantly differ from each other, a HSD.test: Multiple comparisons: Tukey with the agricolae package was used.

```
# A <- aov(Wert~Gruppe, data = Ergebnisse)
TukeyHSD(A)
# HSD = HSD.test(A, "Gruppe", group=TRUE, console=TRUE)
```

Results

A total of 62 species were found in all plots, of which 8 species were found only on Blaueis and 19 only on Watzmann. Thus, a total of 44 species were found at Blaueis (Figure 3) and 54 at Watzmann (Figure 4).

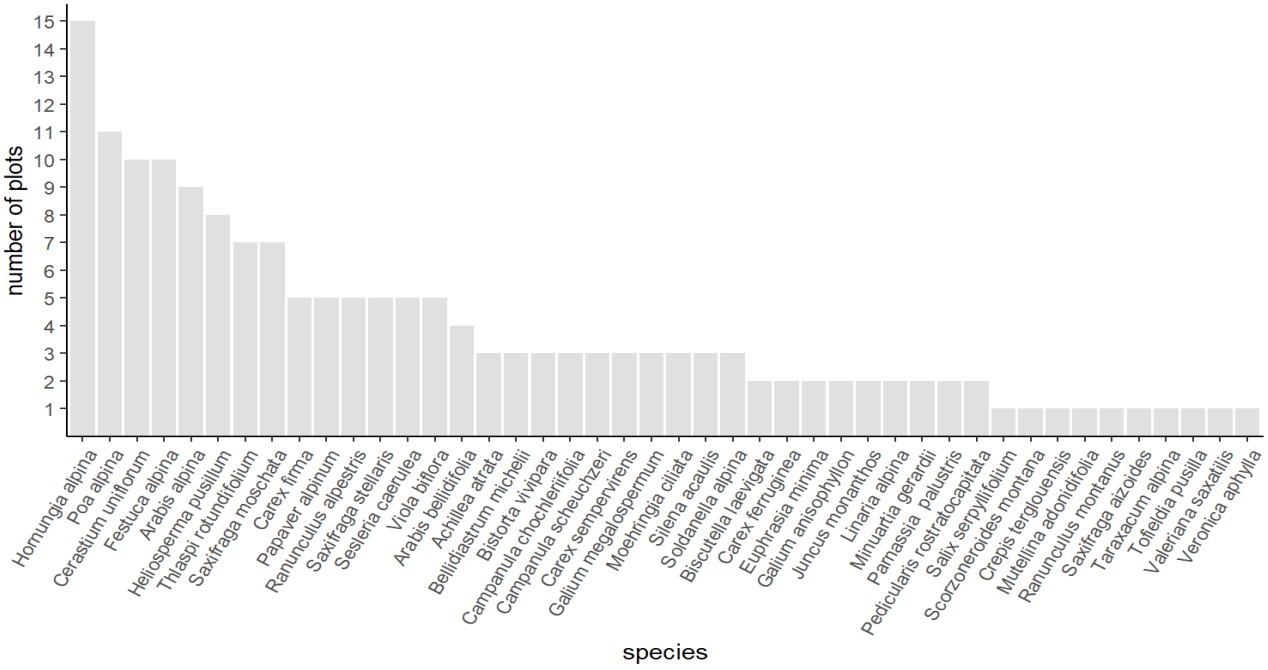

Figure 3: Vascular plant species and their frequency across plots found at the Blaueis forefield.

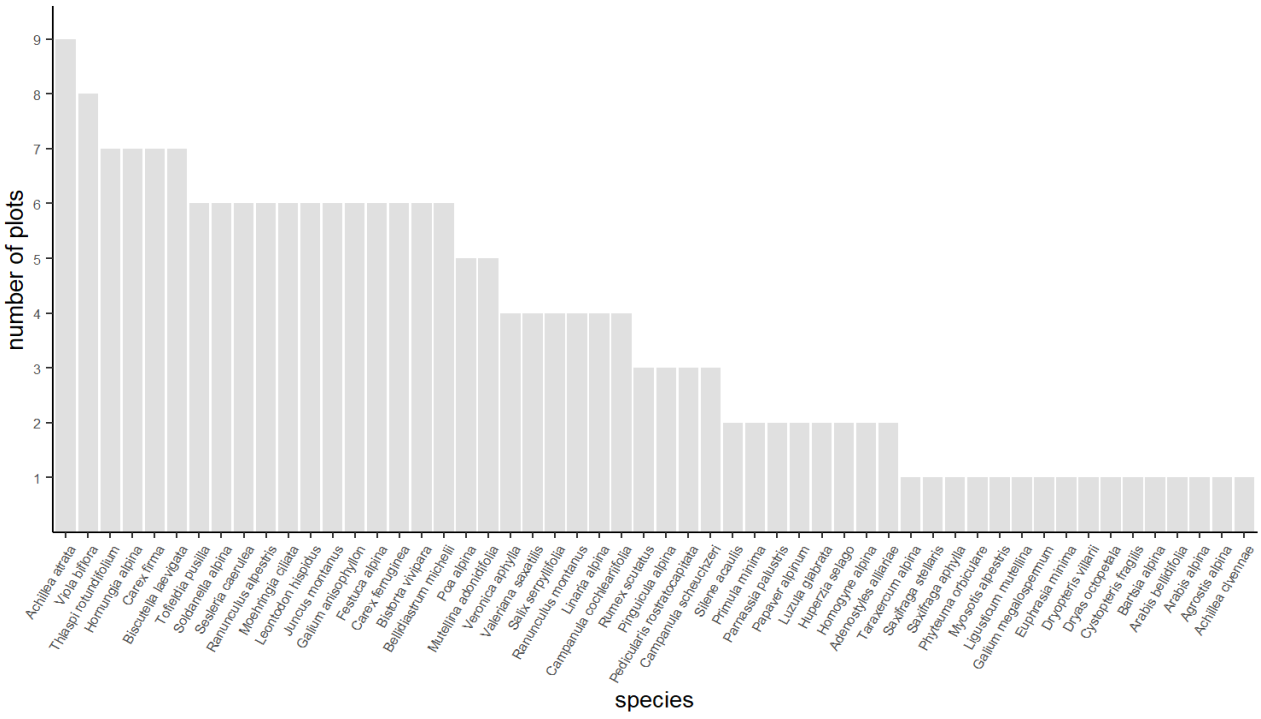

Figure 4: Vascular plant species and their frequency across plots found at the Watzmann gradient.

Blaueis

At Blaueis *Hornungia alpina* was the most common species. This species was found in all plots except BL15 (one of the old reference sites). The second most frequent species was *Poa alpina*, followed *Cerastium uniflorum*, which was not found at all at Watzmann, and *Festuca alpina* (the last two were found with the same frequency) (Figure 3).

In terms of species numbers, a clear trend can be seen at the different age classes. Thus, the most species (28) were found on the oldest age class. This age class represents also the most species-rich plot (BL16 with 21 species). The fewest species were recorded in the youngest age classes (Figure 5).

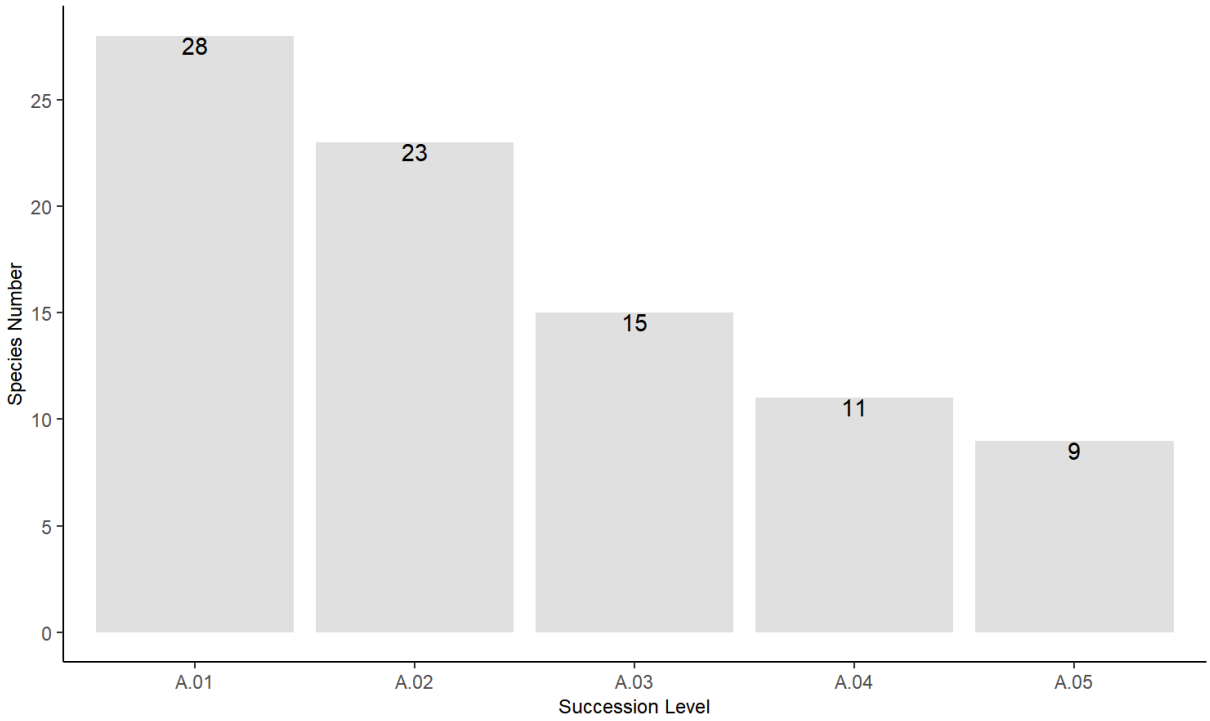

Figure 5: Number of species found at the different age classes (A.01 = Reference plots, A.02 = 100 years, A.03 = 70 years, A.04 = 40 years, A.05 = 10 years).

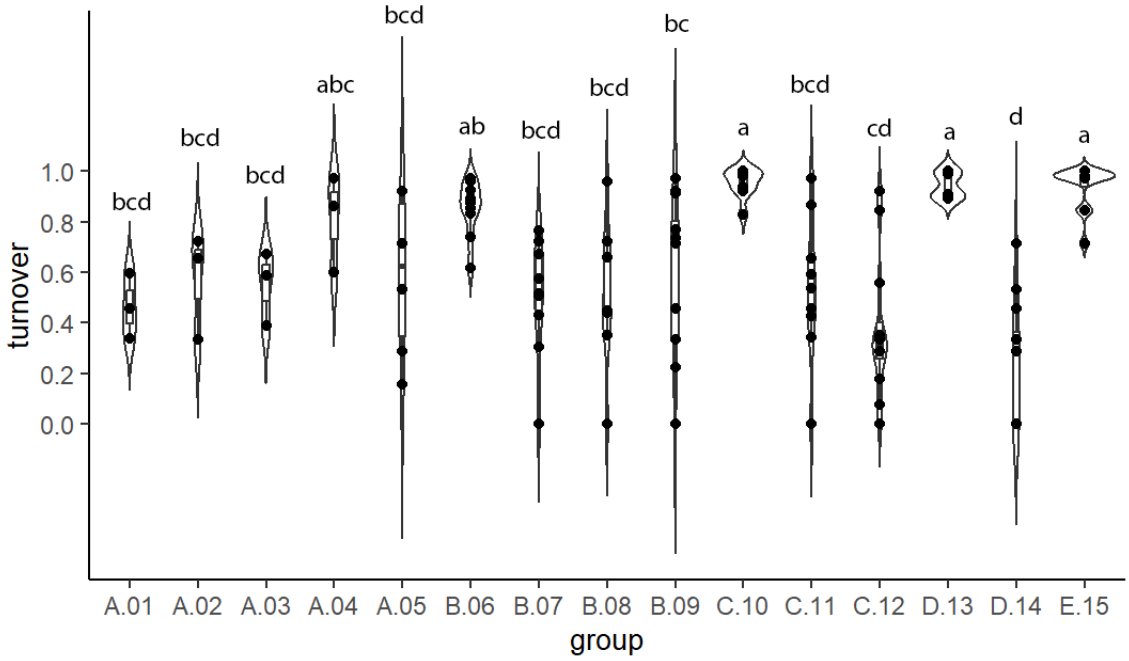

Figure 6: Turnover for the comparisons at Blaueis. The letters indicate whether there are significant differences between the groups. There is no difference when the groups have the same letters and differences when the letters are different. For technical reasons the violin plots range from <0 to >1 although it is computationally impossible.

The turnover values range from 0 to 1 and no clear trend can be seen (Figure 6).

All comparisons, however, between the oldest (reference plots) sites and those 70 years or younger have similar turnover with variation and differ significantly from most other groups (except the comparison of the reference sites (C10, D13) and the 100 years old sites (B06) to younger ones).

Within the same age classes (i.e., group A) there do not seem to be no big differences, only A.04 (40 years old plots) has slightly higher values than the others. The medians range from 0.46 for A.01 to 0.86 for A.04. Group A.05 shows the highest variation.

In group B, B.06 (reference plots vs the oldest successional plots) in particular stands out with the lowest dispersion. This subgroup differs significantly only from subgroups C.12 and D.14 (comparison across longer time scales involving younger plots) and shows the highest median with 0.87 within its own group. B.07, B.08 and B.09, on contrast, show widely scattered values.

A significant difference can be found within group D. D.13 shows much less widely scattered values than D.14. With a median of 0.29, D.14 has the lowest values overall.

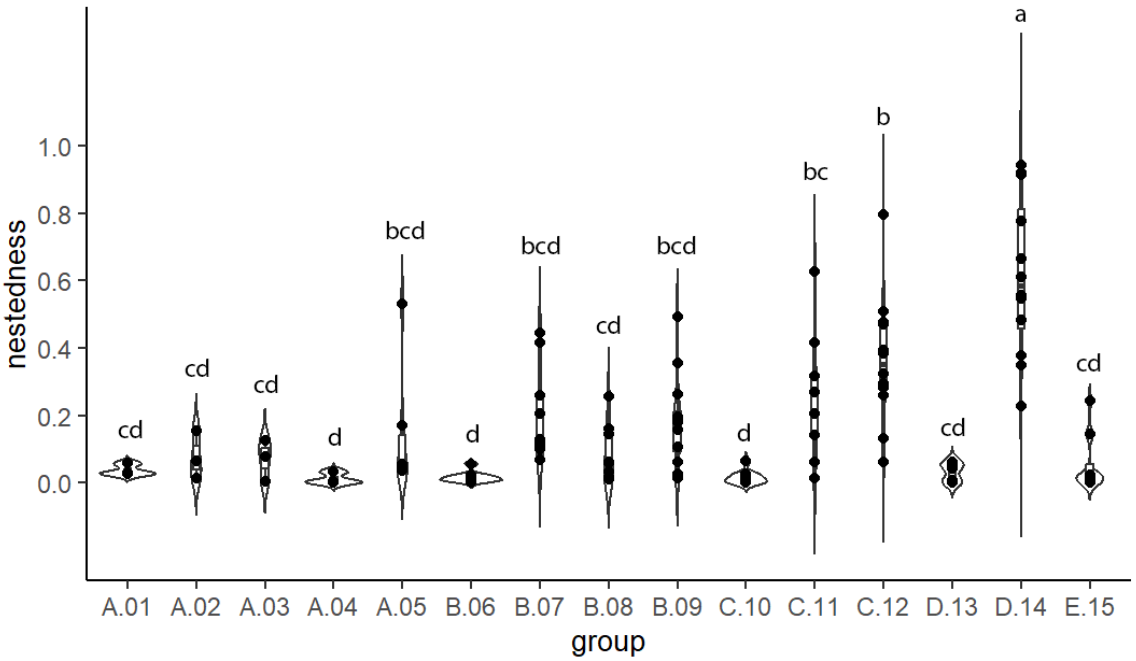

Figure 7: Nestedness for the comparisons at Blaueis. The letters indicate whether there are significant differences between the groups. There is no difference when the groups have the same letters and differences when the letters are different. For technical reasons the violin plots range from <0 to >1 although it is computationally impossible.

The nestedness (Figure 7) is very low overall. Thus, different species occur in different age classes and only a small proportion of species occurs across age classes.

Group A (same age class comparisons) are all comparably low (i.e., share few species), except A05 (the youngest plots). The same is true for all comparisons with the oldest reference sites (B06, C10, D13, E15). Remarkable is the increase in average nestedness and their variation in those sites with two or three age classes difference, excluding the reference sites (i.e., C11, C12, D14).

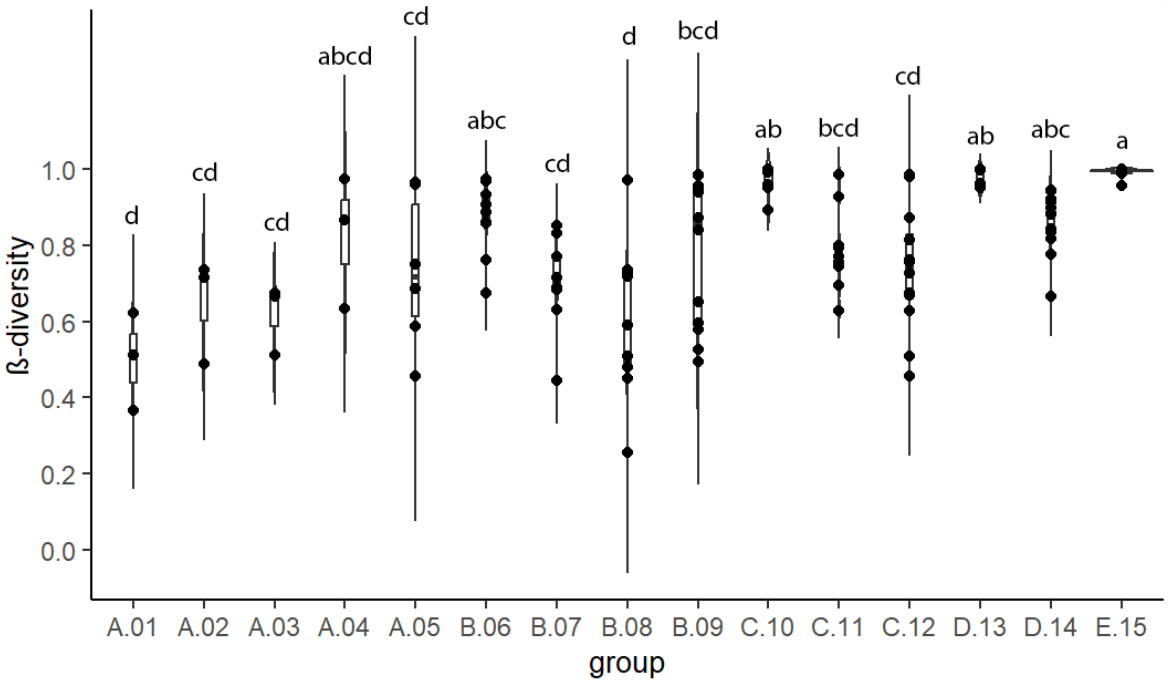

Figure 8: Dissimilarity results of the ß-diversity for the comparisons at Blaueis. The letters indicate whether there are significant differences between the groups. There is no difference when the groups have the same letters and differences when the letters are different. For technical reasons the violin plots range from <0 to >1 although it is computationally impossible.

A slight trend can be seen in β-diversity (Figure 8). The greater the difference between the age groups, the more the values increase. But in general, the results mirror turnover remarkably closely.

The last two groups, D and E, but also subgroup C.10 (i.e. the comparisons across longer time differences or those with the oldest reference sites, respectively), show the lowest fluctuations and highest values, with medians ranging from 0.88 for D.14 to 0.995 for E.15. C.10 shows no significant differences from A.04, B.06, B.09, C.11, D and E. The same is true for D, with D.14 being similar to many more subgroups. E.15 has the most significant differences to other subgroups.

The lowest median with 0.51 has A.01, followed by B.08 with 0.59.

Watzmann

At Watzmann, *Achillea atrata* was the most common species and grew in almost all plots (except WA1, WA10, WA11). It was followed in numbers of plots recorded by *Viola biflora*, which was found only in once plot less and *Thlaspi rotundifolia*, *Hornungia alpina*, *Carex firma*, and *Biscutella laevigata*. The last four with the same frequency (Figure 4).

At succession level I 27 species were found and at level II the most with 35 species. Much fewer species were found in the last two levels. In level III, 18 species were recorded and in IV 20 species were observed (Figure 9).

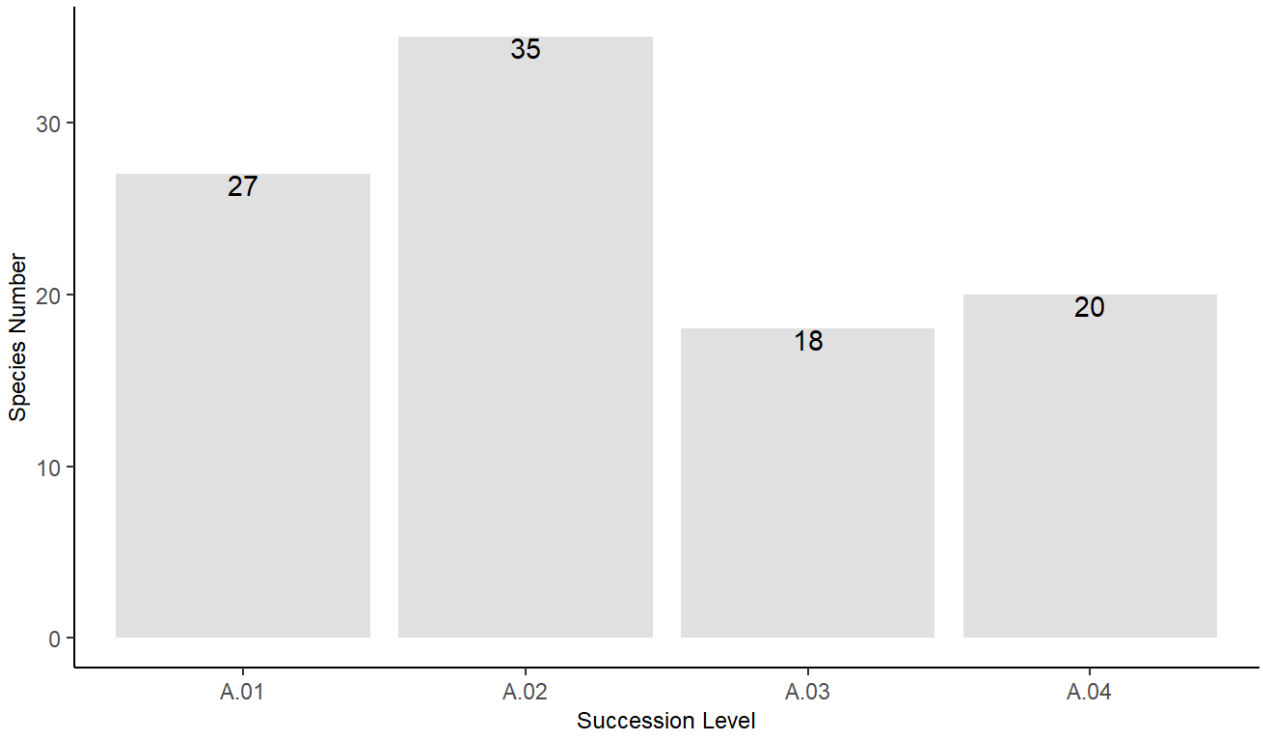

Figure 9: Number of species found at the different succession levels (A.01 = Level I, A.02 = Level II, A.03 = Level III, A.04 = Level IV) at Watzmann.

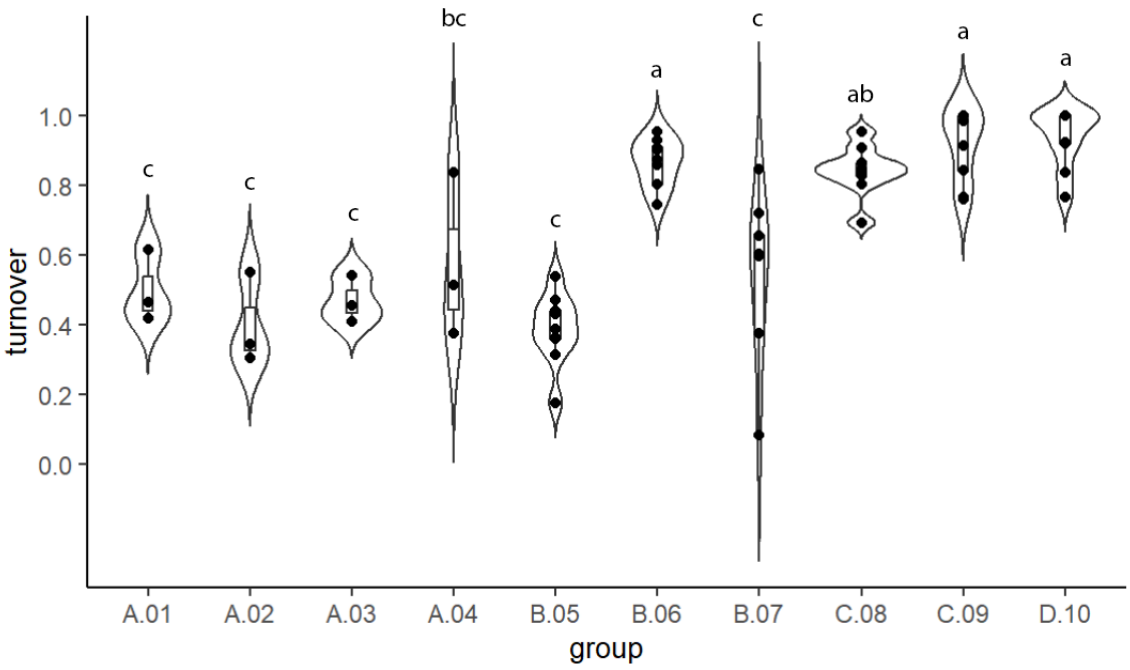

Figure 10: Turnover for the comparisons at Watzmann. The letters indicate whether there are significant differences between the groups. There is no difference when the groups have the same letters and differences when the letters are different. For technical reasons the violin plots range from <0 to >1 although it is computationally impossible.

There is an increasing trend of the turnover from A.02 to D.10 (Figure 10). The subgroup D.10 shows significant differences to most of the other groups (except for subgroup B.06 and both subgroups in group C).

The further apart the plots are, which means the greater the difference in successional levels, the higher the species turnover. In principle, all groups of one age classes and the ones comparing the two oldest age classes are all not significantly different to each other. They differ from the second group (which are comparisons across different age classes (except the oldest ones). Thus, the species composition of the community becomes increasingly different.

An exception is group B. Here the subgroups differ more clearly from each other and a significant difference within the group is seen between B.06 and the other group members. This group compares areas that are covered by open alpine grassland with scree.

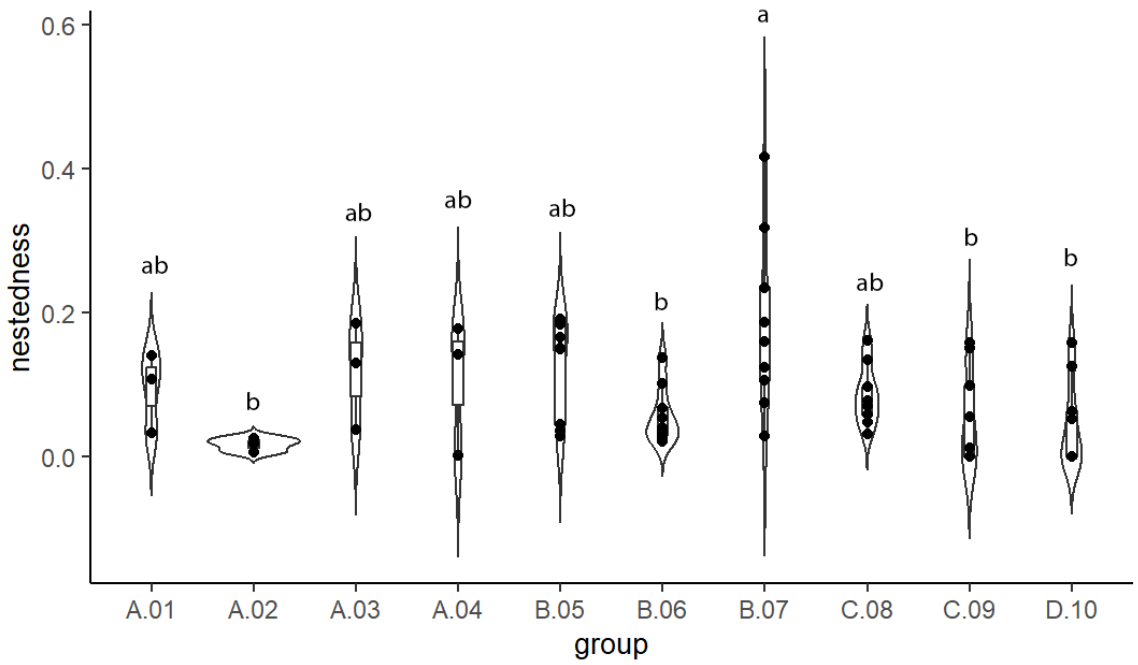

Figure 11: Nestedness for the comparisons at Watzmann. The letters indicate whether there are significant differences between the groups. There is no difference when the groups have the same letters and differences when the letters are different. For technical reasons the violin plots reach <0 although it is computationally impossible.

Nestedness shows relatively consistently low values in all subgroups and little scatter (Figure 11). It can be noted that estedness is lower than turnover and fewer significant differences can be found between the groups. Thus, there seems to be only a small proportion of species that occurs consistently across all plots.

An exception is seen in subgroup B.07, with values ranging from 0.03 to 0.42. It shows the largest distribution and the highest value. There are more species in this comparison (comparison succession level III and IV) than in the other comparisons such as *Hornungia alpina*, *Poa alpina* or *Thaspi rotundifolium*. This subgroup has significant differences to A.02, B.06, C.09 and D.

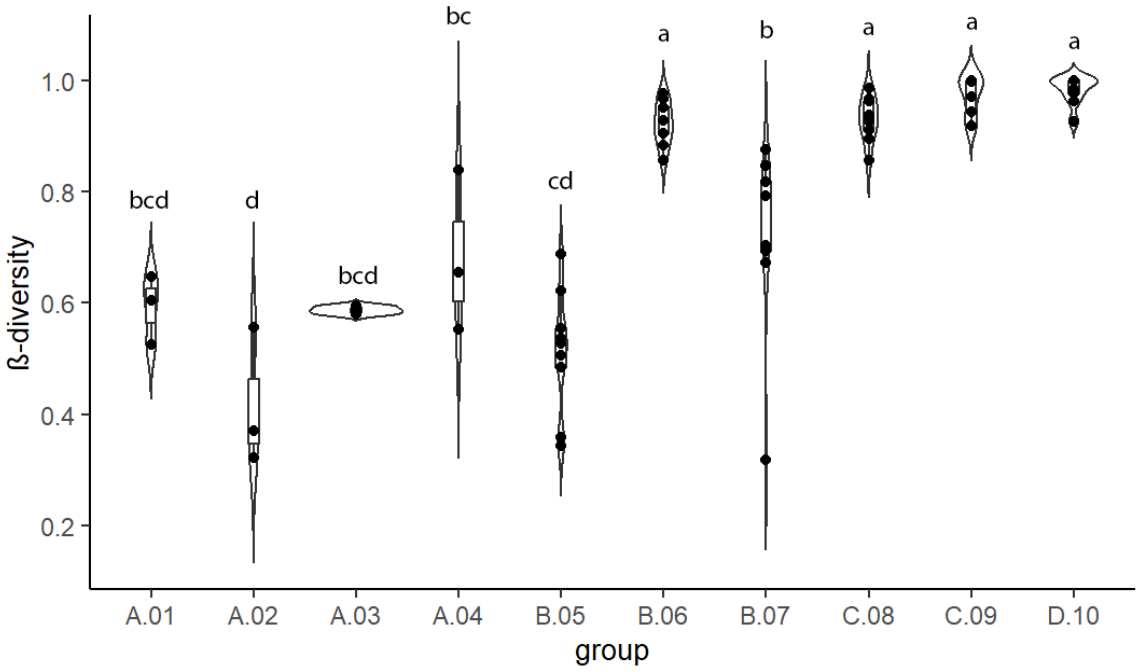

Figure 12: ß-diversity for the comparisons at Watzmann. The letters indicate whether there are significant differences between the groups. There is no difference when the groups have the same letters and differences when the letters are different. For technical reasons the violin plots reach >1 although it is computationally impossible.

The results of β-diversity (Figure 12) resemble those of the turnover. Here, too, an increasing trend can be observed. A.04 (comparison of glacier forefields) stands out with high values within its group. A.02 shows the lowest values for all results in this group. As with turnover and nestedness, B.07 shows the greatest fluctuations in the values.

Group B, which compares succession levels that are directly adjacent to each other, is very different from each other. If the levels are further apart, as in groups C and D, the results are no longer so different from each other. An exception is B.06, which differs from its own group but is equal to C and D (as with nestedness).

Discussion

This study is the first to investigate patterns of β-diversity across plots established in a chronosequence in glaciers forefields of the Northern Limestone Alps (i.e. Watzmann and Hochkalter) and probably one of the first of its kind in glacier forefields of the Alps in general. It assesses changes in species composition and diversity along a successional gradient and age classes of a of a glacier forefield.

The actual goal of this study was to investigate the glacier forefields on Blaueis and Watzmann and then to compare them with each other. However, due to long-lasting snow cover in the year of investigation only the glacier forefields of Blaueis were investigated since most of the glacier forefields at Watzmann were covered with snow. The long snow cover on the glacier forefields at Watzmann is probably related to the fact that the Watzmannkar is much larger than that of Blaueis and is therefore exposed to stronger winds. This leads to snow drifts, which could have been deposited on the glacier forefields.
However, an investigation of the oldest forefields could be carried out. These can thus be compared to most Blaueis plots. The investigation of the further succession plots on Watzmann now serve to see what changes occur when one goes beyond the glacier forefields. The reference plots of Blaueis are probably identical to those of level II at Watzmann.

Blaueis

The results at Blaueis do not reveal a clear trend in turnover, but a very low and constant nestedness along the age classes. In contrast, β-diversity is rather high and a minimal trend can be identified. The further apart the age classes are, the less the values in the individual subgroups scatter and the higher they become.

It can be assumed that there is no major change in species composition between glacier forefield age classes as there is no clear trend in turnover at Blaueis. Only the reference plots, which does not contain glacier forefield areas, shows pronounced turnover compared to all other age classes. The subgroups that contain a comparison to the reference plots show the highest and least scattered values within their group. Thus, there is a change in species composition compared to the reference plots, but not within the glacier foreland plots.

The nestedness shows lower values compared to the turnover on both study plots. There seems to be a certain but small proportion of species that occur constantly on all plots. At Watzmann the values are even lower than at Blaueis, so there is only a small part of species that occurs over all areas. The low values of nestedness were also described in the study by Soininen et al. (2018), which summarized 99 studies in different ecosystems and regions. They found that turnover is generally five times larger than nestedness. Furthermore, the variation caused by differences in richness between sites can be better quantified by nestedness.
The fact that nestedness is often so low seems to be a general problem. Carvalho et al. (2012) developed an alternative approach, which was not known to me at the time of the analysis of this study.

The results of the nestedness at Blaueis thus confirm those of the turnover: The plots of the glacier forefields are quite similar among themselves and only in comparison to the oldest and lowest (reference plots) there is a difference.
There is also only a minimal trend in β-diversity. The values increase slightly with increasing difference between the age groups. Since a change in β-diversity requires turnover processes, no clear trend can be observed here, as strong turnover processes are not present here as already mentioned.

As observed for turnover and nestedness, β-diversity also confirms the discernible difference between the oldest plots (reference plots) and all glacier forefield plots, as well as the similarity among glacier forefields. This is because, the subgroups that contain a comparison to the reference plots show the least widely dispersed values and the highest values within their group. Thus, the difference in age between the age classes within the glacier forefields appears to be not large enough to detect differences. The fact that 17 of the 44 species found at Blaueis only occur in the reference plots highlights the differences between the forefield plots and the reference plots. Among them, for example, the dwarf shrub species *Salix serpylifolia*, but also *Carex ferruginea* and *Soldanella alpina.* At Watzmann, these species also only occur from succession level II, which thus appears to be very similar to the reference plots.
In contrast, the pioneer species *Arabis alpina, Saxifraga stellaris, Cerastium uniflorum* and *Poa alpina* were found exclusively on the glacier forefields.

Watzmann

The situation is different when we step out of the glacier forefield succession and look at the longer and older gradient at Watzmann. The results obtained on the Watzmann show massive turnover and relatively low and constant nestedness along the successional levels. The β-diversity, which has been driven by the turnover, is also very high. It is clearly visible that the further apart the compared plots are or the more differing the succession levels are, the higher the values of turnover and β-diversity are. Cauvy-Fraunié & Dangles (2019) also described an increase in local species diversity and species abundance following glacial retreat. These results were to be expected, because when the succession stage changed, the elevation stage also changed, and with it the ecological conditions for the vegetation. Thus, the farther apart the plots are, the more different the conditions for the plants appear.

The strong trend in β-diversity may be due to the high spatial heterogeneity given by the different successional stages. For example, nutrient availability differs between sites, which can lead to differences in species composition (Soininen et al., 2018). However, the water-energy budget also plays an important role in species distribution (Hawkins et al., 2003). This may be different at the different successional stages studied. For example, water is most likely to run off faster on the upper surfaces than on the lower ones. This is because the soil there consists mostly of gravel and stones and a humus layer is not present. This is different on the lower (older) plots, where at least a clear grass carpet with moss was evident, where water and moisture can be intercepted, retained, and stored (Benninghoff, 1952; Ghestem et al., 2011).

Energy, such as temperature and solar radiation, can also differ between elevation levels and between individual plot locations. Thus, regardless of the age of the plot, meso- and microtopographic variability play a large role in species distribution (Matthews, 1992). In addition, most arctic and alpine species have temperature limitations for reproduction (Erschbamer, 2007; Henry & Molau, 1997). It might be possible, that one plot because it is located in the shade longer than others. This has an effect on the temperatures in these areas. Fewer hours of sunlight also means that plants have less time to photosynthesize and thus grow. For plants, Zellweger et al. (2017) found that climate was the strongest statistical predictor of β-diversity. In contrast Gallardo-Cruz et al. (2009) found in tropical landscapes that β-diversity is more influenced by altitude.

Baselga (2012) also gives high environmental heterogeneity as a likely explanation for why turnover could be the driving factor of β-diversity, rather than nestedness. This is because increasing environmental heterogeneity is seen whenever the number of habitat types and β-diversity increase, as is the case here (Valentine, 2009).
Other disturbing factors in the distribution of species could be rockfall or grazing animals like chamois or marmots. These factors vary on all plots and are hardly measurable, should be considered nevertheless.

It can be observed that the glacier forefield plots on Watzmann are still quite different from each other. The comparison within the glacier forefield plots stands out with quite high values. The glacier forefield plots appear to be more influenced by stochastic processes than those that are older and where succession is more advanced. Hanusch et al. (2022) observed that the first 60 years of succession is characterized by stochastic species additions and the plots are dominated by pioneer species. Subsequently, more deterministic processes occur, such as niche filtering and biotic interactions. After this threshold, pioneer species are progressively replaced by specialists of later successional stages. The threshold between stochastic and deterministic processes seems to occur later on the areas studied here, since the glacier forefield plots are older than 60 years but nevertheless mainly pioneer species have been found there.

It can be assumed that species that were only found on the younger plots were also present on the older plots some time ago. Thus, 19 species were found at Watzmann exclusively on the younger plots of succession levels III and IV, which also reflects the massive turnover. Among them were the pioneer species *Poa alpina, Arabis alpina, Thlaspi rotundifolium, Linaria alpina* and *Taraxacum alpinum*. These pioneer species often appear first in a succession and form the ecosystem engineers and thus the basis for species that follow later. This is because they can germinate under cold and humid conditions, and even high solar radiation does not affect them (Stöcklin & Bäumler, 1996).

Comparison Blaueis and Watzmann

This pioneer phase described can thus be assigned to the glacier forefields at both study sites. At Blaueis only this first succession stage (pioneer phase) is reached, although the sites are up

to 100 years old. Thus, the stochastic processes probably last much longer than described by Hanusch et al. (2022).

In glacier forefields of the Central Alps, the pioneer stage is replaced by the early successional stage after about 15 years (Eichel, 2019), as the pioneer species are partly displaced by other species due to competition, they disappear because they are short-lived species or the environmental conditions at the respective site are no longer suitable for them (Stöcklin & Bäumler, 1996). The changed environmental conditions include, above all, the further development and stabilization of the soil which leads to new species being able to settle more easily (Matthews & Vater, 2015). Thus, species number and vegetation cover increases (Raffl et al., 2006).
This is followed by the Intermediate Successional Stage with the highest species numbers and vegetation cover (Eichel, 2019). In this stage, shrub species that promote soil development and nitrogen fixation increase. The biological mineral cycle is initiated (Matthews, 1992) and the establishment of late successional species is facilitated by these species (Chapin et al., 1994). With the appearance of the first trees, the Late Successional Stage is reached (Eichel, 2019; Nagl & Erschbamer, 2010).

Eichel (2019) interpreted such changes in species composition, as observed here as biogeomorphic succession, which was subdivided into three biogeomorphic succession phases: in the first phase, pioneer species dominate. The dynamics of dispersal are controlled by abiotic processes and geomorphological activity is high. In the second phase, geomorphic processes are increasingly influenced by engineering species and biotic processes come more and more into play and biogeomorphological interaction is high. In the last phase, geomorphic processes decline. As biotic processes such as competition and inhibition now dominate, the engineer species are eventually replaced or superseded by other species. These three phases of biogeomorphic succession are well reflected in the results of this study.

In the Northern Limestone Alps, succession seems to proceed much more slowly than in the Central Alps (Fels, 2022; Kühn et al., unpublished). Because species numbers increase more slowly in the glacier forefields of Blaueis compared to succession in the Central Alps and stochastic processes last longer (Fels, 2022). In this study we are also in the Northern Limestone Alps, which is why it can be assumed that succession is slower here as well. Also, most of the investigated plots at Watzmann are no longer glacier forefields sensu stricto, as they are

probably deglaciated for a long time already. However, since a slower succession can be expected also on these areas, the succession stages of the glacier forefields of the Central Alps can also be transferred to the present gravel and scree areas on Watzmann. In addition, the succession on the Watzmann plots is regularly disturbed by rockfall and new deposits and thus set back, similar as with glacier forefields.

The early successional stage described for the glacier forefields of the Central Alps can be assigned to Level III at Watzmann, since most pioneer species were no longer found from this time on and have probably been displaced by competition (Eichel, 2019).

The intermediate successional stage with the highest species numbers and vegetation cover (Eichel, 2019), is found here at approximately successional level II. Deterministic processes occur more frequently, species that promote soil development or nitrogen fixation such as *Dryas octopetala* are found (Reisigl & Keller, 1994), and shrub species such as *Salix serpylifolia*. At Blaueis, the intermediate stage can be assigned to the reference plots. The shrub species *Salix serpylifolia* is found there.

From successional level I, the first tree species such as *Larix decidua* and *Picea abies* appear and the late successional stage is reached. However, it is important to note the tree line, which is located at about the same elevation level as this successional stage and has a massive influence on the distribution of tree species.

A large change in the turnover and β-diversity can be seen in the comparison of the two succession levels II and III (B.06). The substrate of these plots consists partly of loose sward (level II) and of scree (level III) and seems to play a decisive role. From here on the conditions for the plants seem to change in a way, that a turnover and a change in β-diversity appears. All other comparisons, comparing to level III and IV (the two oldest), remain at approximately the same high level because conditions on the oldest plots appear to be similar. This sharp jump from B.06 may be related to the change in elevation level but also to the successional stage. Successional level I and II and level III and IV appear to be very similar in this regard.

In conclusion, however, the driving factor for the dispersal and diversity patterns cannot be precisely determined, as this study exclusively focussed on patterns of nestedness and turnover and not on their external drivers. This is because this study was limited in scope to what these patterns look like and not what causes them. However, the dispersal ability of species plays an

important role in the emergence of diversity patterns (Dobrovolski et al., 2012; Qian, 2009). It may be that some plant species have not even managed to reach the upper and younger succession areas due to dispersal limitation. Hence, species establishment in the study areas probably originates exclusively from lower sites, with seeds being transported by wind, animals or even humans. Colonization from above is not possible at Blaueis and Watzmann, since there is hardly any vegetation above the glacier surfaces due to the steepness of the adjacent slopes (Nagl & Erschbamer, 2010; Raffl et al., 2006). Therefore, deterministic factors as well as stochastic processes should be equally considered.

Conclusion

With this study it was shown that the investigation of β-diversity is well suited to gain insight into species composition along a successional gradient. Firstly, this study covers succession on different age classes of glacier forefields, and secondly how areas develop where glacial retreat occurred many hundreds to a few thousand years ago.

It was found that the succession process on glacier forefields in the Northern Limestone Alps seems to be slower than compared to the Central Alps. Thus, stochastic processes last much longer and are only later replaced by deterministic ones. The same has already been observed by Fels, (2022) and Kühn (unpublished). For this reason, we can assume that also on the areas of Watzmann outside the glacier forefields a slowed down succession takes place. Therefore, the succession patterns of the glacier forefields in the Central Alps can be transferred and compared to the much older areas on Watzmann.

The results of the β-diversity showed that within the different age classes of the glacier forefields at Blaueis there are still no major changes in species composition. Pioneer species were found here for the most part.

The situation is different along the gradient, which goes beyond the glacier forefields. It could be shown, that the further apart the plots are, or the succession progresses and the age changes, the more they also differ from each other. These results of β-diversity are confirmed by those of turnover and nestedness.

The biggest difference was observed between plots with open alpine grasslands compared to those with scree. Thus, from here on, conditions for vegetation seem to change enough to have

an impact on species compositions.
However, environmental conditions are not the only factors affecting species composition. Stochastic processes, as well as the dispersal capabilities of individual species, should not be ignored.

Outlook

In this study, the changes in species composition were investigated in relation to complex environmental gradients, in this case represented by succession.

By analysing β-diversity, it was possible to show at which stage in succession major changes (change in species composition) occur and that these changes are not found within the glacier forefields. It was also possible to show how the two components nestedness and turnover behave along the gradient. This study can be used as a cornerstone for long-term studies regarding climate change. More and more glaciers are becoming ice-free and thus offer space for vegetation to colonize. In the future it would be interesting to find out if there are differences in succession within the glacier forefields, which have a larger age difference and are further apart from each other.
In order to make comparisons between studies in the long term, the survey of the actual state is important. For this reason, the areas investigated here were marked using GPS so that they can be found again for further studies.

Ecological site factors such as temperature, precipitation etc. should be measured in the future. In this way, the relationship between species occurrence and abundance and the decisive environmental gradient could be assessed. In addition, insights can be gained into whether a response to specific changing environmental gradients occurs only in certain species or species communities respond collectively (Fischer et al., 2011).

Furthermore, comparison to other areas of the Northern Limestone Alps and beyond would be useful to determine if similar results can be found there. It would also be interesting to investigate the functional characteristics to see how they change over succession.

References

Anderson, N. J., Saros, J. E., Bullard, J. E., Cahoon, S. M. P., McGowan, S., Bagshaw, E. A., Barry, C. D., Bindler, R., Burpee, B. T., Carrivick, J. L., Fowler, R. A., Fox, A. D., Fritz, S. C., Giles, M. E., Hamerlik, L., Ingeman-Nielsen, T., Law, A. C., Mernild, S. H., Northington, R. M., … Yde, J. C. (2017). The Arctic in the Twenty-First Century: Changing Biogeochemical Linkages across a Paraglacial Landscape of Greenland. *BioScience*, *67*(2), 118–133. https://doi.org/10.1093/biosci/biw158

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, *19*(1), 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x

Baselga, A. (2012). The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography*, *21*(12), 1223–1232. https://doi.org/10.1111/j.1466-8238.2011.00756.x

Baselga, A. (2017). Partitioning abundance-based multiple-site dissimilarity into components: Balanced variation in abundance and abundance gradients. *Methods in Ecology and Evolution*, *8*(7), 799–808. https://doi.org/10.1111/2041-210X.12693

Baselga, A., Orme, D., Villeger, S., De Bortoli, J., Leprieur, F., Logez, M., Henriques-Silva, R., Mart, S., Mart, R., & Crujeiras, R. (2022). *Package 'betapart.'*

Bayerisches Landesamt für Umwelt (LfU). (2023). *Bayerische Gletscher—Angewandte Geologie—Watzmann-Gletscher*. Umweltatlas Bayern. http://www.bayerische-gletscher.de/wmg.htm

Benninghoff, W. S. (1952). Interaction of Vegetation and Soil Frost Phenomena. *Arctic*, *5*(1), 34–44.

Billings, W. D. (1974). Adaptations and Origins of Alpine Plants. *Arctic and Alpine Research, 6:2, 129-142*, 15. https://doi.org/DOI: 10.1080/00040851.1974.12003769

Burga, C. A., Walther, G. R., & Beisser, S. (2004). Florenwandel in der alpinen Stufe des Berninagebietes – ein Klimasignal? *Berichte Der Reinhold-Tüxen-Gesellschaft*, *16*, 57–66.

Carvalho, J. C., Cardoso, P., & Gomes, P. (2012). Determining the relative roles of species replacement and species richness differences in generating beta-diversity patterns. *Global Ecology and Biogeography*, *21*(7), 760–771. https://doi.org/10.1111/j.1466-8238.2011.00694.x

Cauvy-Fraunié, S., & Dangles, O. (2019). A global synthesis of biodiversity responses to glacier retreat. *Nature Ecology & Evolution*, *3*(12), 1675–1685. https://doi.org/10.1038/s41559-019-1042-8

Chapin, F. S., Walker, L. R., Fastie, C. L., & Sharman, L. C. (1994). Mechanisms of Primary Succession Following Deglaciation at Glacier Bay, Alaska. *Ecological Monographs*, *64*(2), 149–175. https://doi.org/10.2307/2937039

Dobrovolski, R., Melo, A. S., Cassemiro, F. A. S., & Diniz-Filho, J. A. F. (2012). Climatic history and dispersal ability explain the relative importance of turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, *21*(2), 191–197. https://doi.org/10.1111/j.1466-8238.2011.00671.x

Eichel, J. (2019). Vegetation succession and biogeomorphic interactions in glacier forelands. In *Geomorphology of proglacial systems* (pp. 327–349). Springer International Publishing. https://doi.org/10.1007/978-3-319-94184- 4_19

Erschbamer, B. (2007). Winners and Losers of Climate Change in a Central Alpine Glacier Foreland. *Arctic, Antarctic, and Alpine Research*, *39*(2), 237–244. https://doi.org/10.1657/1523-0430(2007)39[237:WALOCC]2.0.CO;2

Fels, L. (2022). *Changes in plant community composition along a successional gradient in the forefields of the Blaueis, Northern Limestone Alps*.

Fischer, A., Blaschke, M., & Bässler, C. (2011). Altitudinal gradients in biodiversity research: The state of the art and future perspectives under climate change aspects. *Waldökologie, Landschaftsforschung Und Naturschutz*, *11*, 35–47.

Gallardo-Cruz, J. A., Pérez-García, E. A., & Meave, J. A. (2009). β-Diversity and vegetation structure as influenced by slope aspect and altitude in a seasonally dry tropical landscape. *Landscape Ecology*, *24*(4), 473–482. https://doi.org/10.1007/s10980-009-9332-1

Gassler, F. (1984). Alpenvereinseinteilung der Ostalpen (AVE). In *Alpenvereinsjahrbuch 1984* (Vol. 108, pp. 215–224). Bergverlag Rudolf Rother GmbH.

Ghestem, M., Sidle, R. C., & Stokes, A. (2011). The Influence of Plant Root Systems on Subsurface Flow: Implications for Slope Stability. *BioScience*, *61*(11), 869–879. https://doi.org/10.1525/bio.2011.61.11.6

Gobbi, M., Caccianiga, M., Cerabolini, B., De Bernardi, F., Luzzaro, A., & Pierce, S. (2010). Plant adaptive responses during primary succession are associated with functional adaptations in ground beetles on deglaciated terrain. *Community Ecology*, *11*, 223–231.

Grabherr, G., Gottfried, M., & Pauli, H. (1994). Climate effects on mountain plants. *Nature*, *369*, 448.

Hagg, W. (2022). *Blaueis*. Bayerische Gletscher. http://bayerischegletscher.userweb.mwn.de/wmg.htm

Hanusch, M., He, X., Ruiz-Hernández, V., & Junker, R. R. (2022). Succession comprises a sequence of threshold-induced community assembly processes towards multidiversity. *Communications Biology*, *5*(1), Article 1. https://doi.org/10.1038/s42003-022-03372-2

Hawkins, B. A., Field, R., Cornell, H. V., Currie, D. J., Guégan, J.-F., Kaufman, D. M., Kerr, J. T., Mittelbach, G. G., Oberdorff, T., O'Brien, E. M., Porter, E. E., & Turner, J. R. G. (2003). Energy, Water, and Broad-Scale Geographic Patterns of Species Richness. *Ecology*, *84*(12), 3105–3117. https://doi.org/10.1890/03-8006

Henry, G. h. r., & Molau, U. (1997). Tundra plants and climate change: The International Tundra Experiment (ITEX). *Global Change Biology*, *3*(S1), 1–9. https://doi.org/10.1111/j.1365-2486.1997.gcb132.x

Koleff, P., Gaston, K. J., & Lennon, J. J. (2003). Measuring beta diversity for presence–absence data. *Journal of Animal Ecology*, *72*(3), 367–382. https://doi.org/10.1046/j.1365-2656.2003.00710.x

Körner, C. (2003). *Alpine Plant Life*. Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-18970-8

Lawinenwarndiest Bayern. (2023). *Archiv Messdaten 2020/2021 Berchtesgadener Alpen, Kühroint/Funtenseetauern*. https://www.lawinenwarndienst-bayern.de/res/archiv/messdaten/saisongrafik.php?id=5&s_saison=2020/2021&geb=6

Lippert, W., Springer, S., & Wunder, H. (1997). *Die Farn- und Blütenpflanzen des Nationalparks: Kommentierte Artenliste: Vol. Nationalpark Berchtesgaden / Forschungsberichte*. Nationalpark-Verwaltung Berchtesgaden.

MacDonald, G. (2002). *Biogeography: Introduction to Space, Time, and Life*. John Wiley & Sons.

Matthews, J. A. (1992). *The Ecology of Recently-deglaciated Terrain: A Geoecological Approach to Glacier Forelands*. Cambridge University Press.

Matthews, J. A., & Vater, A. E. (2015). Pioneer zone geo-ecological change: Observations from a chronosequence on the Storbreen glacier foreland, Jotunheimen, southern Norway. *CATENA*, *135*, 219–230. https://doi.org/10.1016/j.catena.2015.07.016

Mayer, C., Hagg, W., Weber, M., & Lambrecht, A. (2021). *Zukunft ohne Eis Zweiter Bayerischer Gletscherbericht: Klimawandel in den Alpen*. Bayerische Akademie der Wissenschaft Bayerisches, Staatsministerium für Umwelt und Verbraucherschutz.

Mayer, C., Weber, M., Wendt, A., & Hagg, W. (2021). Die bayerischen Gletscher, die verbliebenen Eisreserven Deutschlands. *Polarforschung*, *89*(1), 1–7. https://doi.org/10.5194/polf-89-1-2021

McKnight, M. W., White, P. S., McDonald, R. I., Lamoreux, J. F., Sechrest, W., Ridgely, R. S., & Stuart, S. N. (2007). Putting Beta-Diversity on the Map: Broad-Scale Congruence and Coincidence in the Extremes. *PLoS Biology*, *5*(10). https://doi.org/10.1371/journal.pbio.0050272

Mendiburu, F. de. (2021). *agricolae: Statistical Procedures for Agricultural Research* (1.3-5). https://CRAN.R-project.org/package=agricolae

Müller, K., & Bryan, J. (2020). *here: A Simpler Way to Find Your Files* (1.0.1). https://CRAN.R-project.org/package=here

Nagl, F., & Erschbamer, B. (2010). Pflanzliche Sukzessionen im Gletschervorfeld. Vegetation und Besiedlungsstrategien. In *Glaziale und periglaziale Lebensräume im Raum Obergurgl* (pp. 121–142). Innsbruck University press.

Nationalparkverwaltung Berchtesgaden. (2023). *Klima*. https://www.nationalpark-berchtesgaden.bayern.de/natur/wissenswertes/klima/index.htm

Parolo, G., & Rossi, G. (2008). Upward migration of vascular plants following a climate warming trend in the Alps. *Basic and Applied Ecology*, *9*(2), 100–107. https://doi.org/10.1016/j.baae.2007.01.005

Qian, H. (2009). Beta diversity in relation to dispersal ability for vascular plants in North America. *Global Ecology and Biogeography*, *18*(3), 327–332. https://doi.org/10.1111/j.1466-8238.2009.00450.x

Qian, H., Ricklefs, R. E., & White, P. S. (2005). Beta diversity of angiosperms in temperate floras of eastern Asia and eastern North America. *Ecology Letters*, *8*(1), 15–22. https://doi.org/10.1111/j.1461-0248.2004.00682.x

Raffl, C., Mallaun, M., Mayer, R., & Erschbamer, B. (2006). Vegetation Succession Pattern and Diversity Changes in a Glacier Valley, Central Alps, Austria. *Arctic, Antarctic, and Alpine Research*, *38*(3), 421–428. https://doi.org/10.1657/1523-0430(2006)38[421:VSPADC]2.0.CO;2

Reichelt, G., & Wilmanns, O. (1973). Vegetationsgeographie. In *Das Geographische Seminar: Praktische Arbeitsweisen* (p. 210). Westermann.

Reisigl, H., & Keller, R. (1994). *Alpenpflanzen im Lebensraum—Alpine Rasen Schutt- und Felsvegetation: Vol. Vegetationsökologische Informationen für Studien, Exkursionen und Wanderungen*. Spektrum Akademischer Verlag.

Scholes, R. J., & van Breemen, N. (1997). The effects of global change on tropical ecosystems. *Geoderma*, *79*(1–4), 9–24. https://doi.org/10.1016/S0016-7061(97)00036-0

Shi, G. R. (1993). Multivariate data analysis in palaeoecology and palaeobiogeography—A review—ScienceDirect. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 199–234.

Soininen, J., Heino, J., & Wang, J. (2018). A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems. *Global Ecology and Biogeography*, *27*(1), 96–109. https://doi.org/10.1111/geb.12660

Sommer, C., Malz, P., Seehaus, T. C., Lippl, S., Zemp, M., & Braun, M. H. (2020). Rapid glacier retreat and downwasting throughout the European Alps in the early 21st century. *Nature Communications*, *11*(1), Article 1. https://doi.org/10.1038/s41467-020-16818-0

Stöcklin, J., & Bäumler, E. (1996). Seed rain, seedling establishment and clonal growth strategies on a glacier foreland. *Journal of Vegetation Science*, *7*(1), 45–56. https://doi.org/10.2307/3236415

Valentine, J. W. (2009). Overview of marine biodiversity. In *Marine Macroecology* (pp. 3–28). The University of Chicago.

Wheeler, B., & Torchiano, M. (2016). *lmPerm: Permutation Tests for Linear Models* (2.1.0). https://CRAN.R-project.org/package=lmPerm

Whittaker, R. H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, *30*(3), 279–338. https://doi.org/10.2307/1943563

Wickham, H. (2016). *Ggplot2* (2nd ed.). https://link.springer.com/book/10.1007/978-3-319-24277-4

Wickham, H., Bryan, J., Posit, attribution), P. (Copyright holder of all R. code and all C. code without explicit copyright, code), M. K. (Author of included R., code), K. V. (Author of included libxls, code), C. L. (Author of included libxls, code), B. C. (Author of included libxls, code), D. H. (Author of included libxls, & code), E. M. (Author of included libxls. (2023). *readxl: Read Excel Files* (1.4.2). https://CRAN.R-project.org/package=readxl

Wickham, H., François, R., Henry, L., Müller, K., Vaughan, D., Posit, & PBC. (2023). *dplyr: A Grammar of Data Manipulation* (1.1.0). https://CRAN.R-project.org/package=dplyr

Wilson, M. V., & Shmida, A. (1984). Measuring beta diversity with presence-absence data. *Journal of Ecology*, *72*, 1055–1064.

Wojcik, R., Eichel, J., Bradley, J. A., & Benning, L. G. (2021). How allogenic factors affect succession in glacier forefields. *Earth-Science Reviews*, *218*, 103642. https://doi.org/10.1016/j.earscirev.2021.103642

Zellweger, F., Roth, T., Bugmann, H., & Bollmann, K. (2017). Beta diversity of plants, birds and butterflies is closely associated with climate and habitat structure. *Global Ecology and Biogeography*, *26*(8), 898–906. https://doi.org/10.1111/geb.12598

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Appendix 1

Table S1: Species occurring (X) on the plots of the Watzmann. Sorted by succession level (Recent level = 10-12, second youngest level = 7-9, second oldest level = 4-6, oldest level = 1-3).

Species	WA12	WA11	WA10	WA09	WA08	WA07	WA06	WA05	WA04	WA03	WA02	WA01
Achillea atrata	X			X	X	X	X	X	X	X	X	
Achillea clvennae	X											
Adenostyles alliariae		X			X							
Agrostis alpina									X			
Arabis alpina			X									
Arabis bellidifolia	X											
Bartsia alpina									X			
Bellidiastrum michelii							X	X	X	X	X	X
Biscutella laevigata				X			X	X	X	X	X	X
Bistorta vivipara							X	X	X	X	X	X
Campanula cochleariifolia	X	X		X		X						
Campanula scheuchzeri							X	X		X		
Carex ferruginea							X	X	X	X	X	X
Carex firma	X					X	X	X	X	X	X	
Cystopteris fragilis			X									
Dryas octopetala								X				
Dryopteris villarii			X									
Euphrasia minima	X											
Festuca alpina						X	X	X	X	X	X	
Galium anisophyllon							X	X	X	X	X	X
Galium megalospermum					X							
Homogyne alpina								X	X			
Hornungia alpina	X	X	X	X	X	X		X				
Huperzia selago									X		X	
Juncus montanus	X						X	X		X	X	X
Leontodon hispidus							X	X	X	X	X	X
Ligusticum mutellina												X
Linaria alpina	X			X	X	X						
Luzula glabrata							X	X				
Moehringia ciliate		X		X	X	X		X		X		
Mutellina adonidifolia							X	X	X	X	X	
Myosotis alpestris				X								
Papaver alpinum	X					X						
Parnassia palustris							X			X		
Pedicularis rostratospicata							X		X		X	
Phyteuma orbiculare									X			
Pinguicula alpina							X			X	X	
Poa alpina	X		X	X	X	X						
Primula minima							X		X			
Ranunculus alpestris							X	X	X	X	X	X
Ranunculus montanus								X		X	X	X
Rumex scutatus				X	X	X						
Salix serpyllifolia							X	X	X		X	
Saxifraga aphylla						X						
Saxifraga stellaris		X										
Sesleria caerulea							X	X	X	X	X	X
Silene acaulis							X		X	X		
Soldanella alpina							X	X	X	X	X	X
Taraxacum alpina	X											
Thlaspi rotundifolium	X	X	X	X	X	X	X					
Tofieldia pusilla							X	X	X	X	X	X
Valeriana saxatilis									X	X	X	X
Veronica aphylla	X			X	X	X						
Viola biflora				X	X	X		X	X	X	X	X

Table S2: Species occurring (X) at the Blaueis forefields. Sorted by age class (10 = BL01, BL03, BL06, BL08; 40 = BL02, BL05, BL12; 70 = BL04, BL10, BL11; 100 = BL07, BL09, BL13; Reference plots = BL14-16).

Species	BL 01	BL 03	BL 06	BL 08	BL 02	BL 05	BL 12	BL04	BL 10	BL 11	BL 07	BL 09	BL 13	BL 14	BL 15	BL 16
Achillea atrata														X	X	X
Arabis alpina		X			X	X	X	X	X	X	X	X				
Arabis bellidifolia								X	X				X	X		
Bellidiastrum michelii														X	X	X
Biscutella laevigata														X		X
Bistorta vivipara														X	X	X
Campanula cochleariifolia								X			X	X				
Campanula scheuchzeri														X	X	X
Carex ferruginea															X	X
Carex firma												X	X	X	X	X
Carex sempervirens														X	X	X
Cerastium uniflorum		X		X	X	X		X	X	X	X	X	X			
Crepis terglouensis													X			
Euphrasia minima								X								X
Festuca alpina			X		X		X	X		X	X	X	X	X		X
Galium anisophyllon															X	X
Galium megalospermum											X		X	X		
Heliosperma pusillum					X		X	X	X		X	X	X			
Hornungia alpina	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X
Juncus montanus														X		X
Minuartia gerardii											X	X				
Moehringia ciliate	X				X										X	
Mutellina adonidifolia																X
Papaver alpinum					X		X	X	X							
Parnassia palustris															X	X
Pedicularis rostratospicata															X	X
Poa alpina		X		X	X	X	X	X	X	X	X	X	X			
Ranunculus alpestris											X		X	X	X	X
Ranunculus montanus																X
Salix serpyllifolia														X	X	X
Saxifraga aizoides											X					
Saxifraga moschata		X			X	X			X	X	X	X				
Saxifraga stellaris			X		X						X	X	X			
Scorzoneroides montana								X			X					
Sesleria caerulea								X				X		X	X	X
Silene acaulis								X				X	X	X		
Soldanella alpina														X	X	X
Taraxacum alpina											X					
Thlaspi rotundifolium		X	X				X	X		X	X	X	X			
Tofieldia pusilla														X		
Valeriana saxatilis														X		
Veronica aphylla												X				
Viola biflora											X	X	X	X	X	

Table S3: Species occurrence at Watzmann with species cover at plot-level and succession level.

Plot	Succession level	Species	Species cover (%)
WA01	I	*Bellidiastrum michelii*	2.5
		Biscutella laevigata	1
		Bistorta vivipara	2.5
		Carex ferruginea	37.5
		Galium anisophyllon	1
		Juncus montanus	1
		Leontodon hispidus	2.5
		Ligusticum mutellina	10
		Ranunculus alpestris	2.5
		Ranunculus montanus	2.5
		Sesleria caerulea	37.5
		Soldanella alpina	2.5
		Tofieldia pusilla	1
		Valeriana saxatilis	2.5
		Viola biflora	10
WA02	I	*Achillea atrata*	1
		Bellidiastrum michelii	10
		Biscutella laevigata	2.5
		Bistorta vivipara	1
		Carex ferruginea	20
		Carex firma	0.1
		Festuca alpina	1
		Galium anisophyllon	1
		Huperzia selago	1
		Juncus montanus	1
		Leontodon hispidus	1
		Mutellina adonidifolia	10
		Pedicularis rostratocapitata	1
		Pinguicula alpina	1
		Ranunculus alpestris	10
		Ranunculus montanus	1
		Salix serpyllifolia	0.1
		Sesleria caerulea	20
		Soldanella alpina	1
		Tofieldia pusilla	2.5
		Valeriana saxatilis	10
		Viola biflora	2.5
		Leontodon hispidus	1
WA03	I	*Achillea atrata*	1
		Bellidiastrum michelii	2.5
		Biscutella laevigata	10
		Bistorta vivipara	1
		Campanula scheuchzeri	1
		Carex ferruginea	20
		Carex firma	1
		Festuca alpina	2.5
		Galium anisophyllon	2.5
		Juncus montanus	1
		Moehringia ciliata	1
		Mutellina adonidifolia	1
		Parnassia palustris	1
		Pinguicula alpina	2.5
		Ranunculus alpestris	2.5

		Ranunculus montanus	1
		Sesleria caerulea	2.5
		Silene acaulis	0.1
		Soldanella alpina	1
		Tofieldia pusilla	1
		Valeriana saxatilis	10
		Viola biflora	1
WA04	II	*Achillea atrata*	1
		Agrostis alpina	1
		Bartsia alpina	1
		Bellidiastrum michelii	2.5
		Biscutella laevigata	1
		Bistorta vivipara	1
		Carex ferruginea	20
		Carex firma	1
		Festuca alpina	1
		Galium anisohyllon	1
		Homogyne alpina	1
		Huperzia selago	0.1
		Leontodon hispidus	2.5
		Mutellina adonidifolia	2.5
		Pedicularis rostratocapitata	2.5
		Phyteuma orbiculare	1
		Primula minima	1
		Ranunculus alpestirs	2.5
		Salix serpyllifolia	2.5
		Selseria caerulea	2.5
		Silena acaulis	1
		Soldanella alpina	2.5
		Tofieldia pusilla	2.5
		Valeriana saxatilis	1
		Viola biflora	2.5
WA05	II	*Achillea atrata*	1
		Bellidiastrum michelii	2.5
		Biscutella laevigata	2.5
		Bistorta vivipara	2.5
		Campanula scheuchzeri	1
		Carex ferruginea	20
		Carex firma	1
		Dryas octopetala	0.1
		Festuca alpina	2.5
		Galium anisophyllon	1
		Homogyne alpina	1
		Hornungia alpina	0.1
		Juncus montanus	1
		Leontodon hispidus	1
		Luzula glabrata	1
		Mutellina adonidifolia	2.5
		Ranunculus alpestris	10
		Ranunculus montanus	2.5
		Salix serpyllifolia	0.1
		Sesleria caerulea	2.5
		Soldanella alpina	2.5
		Tofieldia pusilla	1
		Viola biflora	2.5
		Moehringia ciliata	1
WA06	II	*Achillea atrata*	1

		Bellidiastrum michelii	2.5
		Biscutella laevigata	2.5
		Bistorta vivipara	2.5
		Campanula scheuchzeri	1
		Carex ferruginea	10
		Carex firma	10
		Festuca alpina	1
		Galium anisophyllon	1
		Juncus montanus	1
		Leontodon hispidus	2.5
		Luzula glabrata	1
		Mutellina adonidifolia	2.5
		Parnassia palustris	1
		Pedicularis rostratocapitata	2.5
		Pinguicula alpina	1
		Primula minima	0.1
		Ranunculus alpestris	10
		Salix serpyllifolia	1
		Sesleria caerulea	1
		Silene acaulis	1
		Soldanella alpina	2.5
		Thlaspi rotundifolium	0.1
		Tofieldia pusilla	1
WA07	III	*Achillea atrata*	2.5
		Campanula cochleariifolia	2.5
		Carex firma	0.1
		Festuca alpina	0.1
		Hornungia alpina	1
		Linaria alpina	1
		Moehringia ciliata	1
		Papaver alpinum	2.5
		Poa alpina	1
		Rumex scutatus	0.1
		Saxifraga aphylla	1
		Thlaspi rotundifolium	2.5
		Veronica aphylla	1
		Viola biflora	2.5
WA08	III	*Achillea atrata*	2.5
		Adenostyles alliariae	1
		Galium megalospermum	0.1
		Hornungia alpina	1
		Linaria alpina	1
		Moehringia ciliata	1
		Poa alpina	1
		Rumex scutatus	2.5
		Thlaspi rotundifolim	10
		Veronica aphylla	1
		Viola biflora	1
WA09	III	*Achillea atrata*	2.5
		Biscutella laevigata	2.5
		Campanula cochleariifolia	1
		Hornungia alpina	1
		Linaria alpina	1
		Moehringia ciliata	1
		Myosotis alpestris	10
		Poa alpina	1
		Rumex scutatus	1

		Thlaspi rotundifolium	2.5
		Veronica aphylla	2.5
		Viola biflora	10
WA10	IV	*Arabis alpina*	1
		Cystopteris fragilis	0.1
		Dryopteris villarii	0.1
		Hornungia alpina	1
		Poa alpina	2.5
		Thlaspi rotundifolium	2.5
WA11	IV	*Campanula chochleriifolia*	0.1
		Hornungia alpina	1
		Moehringia ciliata	1
		Saxifraga stellaris	1
		Thlaspi rotundifolium	10
WA12	IV	*Achillea atrata*	1
		Achillea clvennae	1
		Adenostyles alliariae	0.1
		Arabis bellidifolia	0.1
		Campanula chochleriifolia	1
		Carex firma	1
		Euphrasia minima	0.1
		Hornungia alpina	1
		Juncus montanus	1
		Linaria alpina	0.1
		Papaver alpinum	1
		Poa alpina	2.5
		Taraxacum alpinum	1
		Thlaspi rotundifolium	1
		Veronica aphylla	1

Table S4: Species occurrence at Blaueis with species cover at plot-level and age class.

Plot	Age classes	Species	Species cover (%)
BL01	10	*Hornungia alpina*	2.5
		Moehringia ciliata	1
BL02	40	*Arabis alpina*	0.1
		Cerastium uniflorum	1
		Festuca alpina	1
		Heliosperma pusillum	1
		Hornungia alpina	2.5
		Moehringia ciliata	2.5
		Papaver alpinum	1
		Poa alpina	1
		Saxifraga moschata	0.1
		Saxifraga stellaris	0.1
BL03	10	*Arabis alpina*	1
		Cerastium uniflorum	0.1
		Hornungia alpina	2.5
		Poa alpina	1

		Saxifraga moschata	0.1
		Thlaspi rotundifolium	1
BL04	70	*Arabis alpina*	0.1
		Arabis bellidifolia	0.1
		Campanula chochleriifolia	1
		Cearastium uniflorum	2.5
		Euphrasia minima	0.1
		Festuca alpina	2.5
		Heliosperma pusillum	1
		Hornungia alpina	2.5
		Papaver alpinum	1
		Poa alpina	1
		Saxifraga moschata	2.5
		Sesleria caerulea	0.1
		Silena acaulis	0.1
		Thlaspi rotundifolium	2.5
BL05	40	*Arabis alpina*	0.1
		Cerastium uniflorum	10
		Hornungia alpina	0.1
		Poa alpina	0.1
		Saxifraga moschata	0.1
BL06	10	*Festuca alpina*	0.1
		Hornungia alpina	0.1
		Saxifraga stellaris	0.1
		Thlaspi rotundifolium	1
BL07	100	*Arabis alpina*	1
		Campanula cochleariifolia	2.5
		Cerastium uniflorum	1
		Festuca alpina	10
		Galium megalospermum	1
		Heliosperma pusillum	0.1
		Hornungia alpina	2.5
		Minuartia gerardii	1
		Poa alpina	1
		Ranunculus alpestris	1
		Saxifraga aizoides	0.1
		Saxifraga moschata	1
		Saxifraga stellaris	0.1
		Scorzoneroides montana	2.5
		Taraxacum alpina	1
		Thlaspi rotundifolium	2.5
		Viola biflora	0.1
BL08	101	*Cerastium uniflorum*	1
		Hornungia alpina	1
		Poa alpina	2.5
BL09	100	*Arabis alpina*	1
		Campanula cochleariifolia	0.1
		Carex firma	0.1
		Cerastium uniflorum	10
		Festuca alpina	10
		Heliosperma pusillum	10
		Hornungia alpina	2.5
		Minuartia gerardii	1
		Poa alpina	1
		Saxifraga moschata	2.5
		Saxifraga stellaris	0.1

		Sesleria caerulea	2.5
		Silene acaulis	1
		Thlaspi rotundifolium	1
		Veronica aphylla	0.1
		Viola biflora	2.5
BL10	70	*Arabis alpina*	2.5
		Arabis bellidifolia	1
		Cerastium uniflorum	2.5
		Heliosperma pusillum	1
		Hornungia alpina	2.5
		Papaver alpinum	1
		Poa alpina	1
		Saxifraga moschata	0.1
BL11	70	*Arabis alpina*	1
		Cerastium uniflorum	10
		Festuca alpina	1
		Hornungia alpina	2.5
		Poa alpina	1
		Saxifraga moschata	1
		Thlaspi rotundifolium	1
BL12	40	*Arabis alpina*	2.5
		Festuca alpina	1
		Heliosperma pusillum	2.5
		Hornungia alpina	1
		Papaver alpinum	2.5
		Poa alpina	2.5
		Thlaspi rotundifolium	0.1
BL13	100	*Arabis bellidifolia*	0.1
		Carex firma	1
		Cerastium uniflorum	0.1
		Crepis terglouensis	0.1
		Festuca alpina	2.5
		Galium megalospermum	1
		Heliosperma pusillum	2.5
		Hornungia alpina	1
		Poa alpina	1
		Ranunculus alpestris	10
		Saxifraga stellaris	1
		Silene acaulis	0.1
		Thlaspi rotundifolium	1
		Viola biflora	10
BL14	250	*Achillea atrata*	0.1
		Arabis bellidifolia	2.5
		Bellidiastrum michelii	2.5
		Biscutella laevigata	2.5
		Bistorta vivipara	1
		Campanula scheuchzeri	2.5
		Carex firma	2.5
		Carex sempervirens	2.5
		Festuca alpina	1
		Galium megalospermum	0.1
		Hornungia alpina	2.5
		Juncus monanthos	2.5
		Ranunculus alpestris	2.5
		Salix serpyllifolia	1
		Sesleria caerulea	2

		Silena acaulis	2.5
		Soldanella alpina	2.5
		Tofieldia pusilla	2.5
		Valeriana saxatilis	1
		Viola biflora	1
BL15	250	*Achillea atrata*	2.5
		Bellidiastrum michelii	2.5
		Bistorta vivipara	1
		Campanula scheuchzeri	2.5
		Carex feruginea	1
		Carex firma	2.5
		Carex sempavirens	1
		Galium anisophyllon	1
		Moehringia ciliata	0.1
		Parnassia palustris	2.5
		Pedicularis rostratocapitata	10
		Ranunculus alpestris	10
		Salix serpyllifolia	2.5
		Sesleria caerulea	1
		Soldanella alpina	1
		Viola biflora	1
BL16	250	*Achillea atrata*	2.5
		Bellidiastrum michelii	2.5
		Biscutella laevigata	2.5
		Bistorta vivipara	1
		Campanula scheuchzeri	2.5
		Carex ferruginea	1
		Carex firma	2.5
		Carex sempavirens	1
		Euphrasia minima	1
		Festuca alpina	1
		Galium anisophyllon	0.1
		Hornungia alpina	2.5
		Juncus monanthos	1
		Mutellina adonidifolia	0.1
		Parnassia palustris	1
		Pedicularis rostratocapitata	2.5
		Ranunculus alpestris	1
		Ranunculus montanus	2.5
		Salix serpyllifolia	2.5
		Sesleria caerulea	2.5
		Soldanella alpina	2.5