



Long-term monitoring confirms limitations of recruitment and facilitation and reveals unexpected changes of the successional pathways in a glacier foreland of the Central Austrian Alps

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Abstract

On a glacier foreland of the Central Austrian Alps, a permanent plot study was performed to investigate the successional pathway on two moraines. We expected that the pioneer stage deglaciated for 25 years will converge to an early successional stage after another 25 years and the early stage deglaciated for 40 years will show trends toward a late successional stage. Different dynamics of species occurrence such as colonization/persistence and cover increase/decrease, were anticipated. Twenty plots of 25 × 25 cm were established in 1996 on each successional stage by selecting vegetated and bare ground plots to account for impacts of facilitation on seedling recruitment. We expected seed and establishment limitations, therefore, also effects of sowing were studied on sown and control plots. Species enrichment occurred on all control and sown plots of both stages. However, the pioneer stage did not converge to an early successional stage as it was expected. On the early successional stage, only on sown plots a development toward a late successional stage was found. Bryophyta were the most efficient colonizers on all plots together with the lichen *Stereocaulon alpinum* at the pioneer stage and the sown species *Anthyllis vulneraria* ssp. *alpicola* at the early successional stage. The pioneer species *Saxifraga oppositifolia* was still present after 25 years on the pioneer and early successional stages, although its cover significantly decreased. We conclude that seed and establishment limitations, drought, facilitation deficits, and ageing of individuals are the essential drivers on the studied glacier foreland, creating ‘quasi-stationary’ communities.

Keywords Colonization · Cover · Diversity · Glacial moraines · Pioneer species · Persistence

Introduction

The vanishing glaciers have attracted scientists for more than 150 years (Matthews 1992; Kaufmann 2001; Raffl and Erschbamer 2004; Raffl et al. 2006; and references therein). On the resulting glacier forelands, new ecosystems develop from zero onward (Matthews 1992), offering a perfect ground to study primary succession. Colonization starts on

a terrain without biological individuals, although inoculation by microbes, seeds, plant fragments, and insects transported by the glacier, cannot be completely excluded (Walker and del Moral 2003; Hågvar et al. 2020). On recently deglaciated sites, climatic and edaphic drivers—called allogenic factors—seem to play a minor role (Schumann et al. 2016), while autogenic factors, such as availability of seeds (Harper 1977; Stöcklin and Bäumler 1996; Niederfriniger Schlag and Erschbamer 2000; Erschbamer et al. 2008), species traits (i.e., germination, growth and reproduction potential; Harper 1977; Tsuyuzaki and del Moral 1995; Stöcklin and Bäumler 1996; Weppler et al. 2006; Mong and Vetaas 2006), mycorrhization (Jumpponen et al. 1998; Mühlmann and Peintner 2008a,b; Mühlmann et al. 2008), and species interactions (facilitation, competition; Walker and del Moral 2003; Dolezal et al. 2013) were identified as essential drivers of primary succession. Nevertheless, allogenic and autogenic factors highly interact, as experimentally demonstrated on the pioneer stage of a central Alpine glacier foreland, where

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drought and seed limitation together constrained seedling recruitment (Erschbamer and Caccianiga 2017).

On stressful alpine environments, facilitative interactions (Bertness and Callaway 1994; Callaway et al. 2002; Anthelme et al. 2014) and positive associations (Losapio et al. 2018) are assumed to be the prevailing mechanisms of colonization, growth and reproduction. Indeed, already established species enhanced the number of seedlings in an Alpine glacier foreland (Niederfriniger Schlag and Erschbamer 2000). In contrast, the role of competition in glacier foreland succession is not yet fully understood (Dolezal et al. 2013). At the plot scale, indications of competitive effects were found on 50 years old moraines, mainly due to shading effects by larger growing species (Erschbamer et al. 2008). To unravel the role of facilitative and competitive interactions, year-by-year observations of species performance are necessary. However, long-term studies are rare (Whittaker 1991; Buma et al. 2017, 2019) and hardly available for the Alps (Richard 1973; Erschbamer et al. 2008; Fickert 2017; Fickert and Grüniger 2018).

Instead, methods based on the chronosequence (Matthews 1992; Foster and Tilman 2004; Walker et al. 2010) have been more frequently applied to investigate primary succession, i.e., with vegetation being surveyed along transects from the youngest to the oldest deglaciated terrain (Schumann et al. 2016). Primary succession may then be predicted from space-for-time substitutions along the temporal gradient. However, climate warming may accelerate colonization dynamics (Cannone et al. 2008; Fickert and Grüniger 2018; Losapio et al. 2021) or slow down germination/establishment due to summer drought (Graae et al. 2009; Marcante et al. 2014; Mondoni et al. 2015) and change successional pathways (Kaufmann 2002; Erschbamer and Caccianiga 2017), making predictions of primary succession using the space-for-time approach unreliable.

The glacier foreland of the Rotmoosferner (Tyrol, Central Austrian Alps) has been object of several phytosociological studies along the successional gradient for more than two decades (Erschbamer et al. 1999; Kaufmann and Raffl 2002; Raffl and Erschbamer 2004; Raffl et al. 2006). The most important inference from this chronosequence-based research was that plant species diversity and cover rapidly increase during the first 40 to 50 years after deglaciation (Kaufmann and Raffl 2002; Raffl et al. 2006) followed by a phase of slower increment on older glacier stages. This holds also for other organismic groups such as insects (Kaufmann 2001; Kaufmann et al. 2002) and microbiota (Tscherko et al. 2003; Dresch et al. 2019).

In parallel, a long-term observation study was started in 1996 on the initial part of the chronosequence. Two sets of permanent plots were established on a pioneer stage deglaciated since 1971 and an early successional stage, deglaciated since 1956–1957 (Niederfriniger Schlag and Erschbamer

2000). In each stage, vegetated and bare ground plots were selected to account for the impact of facilitation on seedling recruitment. Additionally, to avoid drawbacks of seed limitation (Erschbamer and Caccianiga 2017; Zimmer et al. 2018), half of the plots were sown with a mixture of glacier foreland species. The results of the first study years confirmed seed limitation and drought as major challenges for colonization (Niederfriniger Schlag and Erschbamer 2000; Erschbamer et al. 2001, 2008; Erschbamer and Caccianiga 2017).

Here, we studied 25 years of primary succession by analyzing the development of species richness and vegetation cover on vegetated and bare ground plots on the two successional stages, comparing naturally evolving plots with artificially sown plots. We aimed to unravel the processes of colonization, persistence and substitution of species, and to test predictions of community change outlined by the space-for-time method. We assumed that bare ground plots on both moraines can catch up in species number and cover in the course of 25 years. Specific attention was drawn on the changes of two indicator species of the two successional stages, *Saxifraga oppositifolia*, being one of the earliest colonizers, and *Trifolium pallescens*, being one of the most important early successional species (Raffl et al. 2006) and to their substituting species (*Stereocaulon alpinum* and *Anthyllis vulneraria* ssp. *alpicola*, respectively) on both moraines. We hypothesized that after 25 years: (1) sown plots have a significantly higher species richness and cover compared to control plots without seed addition; (2) control bare ground plots on both stages reach a similar species richness and cover as the vegetated plots had on the pioneer stage in 1996; (3) according to space-for-time predictions, the pioneer stage will converge to an early successional stage and the early successional stage will develop toward a late successional stage, these transitions being more pronounced in the sown plots; (4) patterns of species presence/absence and cover increase/decrease vary between the plots and the two moraines.

Material and methods

Study sites

The study sites lie on the glacier foreland of the Rotmoosferner (Obergurgl, Tyrol, Austria) in the Ötztal Alps (46° 49' N, 11° 02' E) and extend between 2380 (moraine of the glacier stage 1956–1957) and 2400 m a.s.l. (moraine of the glacier stage 1971). The two moraines are at ca 300 m distance from each other and show similar topography, the inclination being even (< 10°) and they have a similar exposure slightly to NW (Niederfriniger Schlag and Erschbamer 2000). Both moraines are fairly dry with no streams, gullies or gravelly ground. At the beginning of the study in 1996 the moraine

deglaciated for 25 years (pioneer stage, hereafter m1971) was characterized by a species-poor pioneer community (Raffl et al. 2006) of *Saxifraga oppositifolia*, *S. aizoides*, and *Artemisia genipi*. On the moraine deglaciated for ca 40 years in 1996 (early successional stage, hereafter m1956), *Trifolium pallescens*, *Poa alpina*, *Campanula scheuchzeri*, and *Leontodon hispidus* were the most important species. Pioneer species like *Saxifraga oppositifolia* and *S. aizoides* were still present at this site though in lower abundance. Late successional species such as *Anthyllis vulneraria* ssp. *alpicola*, *Kobresia myosuroides*, *Trifolium badium*, and *Saxifraga paniculata* were first found at sites deglaciated for ca 70 to 80 years and reached high abundances on ca 140 years old moraines (Raffl and Erschbamer 2004; Raffl et al. 2006). These late successional species did not occur at the two studied moraines in 1996 but were part of the seed mixture used in this study (Suppl. Material I).

In June 1996, 10 vegetated plots (V) and 10 plots on bare ground (B) of 25 × 25 cm were randomly selected within 150 m² on each moraine. The plots were marked with iron stakes placed diagonally at two of the four corners, and the sites were protected from grazing and trampling by a fence. Half of the plots of each treatment were sown (VS, BS) in 1996 and in 1997 with seeds collected in autumn 1995 in the same glacier foreland (for seed mixture see Suppl. Material I). The seeds were stored in cotton bags during winter in the field at 1950 m a.s.l. to allow natural stratification. Due to strong winds, almost all seeds were blown away in 1996 and it was necessary to repeat sowing in 1997. In total, 760 seeds per plot were sown in 1996 and 1835 seeds per plot in 1997. The unsown plots served as controls (VC, BC) to analyze natural colonization and development. For further details on plot mapping from 1996 to 1998 see Niederfriniger Schlag and Erschbamer (2000). All plots were monitored in 1996 (i.e., the starting point before seeding). The next recording was carried out in 2002 (only VC and VS of m1971 and VC of m1956). From 2003 onward all plots of m1971 and m1956 were monitored. Plots were divided into 25 subplots of 5 × 5 cm by means of a 25 × 25 cm grid, species cover was recorded in each subplot as percentage, and the average for the plot was calculated. This procedure was repeated yearly during the main growing season from 17th July to 7th August. Due to abundant vegetation cover and canopy height, VC and VS plots of m1956 were recorded only until 2017. On two plots of m1956 recording was terminated early when they were overgrown by a single species (11VC by *Cirsium spinosissimum* in 2008, 13VC by *Salix helvetica* in 2012).

Data analyses

For consistency, the two *Festuca* species (*Festuca pumila*, *F. halleri*) and the two *Gnaphalium* species (*Gnaphalium*

supinum, *G. hoppeanum*) were pooled. *Alchemilla* spec., Bryophyta spec., and *Cladonia* spec. could not be determined individually. Nomenclature of vascular plant species follows Fischer et al. (2008). For species names see Suppl. Material II.

Number of species, cover, and diversity were analyzed by mixed effects models with plot as random factor. Time courses were modeled with a linear regression for the long-term trend from 2002/2003 onward plus an offset for the year 1996 to show discontinuities by sowing effects occurring before 2002/2003. Slope and offset were estimated separately for the groups VC, BC, VS, and BS, but within one model for each moraine (~vegetation*treatment+vegetation: treatment:year96+vegetation:treatment:year+(1|plot)).

For the control plots overall means of these parameters were tested for differences between the moraines, and for differences between bare ground and vegetated plots by mixed effects models (~moraine*vegetation*year+(1|plot)), using pairwise contrasts (with Tukey-adjusted p-values). Analyses were performed in R 4.0.2 (R Core Team 2020) with packages lme4 (Bates et al. 2015), emmeans (Lenth 2020) and lmerTest (Kuznetsova et al. 2017) for calculations and ggplot2 (Wickham 2016) for graphs.

Species cover data were used to analyze community changes by means of canonical correspondence analyses (CCA) in CANOCO 5.15 (Ter Braak and Šmilauer 2018). Empty plots (per definition all bare ground plots 1996) and species with < 5 occurrences were excluded, rare species were downweighted. Monte-Carlo tests of CCA used 4999 permutations.

We used CCA biplots to visualize community changes and differences in the development between sown and control plots together with the species involved. In order to obtain easily readable graphs and a good fit by two axes, separate analyses were required for the two moraines because of their very different species sets and species responses to sowing (CCA with treatment:year as explanatory variable, whereby year was used as categorical variable to allow for nonlinear temporal development). Ordination plots are only shown for the vegetated plots, bare ground plots did not have any significant temporal structure. Time course differences between sown and control plots were tested in separate partial analyses (pCCA) with year as covariate.

A simple correspondence analysis (CA) was performed to evaluate the hypothesized convergence of the pioneer successional stage to the early successional stage; all vegetated plots (VC, VS) of both moraines were used for this analysis.

To classify the species according to their temporal dynamics within each plot, two occurrence schemes based on (1) presence/absence of each species per plot, and (2) species' cover per plot were differentiated. For presence/absence over time, five categories were defined: colonizer (col), persistent (pers), sporadic (spor), temporary (temp)

and vanished (van). Another five categories were described based on changes in cover over time from the regression models: increase (incr), decrease (decr), hump, dip and none. Increase/decrease were given if a linear model was significant at $P < 0.05$. To detect patterns with a maximum or minimum (hump/dip), an additional quadratic term (centred at year 2011) was used. Hump/dip were allocated as pattern only if the quadratic term was significant ($P < 0.05$) and its significance was higher than that of the linear term. A description of each category can be found in Suppl. Material III.

Additionally, the temporal changes in cover (means and standard errors) of *Saxifraga oppositifolia* and *Stereocaulon alpinum* as important pioneer and early successional species, respectively, and of *Trifolium pallescens* and *Anthyllis vulneraria* ssp. *alpicola* representative for early and late successional species, respectively, were shown.

Results

Natural development in control plots

All control plots (VC, BC) showed an increase in species richness (Fig. 1) over the investigated period. Overall means of species richness on the vegetated plots were significantly higher on m1956 compared to m1971 ($P = 0.003$, Suppl. Material IV). VC on m1971 started with a minimum of 3.8 ± 0.8 species per plot in 1996 and reached a maximum

of 15.6 ± 2.4 species in 2021. On m1956, VC had 7.6 ± 1.3 species in 1996 and increased to a maximum of 16.7 ± 1.8 in 2013. After 25 years, BC of both moraines reached a species number slightly higher than the starting point of VC on m1971 in 1996 (5.8 ± 0.7 on m1971 and 4.6 ± 0.7 on m1956).

Vegetation cover (Fig. 2) and diversity H' (Suppl. Material V) also increased on VC and BC, with exception of VC of m1956. Here, cover of VC decreased until 2013 and rapidly increased afterwards (Fig. 2). On BC plots, cover developed on much lower levels than on VC ($P < 0.001$ on both moraines, Suppl. Material IV); being far from the initial cover of VC in 1996. Shannon diversity H' on m1971 did not follow the increase in species number, indicating a decrease in evenness and an increase in dominances (Suppl. Material V). The overall means of cover and Shannon diversity H' were not significantly different between the two moraines (Suppl. Material IV).

Rates of increase (Suppl. Material VI) ranged between 0.2 and 0.5 species per year for species number and 0.5 to 1.5% per year for cover (except VC on m1956 as mentioned above) with no systematic difference between BC and VC.

Sowing effects

Sowing clearly increased species numbers on VS over at least 13 years (Fig. 1). A significantly increasing step was observed between 1996 and 2002/2003 (m1971 + 7.4 species, m1956 + 12.7 species; Suppl. Material VI), higher than

Fig. 1 Number of species per recording year (means $\pm$ standard error) at m1971 (upper panel) and m1956 (lower panel) on vegetated plots (VC filled circles, VS open circles) and bare ground plots (BC filled squares, BS open squares). Dashed lines = regression models with optional offset 1996

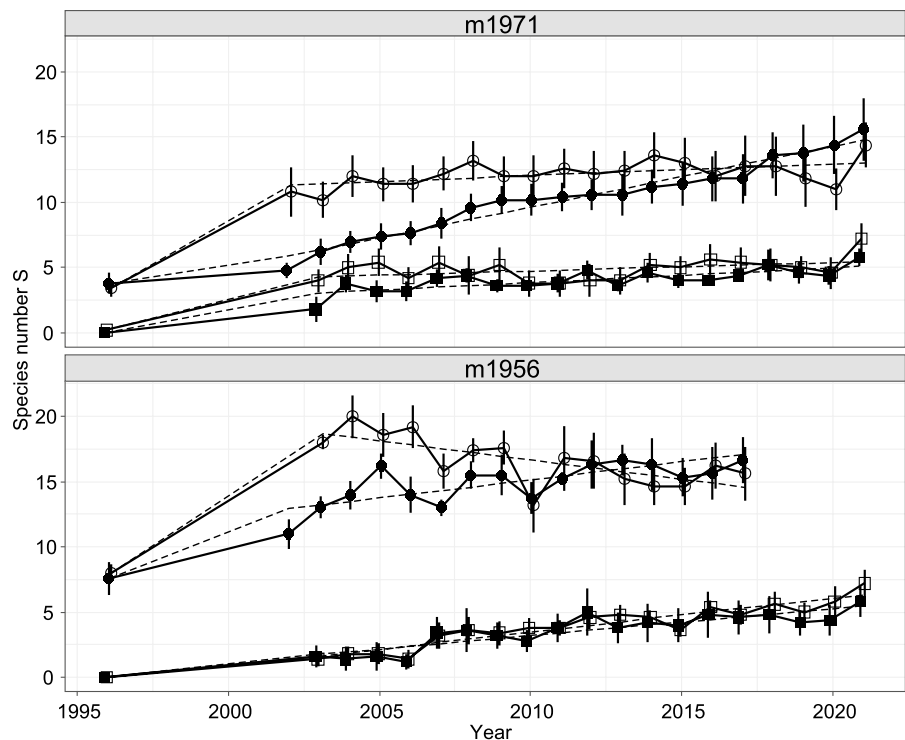


Fig. 2 Plot cover per recording year (means $\pm$ standard error) at m1971 (upper panel) and m1956 (lower panel) on vegetated plots (VC filled circles, VS open circles) and bare ground plots (BC filled squares, BS open squares). Dashed lines = regression models with optional offset 1996

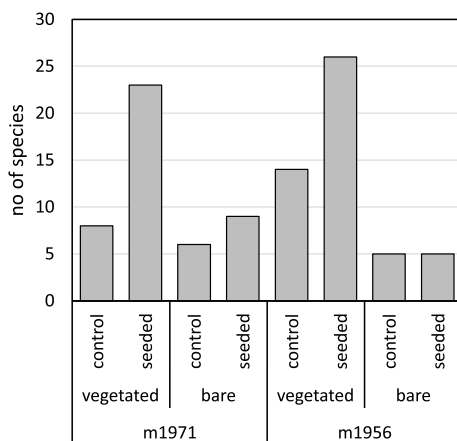
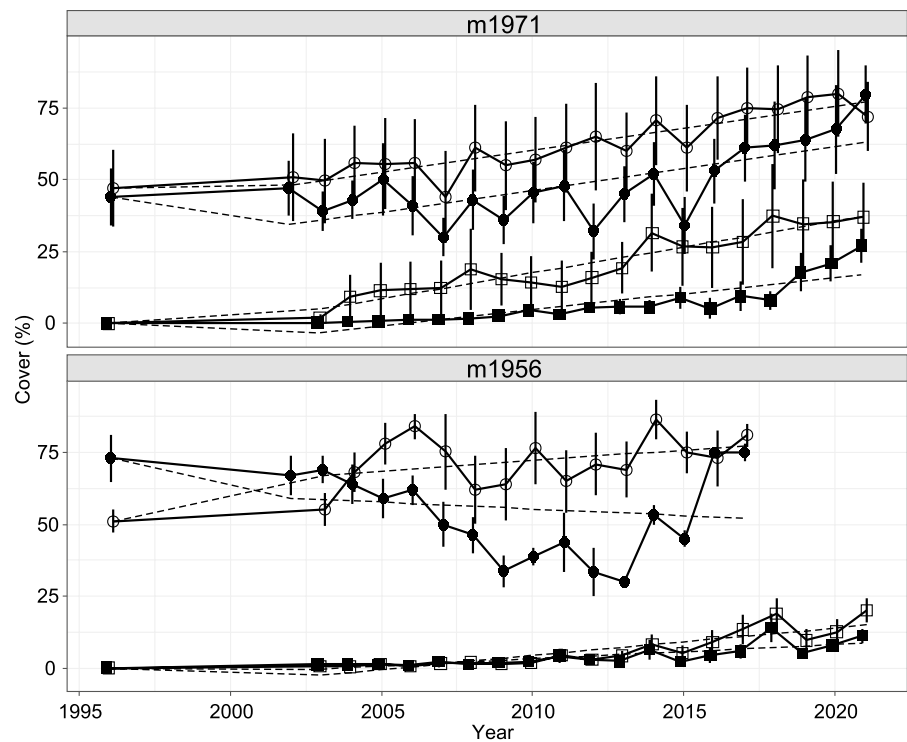


Fig. 3 Number of new species appearances in 2002/2003 on the plots of the two moraines m1971 and m1956

on VC (m1971 n.s., m1956 + 3.66 species; Suppl. Material VI). In the following years the effect declined and species numbers of sown plots converged with the controls by 2015 (Fig. 1), either by slower increase (m1971) or even decrease (m1956). On BC this effect was either small (m1971) or absent (m1956, Fig. 1). On vegetated plots new appearances were at least doubled by sowing, while on bare ground this effect was weak (m1971) or absent (m1956, Fig. 3).

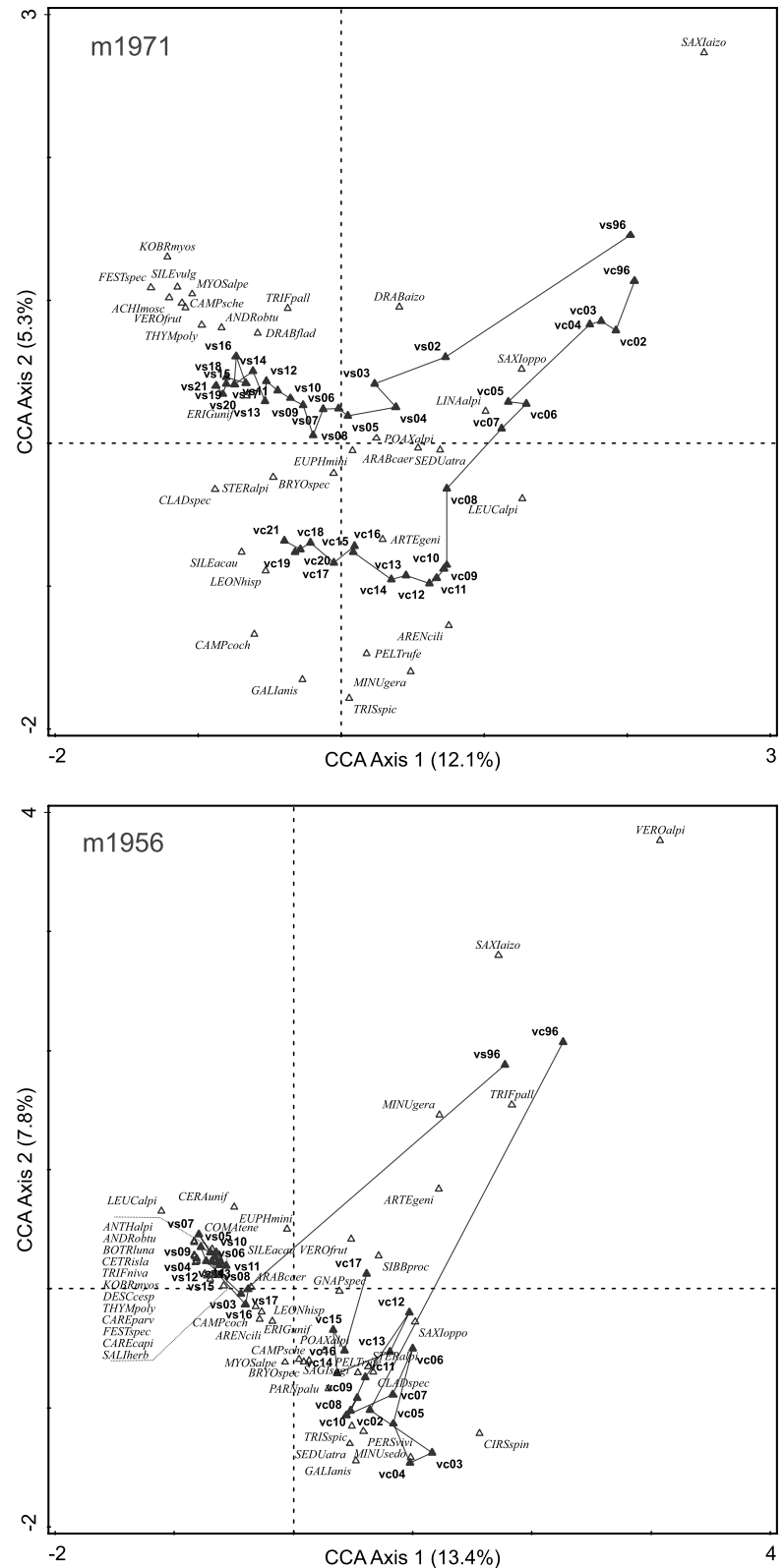
Sowing effects on cover were less clear (Fig. 2, Suppl. Material VI). Even though cover was generally higher on sown than on control plots, the increase occurred later and

was not yet the case in 2002/2003 when the sowing effect would have been expected. On bare ground plots, sowing effects on cover were not significant neither on m1956 nor on m1971. Shannon diversity H' did not reflect the sowing effect in the same way as species number (Suppl. Material V).

Community changes

Community development on the two moraines is shown by a CCA (Fig. 4), 26.9% on m1971 and 34.6% on m1956 of variation being explained by years and sowing effect (two relevant axes in both cases). On m1971, VC and VS started with a species-poor pioneer community in 1996 and developed in a similar direction. However, VS showed a large sowing effect between 1996 and 2002 followed by only small changes after 2003, while VC changed continually until 2009, slowing down then. The two trajectories diverged, being significantly different (tested in a separate pCCA, pseudo- $F = 1.5$, $P = 0.0002$). On VC, the community of *Saxifraga* spec. and *Artemisia genipi* was enriched by several pioneer and early successional species (e.g., *Arenaria ciliata*, *Leucanthemopsis alpina*, *Minuartia gerardii*, *Peltigera rufescens*, *Silene acaulis*) and few late successional species (*Galium anisophyllum*, *Leontodon hispidus*), while on VS mainly species from the seed mixture prevailed (*Achillea moschata*, *Androsace obtusifolia*, *Campanula scheuchzeri*, *Draba fladnizensis*, *Festuca* spec., *Kobresia myosuroides*,

Fig. 4 Community changes in vegetated control (VC) and seeded plots (VS) of m1971 (upper panel) and m1956 (lower panel), visualized by CCA analyses. Lines are temporal trajectories (=explanatory variables), years abbreviated to the last two numbers. Percentages of explained variation given with axes labels. For species abbreviations see Suppl. Material II



Myosotis alpestris, *Silene vulgaris*, *Thymus polytrichus*, *Veronica fruticans*).

On m1956, VC and VS had similar initial communities in 1996 too, but quickly diverged into two distinct clusters for all later years where no further directional community

changes were observed (Fig. 4), with significantly different trajectories (pCCA, pseudo- $F = 1.9$, $P = 0.0002$). VC plots were differentiated from VS by species which were already present in 1996 (*Campanula scheuchzeri*, *Galium anisophyllum*, *Minuartia sedoides*, *Parnassia palustris*, *Poa alpina*, *Stereocaulon alpinum*, *Trisetum spicatum*). Within the VS cluster the sown species *Anthyllis vulneraria* ssp. *alpicola* became dominant together with more sporadically occurring sown species such as *Androsace obtusifolia*, *Carex capillaris*, *Carex parviflora*, *Salix herbacea*, *Silene acaulis*, and *Trifolium pratense* ssp. *nivale*.

On the bare ground plots, the CCA could not detect significant temporal changes on either moraine. Note, however, that this refers to years from 2003 onward since the empty recordings from 1996 were excluded. The newly appearing species on BC in m1971 were mainly pioneer species including Bryophyta and lichens; only on two BS plots seeding effects were recognizable. On m1956, some BC plots remained rather species-poor, while others were colonized by species from VC or species from the seed mixture.

In the course of 25 years the community on m1971 did not develop toward an early successional stage, i.e., to the early successional stage of m1956 observed in 1996 (Fig. 5). The two moraines remained clearly separated along CA axis 1, both the VC and VS plots (only axis 1 was really relevant in this respect, higher order axes were weak). In contrast, on m1956, the high dominance

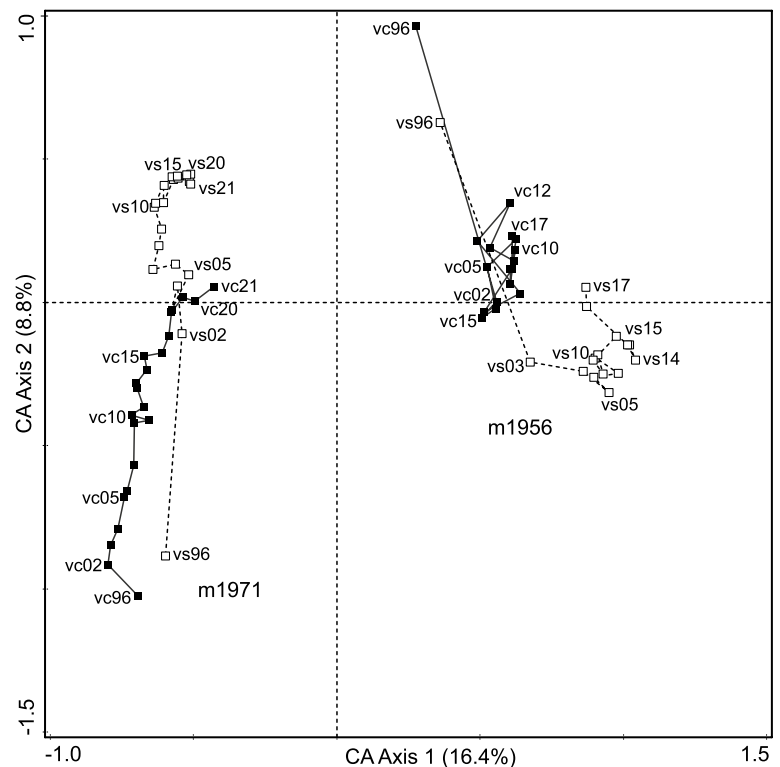
of *Anthyllis vulneraria* ssp. *alpicola* in VS suggests a converging community toward a late successional stage.

Temporal patterns of species occurrences

Regarding the temporal pattern, no remarkable differences between the two moraines were observed (Fig. 6). Compared to m1971, the percentage of colonization events was slightly lower in VC and VS of m1956. BC of m1971 had less colonizers compared to BS. VC on m1971 had slightly more colonization events than VS (Fig. 6). The most important colonizers on m1971, occurring on most plots, were Bryophyta, *Stereocaulon alpinum* (Fig. 7), *Sedum atratum* and *Artemisia genipi* (Table 1). Among the persistent species, *Saxifraga oppositifolia* was the most important one, occurring at VC and VS, however significantly decreasing in cover over the years (Fig. 7). Despite this cover reduction, the species did not vanish after 25 years, neither in VC nor in VS. On BS one persistent species (*Artemisia genipi*) occurred, being present from the plot establishment in 1996 onward (Fig. 6). In all other bare ground plots, the categories persistent and vanishing were missing by definition.

On m1956, there was more colonization on the bare ground than on the vegetated plots (Fig. 6). The most important colonizers were Bryophyta, *Leontodon hispidus*, *Anthyllis vulneraria* ssp. *alpicola*, *Campanula scheuchzeri*, *Erigeron uniflorus*, *Euphrasia minima* (Table 1). Among them, only *Anthyllis* (Fig. 7) did not

Fig. 5 Comparison of VC and VS plots on m1971 and m1956 by means of a CA, visualized on axis 1 and 2. No convergence of m1971 towards m1956 can be recognized. Recording years abbreviated to the last two numbers. Percentages of explained variation given with axes labels



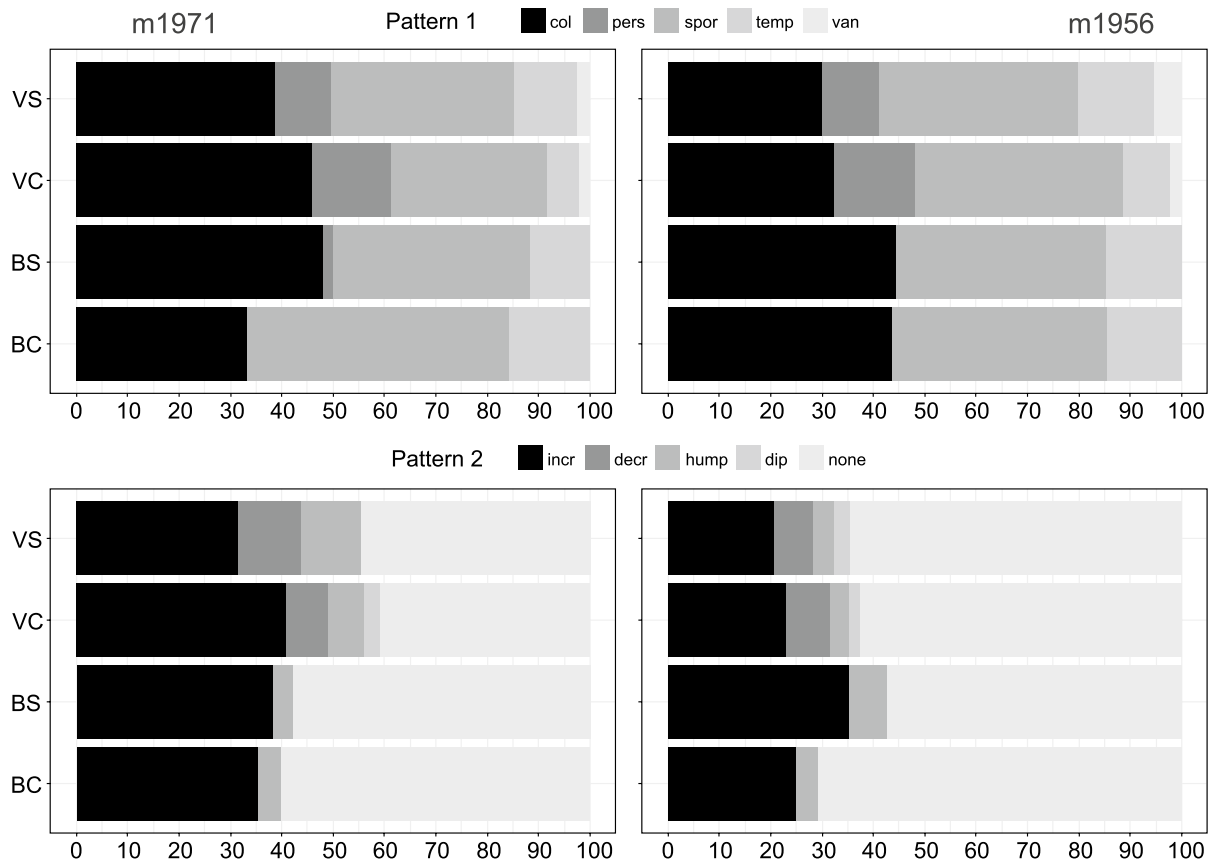


Fig. 6 Temporal pattern of occurrences on the two moraines (left m1971, right m1956). Percentages are given. Pattern 1: colonizer, persistent, sporadic, temporary, vanished (upper panel). Pattern 2:

increase, decrease, hump, dip, none (lower panel). For further explanations of the pattern categories see Material and Methods and Suppl. Material III

occur at the site in 1996 while all others were already present in some permanent plots. The most prominent vanishing species on m1956 was *Saxifraga aizoides*. *Trifolium pallescens* was overgrown by *Anthyllis* in VS plots, which developed 30–40% cover between 2005 and 2015 (Fig. 7). Several *Trifolium pallescens* seedlings occurred in these plots throughout the years, but hardly increased in cover. On VC plots, *Trifolium pallescens* declined rapidly too and *Anthyllis vulneraria* ssp. *alpicola* reached notable cover from 2014 onward (Fig. 7).

A relatively high percentage of species appeared sporadically on both the moraines and in all plots. The number of vanishing species was low on vegetated plots. Results of all species per moraine are shown in Suppl. Material VII and VIII.

Most species (40–70%) did not show any significant pattern of cover change on both moraines (Fig. 6). The percentage of species with increasing cover was slightly higher on m1971 (30–45%) than on m1956 (20–35%). In around 10% of the vegetated plots on both moraines

decreasing cover patterns were recorded. Species with hump shaped pattern were found on all plots while dip shaped were rare and present only on vegetated plots.

Discussion

Plot development

Species richness and diversity of naturally developing plots (VC, BC) increased over a period of 25 years on both moraines. This is in line with chronosequence studies (Raffl et al. 2006; Burga 2010; Buma et al. 2017), showing considerable diversity increases until 40–50 years after deglaciation. After ca 50–70 years, diversity levels more or less stagnate mainly due to the increasing dominance of late successional grasses and herbs (Raffl et al. 2006) or decreases due to the invasion of tall shrubs and trees (Buma et al. 2019). In the long term, *Salix helvetica*, the only tall shrub present on m1956, might have a similarly negative effect on

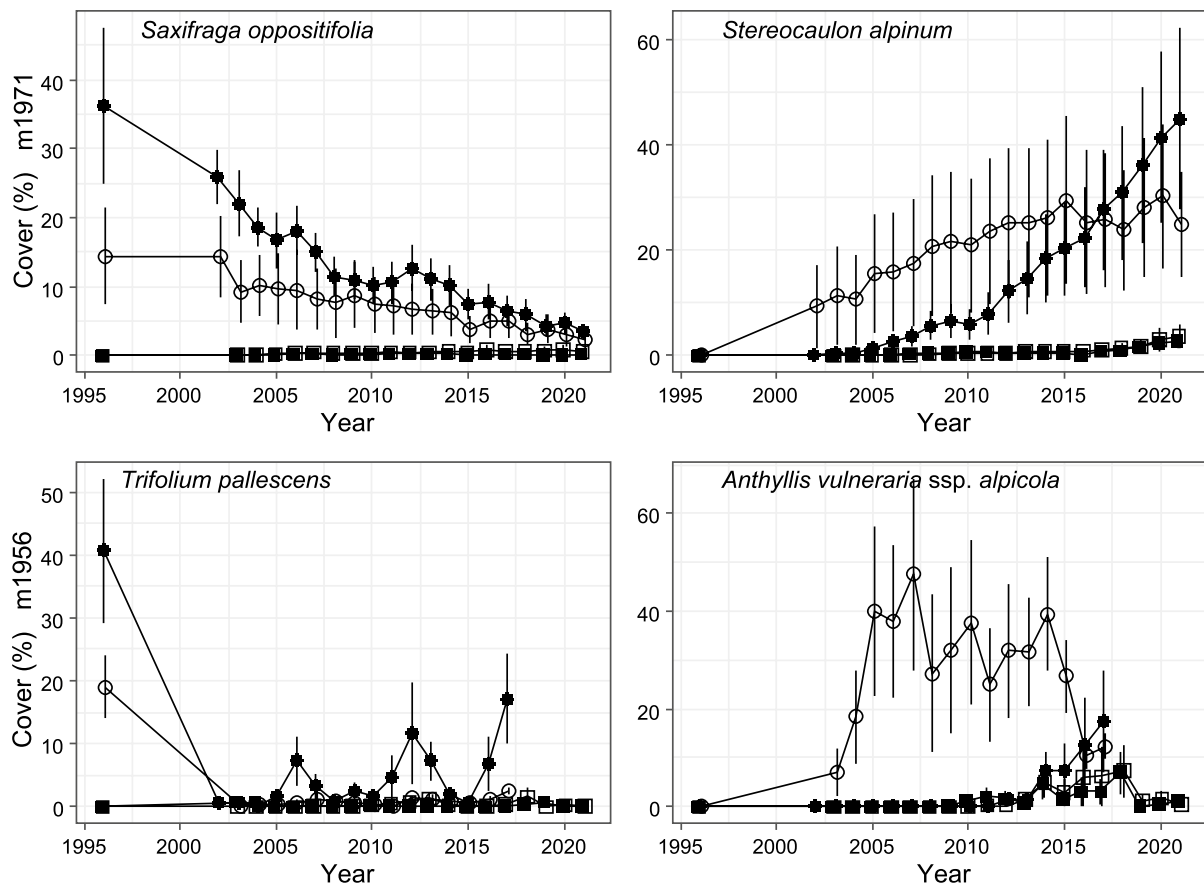


Fig. 7 Cover changes of *Saxifraga oppositifolia* (upper left) and *Stereocaulon alpinum* (upper right) on m1971 and of *Trifolium pallescens* (lower left) and *Anthyllis vulneraria ssp. alpicola* (lower right) on m1956 from 1996 to 2021 (m1971) and from 1996 to 2017

(m1956), respectively. Mean cover $\pm$ standard error for vegetated plots (VC filled circles, VS open circles) and bare ground plots (BC filled squares, BS open squares)

Table 1 Species with significant temporal pattern (for abbreviations, see Material and Methods and Suppl. Material III) at the two moraines m1971 and m1956

	m1971		m1956	
	Pattern 1	Pattern 2	Pattern 1	Pattern 2
Bryophyta	col (19/20)	incr (14/20)	col (15/19)	
<i>Stereocaulon alpinum</i>	col (16/19)	incr (14/19)	col (7/14)	
<i>Leontodon hispidus</i>			col (12/16)	incr (13/16)
<i>Campanula scheuchzeri</i>			col (10/15)	hump (6/15)
<i>Anthyllis vulneraria ssp. alpicola</i> *			col (10/16)	
<i>Erigeron uniflorus</i> *	col (7/12)	incr (7/12)	col (9/15)	
<i>Euphrasia minima</i>			col (8/13)	
<i>Sedum atratum</i>	col (9/20)		col (7/16)	
<i>Cladonia spec</i>			col (6/10)	
<i>Arenaria ciliata</i> *			col (6/9)	
<i>Silene acaulis</i>			col (5/9)	incr (5/9)
<i>Androsace obtusifolia</i>	col (6/9)	incr (4/9)		
<i>Minuartia gerardii</i>	col (5/8)	incr (3/8)		
<i>Artemisia genipi</i>	col (8/17)	incr (11/17)		

Species with asterisks (*) were present only in the seed mixture of 1996 and 1997, respectively, and missing in the plots 1996. First number in parenthesis shows the number of plots with significant pattern, second number gives the total number of plots with the species

diversity as observed by Buma et al. (2019). The species was overgrowing one plot but several individuals constantly increased on m1956 throughout the years, probably leading to a decrease in diversity in the next future on this site.

Seed addition provoked a steep increase in species numbers from 1996 to 2002/2003 on vegetated but not on bare ground plots. This can be interpreted as seed limitation (or dispersal limitation, Zimmer et al. 2018) but it may also be attributed to facilitative effects for recruitment in vegetated plots. However, in the long-term, the effect vanished, i.e., the regression lines flattened (m1971) or even dropped (m1956; Fig. 1). Therefore, the hypothesized higher species number in sown plots (hypothesis 1) cannot be confirmed at the end of the study. We observed that the species from the seed mixture reproduced regularly and most likely contributed to the seed rain and seed bank at the site scale. As a consequence, some of the sown species colonized VC plots, leading to a more continuous increase as compared to VS, and therefore masking potential differences due to the sowing treatment.

Plot cover showed considerable variation between recording years with a decrease on VC of m1956 until 2013, while for VS plots an increase was observed. This unexpected cover decrease in VC of m1956 might be due to a combination of ageing and failing recruitment of some species. The originally dominant species on this site, *Trifolium pallescens*, has a maximum life span of only 6 to 8 years (Kuen and Erschbamer 2002), and recruitment could not compensate the losses (Fig. 7). In glacier forelands, weak cover increase was attributed to seed and establishment limitations (Chapin et al. 1994; Jones and del Moral 2009; Zimmer et al. 2018). Interestingly, the cover decreases in VC of m1956 started in 2004, i.e., after the severe summer drought of 2003 (de Bono et al. 2004). Due to sparser canopy, VC were obviously more affected by desiccation than the densely covered VS. *Anthyllis vulneraria* ssp. *alpicola*, the species introduced by sowing, is more drought tolerant than *Trifolium pallescens* (see moisture values in Flora Indicativa, Landolt et al. 2010). During the last two monitoring years, a slight recovery of VC cover on m1956 was visible (Fig. 2), mainly due to the new appearance of *Anthyllis* in these control plots (Fig. 7).

Colonization of bare ground plots

After 25 years, BC on m1971 had slightly more species numbers (5.8 species per plot) than VC exhibited in 1996 on m1971 (i.e., 3.8 species per plot); BC on m1956 had 4.6 species per plot, the differences between the two moraines not being significant. While these results corroborate hypothesis (2) in terms of species numbers, plot cover remained very low, especially on m1956. Seed limitation and drought effects were clearly shown by a multifactorial experiment on bare ground on m1971 (Erich Schwenbacher unpubl. data;

Erschbamer and Caccianiga 2017) where the factor ‘sowing × irrigation’ achieved the highest number of seedlings followed by ‘sowing’ alone. On the other hand, seedling establishment is one of the essential bottlenecks in the glacier foreland (Marcante et al. 2009; Winkler et al. 2015). Additionally, drought and heat stress (Marcante et al. 2014) were identified as most important limiting factors in summer while frost might be a problem for seedlings in spring and in late autumn (Marcante et al. 2012).

The relatively low colonization and cover increase on bare ground plots could also be explained by a facilitation deficit of recruitment (Anthelme et al. 2021). It is well known that facilitative interactions are decisive in temperate alpine environments (Callaway et al. 2002; Callaway 2007) as well as in tropical glacier forelands (Zimmer et al. 2018). On the study site, safe sites such as larger stones are missing on bare ground (Erschbamer et al. 2008) and most established plants are still too small to act as ‘nurse or protégé plants’ (Filazzola and Lortie 2014). Nevertheless, on BS of m1971 already established plants seem to be more efficient safe sites than those on m1956, leading to an increase in cover on m1971.

Another explanation for low cover increases in bare ground plots could be microtopography (Matthews and Whittaker 1987; Andreis et al. 2001; Burga et al. 2010; Garibotti et al. 2011) and local environment (Bayle et al. 2022). Even though our two study sites are nearly level, slight topographical unevenness provokes a patchy distribution of vegetated and bare ground stripes. This heterogeneity determines, among others, the course of melting water in spring. Soil analyses on m1956 proved that bare ground plots had a much higher amount of fine sand in contrast to vegetated plots (Erschbamer et al. 1999). Fine sand was found to inhibit root formation (Chambers et al. 1991; Tsuyuzaki et al. 1997) and survival/growth of seedlings (Marteinsdóttir et al. 2013). In addition, the structure of the substrate determines the impact of drought and heat (Marcante et al. 2014), being responsible for seedling death or survival. All these factors seem to reduce seedlings on m1956 even more than on m1971. We therefore conclude that bare ground plots on m1956 are virtually permanent while those on m1971 are potentially colonizable provided that enough seeds are available.

Successional change

The significant sowing effect on m1956 corroborates hypothesis (3) of a community convergence toward a late successional stage. Cover increases of the seeded species *Anthyllis vulneraria* ssp. *alpicola* until 2007 in VS and colonizing individuals during the last recording years in the VC (Fig. 7) underline this trend. We suggest that especially those plots with the regenerating *Anthyllis* together with graminoid

species recruited from the seed mixture might have a good chance to develop to a late successional stage. But, following Buma et al. (2017), it will take again several decades before a complete change of the community will occur at the site.

In contrast, the community on m1971 did not develop toward an early successional stage (Fig. 5), as predicted by the space-for-time substitution model. Thus, hypothesis (3) cannot be confirmed for the younger moraine. Until the end of the studied period, m1971 showed high community consistency, although species enrichment occurred. During the 25 study years, the pioneer species *S. oppositifolia* on m1971 was not outcompeted, although cover decreased significantly due to the dominance of the lichen *Stereocaulon alpinum* in some plots. The expected enhancement of colonization speed and pathway due to climate change (Kaufmann 2002; Erschbamer and Caccianiga 2017) could not be observed on this moraine, although growing seasons extended at the study site (Erschbamer 2013) and temperatures increased (Kuhn et al. 2013).

Temporal pattern of species occurrence

The occurrence patterns of the species were rather similar between the two moraines. Thus, hypothesis (4) cannot be confirmed. On m1971, natural invaders such as Bryophyta and the lichen *Stereocaulon alpinum* were the most widespread colonizers. Lichens arrive only about 20 years after deglaciation in the study area (Türk and Erschbamer 2010) while Bryophyta may appear very soon on recently deglaciated areas but they often remain highly ‘volatile’ due to prevailing strong winds in front of the glacier (Roland Mayer, unpubl. data from glacier stage 2009).

On m1956, Bryophyta, *Leontodon hispidus* and *Anthyllis vulneraria* ssp. *alpicola* were the most successful colonizers, the latter species dominating between 2004 and 2015 on VS. Without sowing, *Anthyllis* would have hardly reached the study site in the course of 25 years, as shown by the absence of the species in the surrounding of the study site. This underlines the problem of seed limitation on the glacier foreland, being one of the essential interferences of primary succession (Erschbamer et al. 2008; Zimmer et al. 2018). *Anthyllis* dominated on the VS of m1956 from 2004 onward with several alternating diebacks and smaller peaks till 2015. In the last two monitoring years a considerable cover decrease occurred in VS, most likely attributable to ageing of the individuals. The species is able to reach a maximal age of 8 years (Erschbamer and Retter 2004).

On the other hand, *Anthyllis* showed a good reproduction and seed germination at the site. The sown species highly influenced the cover of persistent species such as *Trifolium pallescens* and other species, but did not completely suppress their occurrence (exception: *S. aizoides*). Competitive vs facilitative species interactions are still a matter of

debate in glacier foreland succession (Dolezal et al. 2013; Erschbamer and Caccianiga 2017). Following Dolezal et al. (2013), competitive interactions should occur only on successional stages much older than that of m1956. Our observations suggest that the remarkable cover reduction of *Trifolium* individuals is a sign of competition although their seedlings seem to be ‘nursed’ by adult *Anthyllis* individuals.

The pioneer species *Saxifraga aizoides* completely vanished from the study plots on m1956. Competitive displacement of *S. aizoides* cannot be excluded but this species probably suffered also by the increasing drought at the site. It needs more moisture (Landolt et al. 2010) compared to *S. oppositifolia* which was even able to newly establish in two plots of m1956.

Climate change effects

Repeated drought periods might be an explanation not only for weak or failing germination and establishment but also for established species diebacks. In the Alps, the years 2003, 2015, 2018 were extreme climatic outliers with heat and drought during summer (Stephan et al. 2021). In a paper review, Vázquez-Ramírez and Venn (2021) outlined that climate warming has positive effects on all plant life stages with exception of seedling establishment while decreasing precipitation has highest negative effects on seedling survival and establishment. In ‘normal’ years without climatic extremes, plant communities in high elevations of the European Alps are not endangered by drought (Körner 2003, 2019; Nagy and Grabherr 2009) with exception of some extreme topographic sites. With climate change this will be considerably altered especially if the frequency of drought periods increases even in the alpine environment. Community changes in the alpine zone have already been related to precipitation changes (Cannone et al. 2007). In the Central Austrian Alps, cover of high alpine summit species decreased already at the lower margins of their occurrence (Lamprecht et al. 2018; Steinbauer et al. 2020) and precipitation decrease was found to be related to species disappearance. Drought together with increasing temperatures might affect colonization and establishment of pioneer species (Erschbamer 2007) but also survival of some early and late successional species may be at risk as most of them are adapted to conditions without moisture shortage. Models anticipated that in glacier forelands species extinctions will occur especially when glaciers completely disappear due to climate warming (Losapio et al. 2021).

Conclusions

According to the space-for-time substitution model we expected that after 25 years the plots of the pioneer stage on m1971 should reach the next successional phase, i.e., the early successional stage, shown in 1996 on the moraine m1956. However, our observations do not confirm such a convergence. Therefore, at least in the Central Austrian Alps, space-for-time substitutions on younger moraines of the glacier forelands should be used with caution. The plot pattern of the glacier foreland is governed by facilitation deficit and recruitment limitation on bare ground while vegetated plots without sowing are driven by seed - as well as establishment limitation. Species ageing and failing regeneration due to drought effects can be regarded as essential obstacle for primary succession. Thus, the key factor for present-day primary succession processes is climate change (i.e., increase of temperature, extension of growing season, and more frequent and longer drought periods during the growing seasons), which not only delays succession but completely changes the successional pathways valid until present.

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Author contributions Study conception and design were performed by BE and RNS. Species mapping per plot in 1996 and seeding in 1996 and 1997 were carried out by RNS. Data collection from 2002/2003 onward was done by BE, with helping hands of PC in 2021. Data analyses were performed by RK. The first draft of the manuscript was written by BE with suggestions of RK. All authors commented on previous versions of the manuscript. All authors read, commented, and approved the final manuscript.

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Declarations

Competing interest The authors declare no competing interests.

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