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Rapid plant colonization of the forelands of a vanishing glacier is strongly associated with species traits

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ABSTRACT

Recently developed glacier forelands provide valuable insights into vegetation dynamics. We studied the vascular plants in the glacier forelands of the Ålmajallojekna glacier in comparison to the plants in the surrounding area. The glacier is retreating rapidly at an average rate of 0.17 km^2 per year from 1898 to 2012. In the newly emerged glacier forelands, we found that 32 percent of the 381 plant taxa occurred in the surrounding region. Sixty-eight plant species were present on the youngest terrain (0–31 y), an additional thirteen species occurred on terrain aged 32–53 years, and an additional forty-two species were detected on terrain aged 54–114 years. Of the surrounding species pool, plant species that had successfully established in recently deglaciated terrains were characterized by high regional abundance and low seed weight, and they were more likely to be members of the plant families Saxifragaceae, Salicaceae, and Asteraceae. Woody plant species with a preference for well-drained soils were more likely to be present in the youngest terrain. Our results show that the vegetation of glacier forelands is developing rapidly depending on the plant species in the surrounding area and the species' life-history traits.

Introduction

Climate change is especially pronounced in the Arctic, where temperatures have increased from two to three times more than the global average during the past fifty years (Post et al. 2009; Pachauri and Meyer 2014). This coincides both with widespread vegetation shifts (Kullman 2004; de Vernal and Hillaire-Marcel 2008; Kullman and Öberg 2009), decreasing the extent and thickness of glaciers (Hodkinson et al. 1998), and with the exposure of new glacier forelands. For decades, recently deglaciated lands have provided excellent opportunities to study the development of emerging ecosystems, to understand the mechanisms of primary succession, and to disentangle the role of species characteristics in colonization ability (Matthews 1992; Chapin et al. 1994; Stöcklin and Bäumler 1996; Rydgren et al. 2014; Klaar et al. 2015).

With an increasing area of new glacier forelands forming as the climate continues to change, thorough knowledge of the drivers of vegetation development can inform us about the susceptibility of species to climate change and about the importance of emerging habitats in mitigating the loss of habitats in arctic areas (Callaghan et al. 2013; Egerton 2015). Plants are colonizing glacier forelands relatively fast, with species composition changing rapidly from predominantly moss-dominated early vegetation to evergreen dwarf shrub-moss tundra (Jones and Henry 2003). Post-glacial plant colonizations have been studied intensively because they are suitable areas for studies of chronosequences where space is substituted for time in determining the sequences of the succession of plants, nutrients, and soil development (Crocker and Dickson 1957; Lawrence et al. 1967; Hobbie, Macko, and Shugart 1998). Several studies have been provided as textbook examples of primary succession on glacial till following ice retreat (Cooper 1939; Begon 2005).

Species composition in successional habitats often reflects that of surrounding habitats and nearby seed sources (Campbell, Rochefort, and Lavoie 2003; Kullman 2010). The ability of species from the surrounding

landscape to disperse and establish in emerging habitats is related to their dispersal and persistence ability. Life-history traits such as height, seed weight, and seed number can be linked to the ability to colonize new habitats, and have often been used as a proxy for both dispersal and establishment success (Grime 1974; Moles and Westoby 2006; Thomson et al. 2011). Pioneer plant species are often efficient in terms of both dispersal and establishment success (Chapin, Autumn, and Pugnaire 1993; Pywell et al. 2003; Meiners et al. 2015), have rapid reproduction strategies (Elven 1980), and belong to opportunistic taxonomic families with corresponding life forms (McIntyre, Lavorel, and Tremont 1995; Alsos et al. 2007).

We explored how vegetation has developed in the glacier forelands in one of Europe's most remote areas, examining a period covering 114 years. We were interested in whether plant occurrences in new terrain are related to species traits. By combining unique information about the current plant species occurring in the glacier forelands and the historical distribution of plant species in the region we tested whether species life-history traits, abundance, and distribution explain why certain species occur in the new terrain. We also explore glacier retreat in the study area and discuss the potential influence of temperature on glacier retreat and plant occurrences.

Material and methods

Study area

The study was conducted in the northwestern part of Swedish Lapland. Here, Sten Selander extensively studied the flora from 1941 to 1946 and published a plant atlas describing the distribution of each plant species in the region, covering 4,013 km^2 (Selander 1950). Selander subdivided the area into eight districts (Figure 1), and mapped plant occurrences and abundancies in each
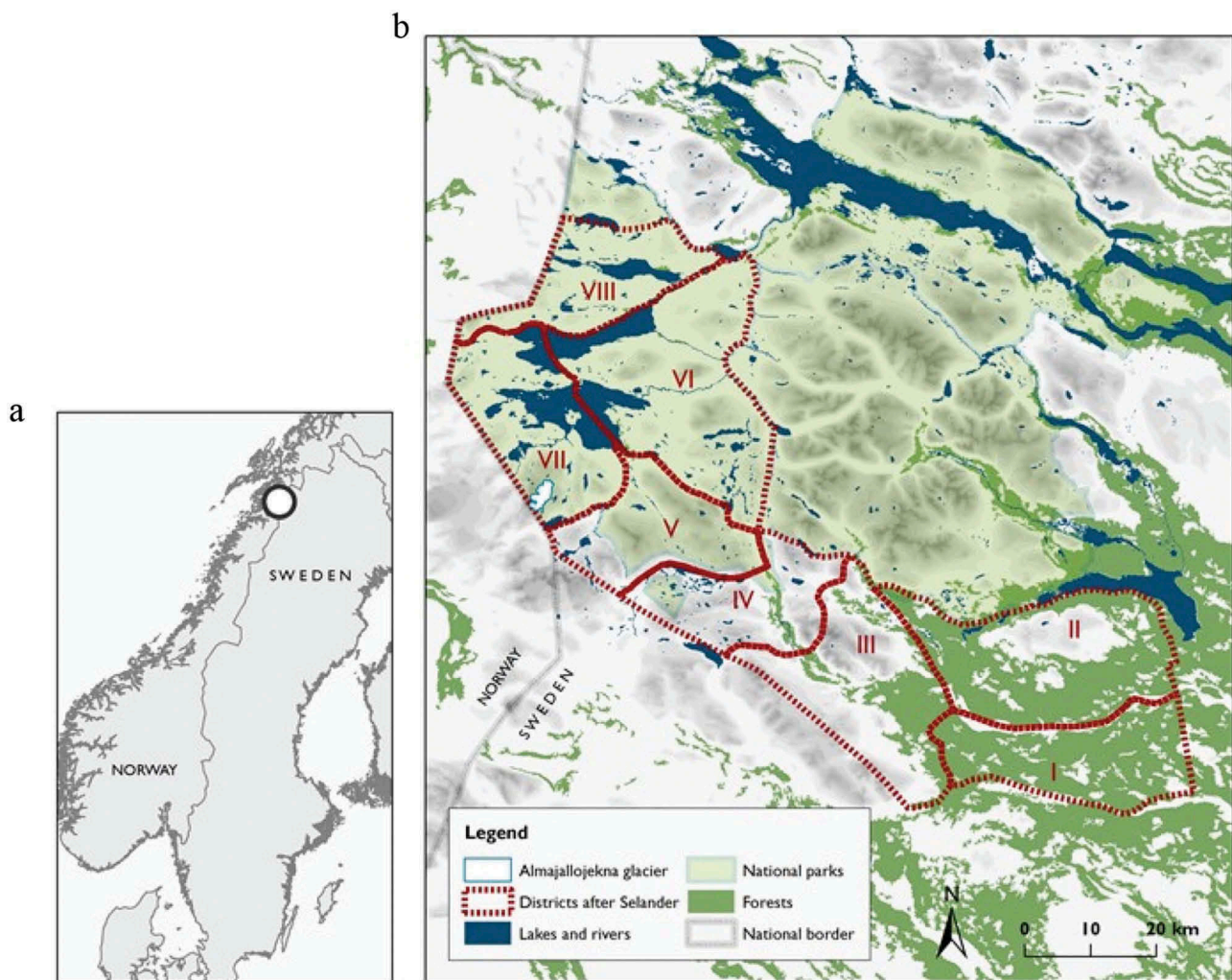

Figure 1. (a) Location of the study area in northern Scandinavia. (b) Location of the eight districts surveyed by Selander (1950) and the Ålmajallojekna glacier (located south of the label VII). Dark green areas indicate spruce forests, light green indicates birch forests, grey indicates the area above the tree limit, blue indicates lakes.

district. Most of Selander's districts are within the UNESCO World Heritage site Laponia, and cover large parts of the national parks Padjelanta and Sarek. The atlas published by Selander is the only detailed vegetation survey available for the study region, and lists 381 plant taxa. Selander was very interested in plant succession patterns and studied the area surrounding the glaciers extensively, including the nunataks inside the glacier Ålmajallojekna.

We studied the glacier forelands around what used to be the largest glacier in Sweden, the Ålmajallojekna glacier (N67°16′25, E16°22′45), which is located within Selander's study area. The Ålmajallojekna glacier is on the border between Sweden and Norway in the northern part of the Scandes (Scandinavian mountain range) in Padjelanta National Park (Figure 1). There are no roads and no permanent human inhabitants in the area and the closest village, Kvikkjokk, is situated 70 km away in a straight-line east of the glacier. The Ålmajallojekna glacier and its forelands nestle in a typical alpine landscape dominated by rocks and mountain heathlands, stretching from 950 m a.s.l. to 1,300 m a.s.l. From the Ålmajallojekna glacier, the closest fjord in Norway is only 35 km away and relatively warm and moist winds from Norway reach the site. The growing season is limited to the period from mid-June to the end of August and is characterized by high precipitation, amounting to about 1,500 mm per year (von Sydow 1983). There is no meteorological station available within 50 km from the study area. Occasionally, large areas are still covered by snow in July, as happened in 2012. The presence of Cambro Silurian bedrock containing calcareous phyllites and limestone has led to the development of a species-rich and specially adapted flora (Figure S1), with some species solely restricted to this region in Scandinavia (von Sydow 1983).

Characteristics of the Ålmajallojekna glacier and survey of its retreat

Ålmajallojekna glacier has a southeast-facing slope, with multiple ridges and swales (Figure 2).Westman (1899) was the first person to study the Ålmajallojekna glacier thoroughly, mapping its spatial extent and establishing reference cairns that are still present. In 1898, the glacier covered an area of about 22 km^2; since then, it has continuously retreated to an area of 2.8 km^2 in 2013 (Figure 2). Because of this glacial retreat, new terrain with rivers, lakes, and rocks have been exposed in the formerly glaciated area.

We measured the glacial retreat by analyzing maps from 1898 (Westman 1899), aerial photographs from both 1957–1958 and 1980, SPOT-5 satellite images from 2012,

as well as data from our field visits from 2011 to 2013. For each year, glacier cover was based on information from July to September when the glacier was fully exposed. Based on the extent of the glacier, we classified the glacier foreland into three age classes: areas that had been deglaciated for 0–31 years, 32–53 years, and 54–114 years. The age classes were defined based on the years from which maps, aerial photographs, and satellite images were available and in which the extent of the glacier could be clearly defined. No information about the thickness of the glacier is available.

Plant survey in the glacial forelands

From the plant studies in the 1940s Selander gives detailed information about plants that occur in new terrain in a paragraph titled "The vegetation on 'new soil'" (Selander 1950, 122–27). He also stated that he investigated the area surrounding Ålmallojekna glacier, and *Saxifraga rivularis* was the only vascular plant species present on the new terrain (that had been free from ice for approximately 50 years). Further, in the legend to a photograph (see Figure 2c) Selander wrote: "Recently formed 'nunatakk' on the glacier of Ålmallojekna, seen from Mt Kasakpuolta. On the raw gravel in the foreground no phanerogam vegetation but *Saxifraga rivularis* was found. The 'nunataks' were completely devoid of phanerogam vegetation." The few plant individuals that occurred in the glacier forelands at this time might reflect that the terrain was young, the large glacier was cooling the area, and previous years from 1943 to 1946 had been cold with large snowfields covering the area even during the summers (Figure 2c).

Our fieldwork was carried out from July 20 to August 3, 2011, and from August 3 to August 17, 2012. We established twelve transects (six were surveyed in 2011 and six in 2012) in the glacier foreland, stretching from the present glacier edge to where the edge was in 1898 (Table S4; Westman 1899). The transects had a total length of 11,185 m (average 1,016 m, ranging from 634 m to 1,828 m; Figure 2a). The altitude along the transects ranged between 1,020 m a.s.l. and 1,200 m a.s.l. The youngest terrain that each plant taxon occupied was determined by recording the closest occurrence to the glacier edge along each transect (Table S4). We recorded the first time each plant taxon occurred in a fixed-width band of 1 m along each transect. To estimate the relative frequency of each taxon, we also identified all plant taxa in 1,507 plots of 50 cm × 50 cm that were placed approximately every 50 m (on neutral-aspect ground) along each transect. To obtain a complete picture of the plants occupying the former glacier-covered area, as well as the age of
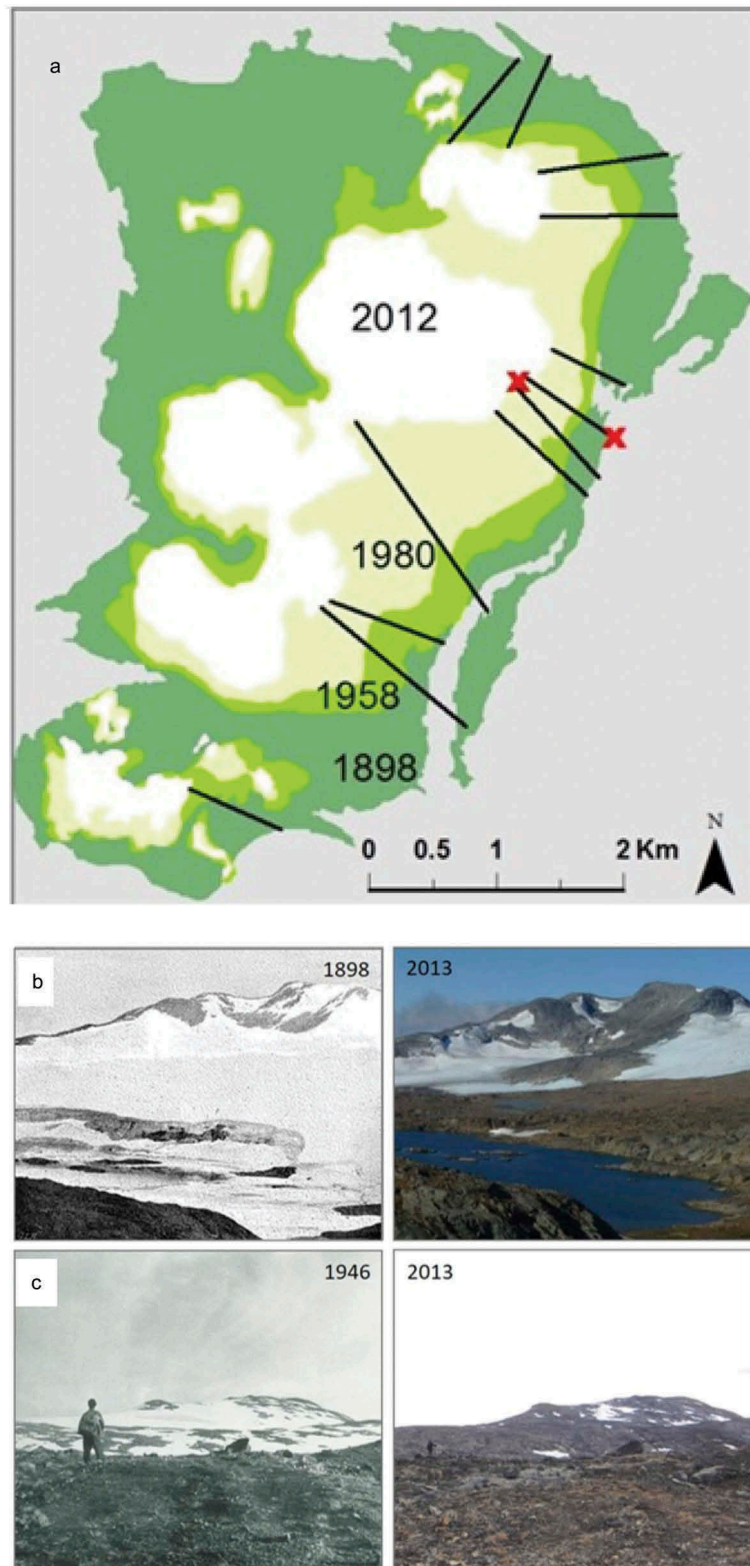
Figure 2. (a) The extent of the Ålmajallojekna glacier in 1898 (dark green), 1958 (green), 1980 (light green), and 2012 (white), as well as the twelve transects used for the plant survey undertaken during this study. The red crosses show the positions of the two temperature loggers. (b) Photo point XII in Westman (1899) showing the eastern parts of Ålmajallojekna. The photographs were taken July 30, 1898 (left), and September 5, 2013 (right). (c) Photo point from Selander (1950) (seen from Mt. Kasakpuolta) photographed July 26, 1946 (left), and September 5, 2013 (right). Selander (1950) described the area in the photo as "Recently formed nunatak" (i.e., area completely devoid of phanerogam vegetation) and on the bare gravel in the foreground he found no phanerogam vegetation other than *Saxifraga rivularis*. Photos from 2013: Markus Franzén.

the terrain that they had occupied, we also recorded plant taxa (with the exact coordinates) that had not been observed along any transects while walking in the glacier foreland (for about 25 h each year). Most taxa were recorded along the transects and only seven additional taxa (of 123) were recorded during the random walks. We focused the plant survey on the western part of the former glacier because this area is easiest to access and has no great altitudinal differences. Two hybrid taxa were recorded: *Betula nana* x *pubescens* and *Carex capitata* x *arctogena*. Some individuals were impossible to identify to species level, especially among *Salix* spp. and *Poa* spp. Hybrids and individuals that were not identified to species level were deliberately excluded from the analyses. *Draba oxycarpa* was only recently split from *Draba alpina* and the two species were merged in the statistical trait analyses in line with the older data (Selander 1950). A few plant individuals could only be identified to genus level and these were attributed to the most common taxa in the genus that was found in the deglaciated area. We applied a chronosequence approach, and all plant occurrences were cross-referenced to the age of the terrain. Each occurrence was attributed to one of the three age classes based on where they occurred in the former glaciated area: 0–31, 32–53, and 54–114 years. Based on the extent of the glacier in 1898, 1957, 1980, and 2012, as well as the plant-species distribution in the glacier forelands in 1946 (Selander 1950) and 2011–2012, we explore the plant-species richness at each age class. In addition, we give broad estimates of the successful colonization rate by linking the plant richness and the age of the terrain for five time periods (1898–1946, 1898–2012, 1946–2012, 1957–2012, and 1980–2012).

Information about plant-species characteristics

All 381 plant species found by Selander (1950) were treated as our species pool, consisting of species that could potentially occur in the deglaciated Ålmajallojekna area (Table S5). For each species in the species pool, we extracted information for eight different species-related variables as follows: from Selander (1950) we obtained data on (1) local abundance, (2) distribution area in the eight districts, and (3) distance to the nearest district in which the species was recorded (Figure 1). *Species local abundance* represents the number of single plant occurrences in Selander (1950) and ranges from one to forty, where ubiquitous species were allocated the maximum number of occurrences recorded for any single species (40). *Distribution area* was defined as the number of occupied districts. For each plant species found during our study in the glacial foreland, we estimated the distance between the nearest district that it occupied in 1950 and

the glacier edge in 1898. These distances ranged from 0 km to 67 km, where the Ålmajallojekna glacier district was allocated a distance value of zero (Figure 1).

For each of the 381 species we also collated information about species taxonomy at the family level (4), habitat preferences (5), life form (6), pollen vector (7), and seed weight (8). Species habitat preferences (soil moisture [F], soil nitrogen [N], and soil reaction [R]) were obtained using Ellenberg indicator values for the Faroe Islands (Lawesson, Fosaa, and Olsen 2003). The Faroe Islands are environmentally similar to the study area and represent the only colder region for which Ellenberg values have been calibrated (cf. Hedwall, Brunet, and Diekmann 2019). When information was missing for some species in Lawesson, Fosaa, and Olsen (2003), original Ellenberg values were used as described in Ellenberg et al. (1992), and when still missing, values from Hill (1999) were used. Life-form classifications were adapted from Ellenberg and Mueller-Dombois (1967) and Raunkiaer (1934), and included the following: phanerophytes (self-supporting woody perennials that grow taller than 25–50 cm), chamaephytes (self-supporting woody plants whose mature branch or shoot system remains perennially within 25–50 cm above the ground surface), hemicryptophytes (self-supporting perennial [including biennial] herbaceous plants with periodic shoot reduction to a remnant shoot system that lies relatively flat on the ground surface), geophytes (self-supporting perennial and biennial herbaceous plants with periodic reduction of the complete shoot system to storage organs that are buried in the soil), hydrophytes (free-moving water plants and partly submerged, amphibious plants), and therophytes (self-supporting annual plants whose shoot and root system dies after seed production and which complete their entire life cycle within one year). The pollen vector for each plant species was catagorized as follows: (1) predominantly insect pollinated, (2) predominantly selfing, (3) predominantly wind pollinated, or (4) no pollen (e.g., ferns). Seed and spore weight were classified into three weight classes: (1) spores and small seeds (<0.5 mg), (2) intermediate-sized seeds ($0.5 \leq 1.0$ mg), and (3) large seeds (>1.0 mg). In our analysis height was captured by the trait "life form" and we considered height to be a less reliable trait because most plants did not grow to their full height in our study area.

Species information was extracted from the following individual studies: Grime, Hodgson, and Hunt (1988); Ellenberg et al. (1992); Hill (1999); Lawesson, Fosaa, and Olsen (2003); Molau, Nordenhall, and Eriksen (2005); and Welling, Tolvanen, and Laine (2005), as well as from the databases LEDA (Kleyer et al. 2008), BiolFlor (Klotz, Kühn, and Durka 2002), The Seed Information Database (Royal Botanic Gardens 2019, data.kew.org/sid/), Flora of

Svalbard (svalbardflora.no/), FloraWeb (www.floraweb.de/index.html), Flora of the Canadian Arctic Archipelago (Aiken et al. 2007), The PLANTS Database (plants.usda.gov), Interactive Flora of NW Europe (wbd.etibioinformatics.nl/bis/flora.php?menuentry=inleiding), and the Online Atlas of the British and Irish flora (https://www.brc.ac.uk/plantatlas/index.php?q=title_page). All online resources were accessed April 15, 2016. The taxonomy follows The Plant List 2017 (www.theplantlist.org).

Temperature data

To monitor the temperature range in the recently established terrain available for plant colonization we collected daily temperature data using iButton dataloggers (model DS1922L; accurate to 0.4°C): one logger was placed at the site of the glacier edge in 1898 and one at the glacier edge in 2011 (Figure 3). The loggers were fixed at a height of 120 cm on poles in radiation shade and they recorded the temperature each hour from July 2011 to July 2012 as described in Franzén and Dieker (2014). The dataloggers provide a temperature gradient across the foreland unrelated to change over time.

We also extracted yearly temperature data from a grid with a resolution of 10′ latitude times 10′ longitude that intersected the former glacier area in 1898. These data were extracted from Mitchell et al. (2004) for the period 1900–2000 and from GISTEMP-Team (2016) for the period 2001–2012 and were used to calculate the yearly change in temperature among the time periods 1898–1957, 1898–1980, 1898–2012, 1957–1980, 1957–2012, and 1980–2012. In addition, temperature anomalies were calculated for each decade. These were based on the difference

from the average temperature for the entire area that the glacier covered from 1900 to 2013.

Statistical analyses

To analyze variables potentially associated with the vascular plant colonization of glacier forelands, we carried out the following analyses: (1) We performed a hierarchical cluster analysis of the seven continuous variables based on the complete linkage method (Dormann et al. 2012) to avoid further problems potentially arising from collinear variables when including the variables in general linear modeling (Figure S2). The hierarchical cluster analysis revealed a strong correlation among abundance, distribution, and the distance from the glacier (Figure S2). Thus, we could not separate effects from these three variables and, therefore, only included abundance (which is the most ecologically relevant trait [Brown 1984] in the statistical analyses). (2) We performed logistic regressions with binomial error distribution and the log link function, using species presence/absence in the glacier foreland as response variables and the six uncorrelated species traits as predictor variables. The combined information from the surrounding species pool in the 1940s (Selander 1950) and the species present in the formerly glaciated area recorded in 2011–2012 were used to classify the species as either present or not in the glacier foreland. The final model with the lowest AIC value (Burnham and Anderson 2002) was selected. (3) We explored whether any species traits were related to the age of the terrain that has been exposed since 1898 using plant occurrences only within the former glacier area. As response variables in the models, we assigned each species present in the glacier foreland to the youngest of the three
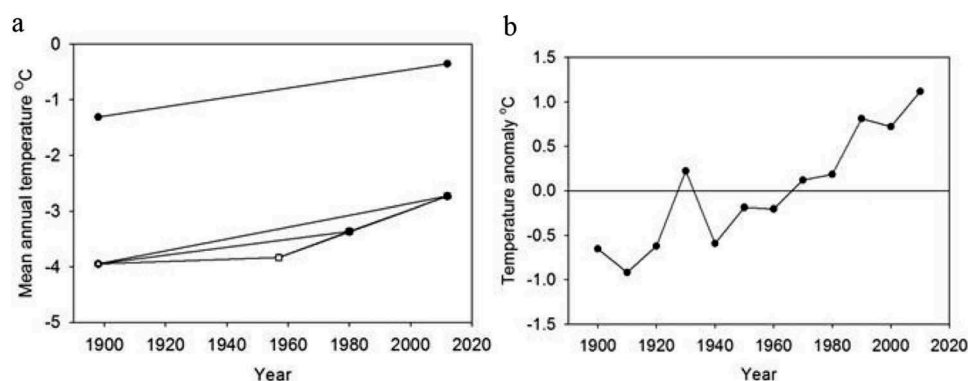
Figure 3. (a) Annual mean temperature from the temperature logger placed at the location of the 1898 glacier edge (−0.35°C) and at the glacier edge in 2011 (−1.31°C), indicating a temperature increase of 0.008°C per year (upper line). The mean annual temperature of the entire glacier area is based on extrapolated temperature data on grids for the six periods 1898–1958 (slope = 0.0019), 1898–1980 (slope = 0.0071), 1898–2012 (slope = 0.0107), 1958–1980 (slope = 0.0212), 1958–2012 (slope = 0.0203), and 1980–2012 (slope = 0.0197) (lower lines). The colder temperature from the yearly data according to the grids is because the grid extends across the entire glacier area, which is mainly covered by ice and includes higher altitudes. (b) Temperature anomalies calculated for each decade from 1900 to 2015 (1900 is based on extrapolated yearly mean temperature data covering the entire glacier area from 1900 to 1909, 1910 is based on data from 1910 to 1919, and so on).

age classes in which a given species was found: 0–31, 32–53, and 54–114 years. The six remaining species traits were included as predictor variables. Model selection was conducted as described previously. (4) We explored the relationship between the analyzed trait states across the species using correspondence analysis (CA) in which all noncontinuous trait states were dummy coded (Figure S3). This was investigated because some states of different characteristics might be linked, and the hierarchical cluster analysis (see previously) can only handle continuous variables. Species with missing trait data were excluded from the statistical analyses ($n = 128$, Table S5). All models were developed using the R software version 3.3.2 (R Development Core Team 2016) and the multivariate CA was performed in Canoco version 4.5.

Results

The Ålmajallojekna glacier has been retreating at an average rate of 0.17 km^2 per year from 1898 to 2012 (Figure 2). The mean temperature increased during the study periods, with the increase ranging from 0.0012°C per year (1898–1946) to 0.021°C per year (1958–1980; Figure 3). Temperature anomalies calculated for each decade (based on daily average temperatures from 1900 to 2015) also showed that the temperature had increased every decade since 1960, ranging from 0.11°C in the 1960s to 1.12°C in the 2000s (Figure 3). The annual mean temperature measured from 2011 to 2012 varied between –0.35°C at the 1898 glacier edge and –1.31°C at the 2011 glacier edge (Figure 3).

Of the 381 vascular plant taxa in the surrounding species pool, 123 were present on the glacier forelands that have been deglaciated since 1898 (Table S5). Sixty-eight plant species were present on the youngest terrain (0–31 years), an additional thirteen species occurred on terrain aged 32–53 years, and forty-two additional species occurred only on the terrain aged 54–114 years. All the plant species that were present in the youngest terrain were also found in the oldest terrain. We obtained estimates of the rate of the number of plant species establishing in the deglaciated areas by linking the number of species with the age of the deglaciated terrain on which they occurred. The youngest terrains have obtained species at a rate of approximately 2.34 taxa per year from 1980 to 2012, while the oldest deglaciated terrains have gained species at a rate of approximately 1.04 taxa per year between 1898 and 2012 (Figure 4). Twenty-nine species were only recorded once and seven species only outside of the transects. Of the 123 species present in the glacier foreland most species were locally abundant and ninety species were classified as very abundant by Selander (1950) in the glacier's surroundings. In the recently exposed glacier forelands *Poa alpina* was the most abundant species, followed by *Salix herbacea* and *Saxifraga oppositifolia* (Figure S1), all of which were present in more than 20 percent of the 1,507 plots.

Plant-species characteristics

To determine whether species characteristics were influencing the ability to occupy the glacier forelands, we included the six uncorrelated trait variables in the same general linear model. The best-fitting model revealed that local abundance (positively), seed weight (negatively), and taxonomic family were the most important traits influencing the species' ability to occur in the glacier forelands (Table 1). The proportion of species occupying the new
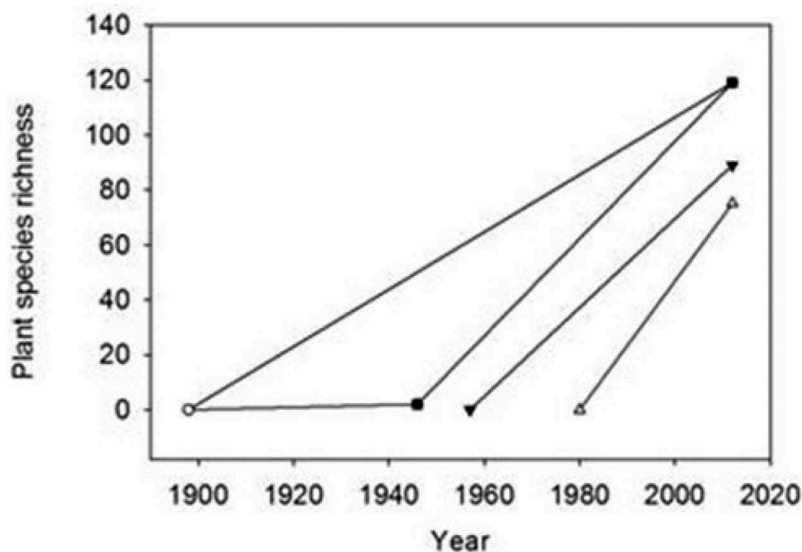

Figure 4. Plant-species richness at the different age classes of the deglaciated terrain among the time periods 1898–1946 (slope = 0.04), 1898–2012 (slope = 1.04), 1958–2012 (slope = 1.64), and 1980–2012 (slope = 2.34). The year 1946 represents the date Selander (1950) visited the glacier area and found only one plant species in the recently deglaciated terrain.

Table 1. The final best-fitting generalized linear model (lowest AIC) for the relationship between plants occurring on the recently established terrain or only outside (in the species pool) and the traits abundance, seed weight, and taxonomic family. For differences between each family, see Figure S6: $df = 252$, $N = 264$, $R^2 = 0.45$; AIC = 204.5.

Source of Variation	Estimate	SE	z Value	p Value
(Intercept)	−0.827	0.829	−0.998	0.32
Abundance	0.119	0.012	8.567	<0.001
Seed weight	−0.447	0.281	−1.591	0.111
Family (Asteracaea as reference)				
Family Brassicacea	−0.015	1.277	−0.012	0.991
Family Caryophyllacea	−0.710	0.910	−0.711	0.477
Family Cyperaceae	−1.366	0.945	−1.445	0.148
Family Ericaceae	−1.410	1.103	−1.278	0.201
Family Juncaceae	−0.437	1.068	−0.410	0.681
Family Other	−1.768	0.821	−2.153	0.031
Family Poaceae	−2.844	1.001	−2.839	0.004
Family Ranunculaceae	−1.323	1.118	−1.183	0.236
Family Salicaceae	0.425	1.214	0.351	0.725
Family Saxifragaceae	1.660	1.391	1.193	0.232

terrain was higher among species within the families Saxifragaceae, Salicaceae, and Asteraceae compared with Cyperaceae, Poaceae, Orchidaceae, and Rosaceae. Plant occurrences within the area that had been deglaciated since 1898 were associated with two life-history traits: life form and the preference for soil moisture. Chamaephytes and species preferring well-drained and drier conditions were more frequent at the youngest terrain (Table 2).

Discussion

Of the 381 plant species occurring in the surrounding region, 123 were present in the recently deglaciated terrain. The glacier foreland has rapidly been colonized by species with certain characteristics at a recent rate of more than two species per year. In our analysis, the occurrence patterns of plants in the glacier foreland were associated with several species characteristics. Important variables in determining occupancy patterns were species local abundance, seed weight, and taxonomic family, indicating the importance of dispersal-related factors to reach new terrain. Within the former glacier area, life form and habitat

Table 2. Results from the best-fitting model analyzing the plants that only occur inside the recently deglaciated terrain and whether traits determine the ability to occupy younger terrain. Soil moisture and life form were linked to the ability to occupy younger terrain: $df = 74$, $N = 78$, $R^2 = 0.12$; AIC = 201.1.

Source of Variation	Estimate	SE	z Value	p Value
(Intercept)	0.503	0.431	1.167	0.247
Soil moisture	0.143	0.068	2.101	0.039
Life form				
(Chamaephyte as reference)				
Geophyte	0.437	0.319	1.370	0.175
Hemicryptophyte	0.468	0.217	2.159	0.034

preference were linked to species' ability to establish on young terrains, indicating that characteristics related to plant establishment are important when determining persistence in a new environment following arrival (see also Rydgren et al. 2014).

Dispersal-related factors and regional abundance: Key traits for successful establishment in the glacier foreland

We found evidence for a strong selection toward dispersal-related characteristics, and large impact of the abundance on the species occurring in glacier forelands. Establishment success was high among the species from the surrounding species pool that had high local abundance, low seed weight, and were members of certain taxonomic families, demonstrating the importance of propagule pressure (seed availability) in the successful colonization of new terrains (Chapin et al. 1994; Ehrlén and Eriksson 2000; Moles and Westoby 2002; Martin and Wilsey 2006). Abundance was correlated with range size and the distance to the nearest population from the glacier edge and we conclude that each of these traits represents a different measure of rarity—measures that are often very strongly correlated (Figure S2; Gaston 1993; Violle et al. 2017). Rare, range-restricted species, or species with small population sizes, are more often absent from new terrain because of a reduced ability to colonize otherwise suitable areas (Gardner and Engelhardt 2008). Thus, the number of diaspores arriving can be more important in shaping the glacier foreland species composition than specialized adaptations for tolerating stressful environmental conditions. Propagules of more abundant species and of those occurring closer to the glacier foreland have a higher probability of reaching newly available sites (Brown and Kodric-Brown 1977). The significance of propagule pressure in determining the species composition of glacier forelands has previously been emphasized in other studies (Stöcklin and Bäumler 1996; Erschbamer, Niederfriniger Schlag, and Winkler 2008; Erschbamer and Mayer 2011). The importance of propagule availability and dispersal-related factors were likewise manifested in the results found for species life-history traits. We found that heavier seeded species are less likely to occur in the glacier foreland compared to their presence in the surrounding species pool (Table 1). Although larger seed weight would enable species to establish more easily (because they have more resources available; Moles and Westoby 2002), their dispersal ability is reduced and thus they are less likely to reach new habitats than species with smaller seeds (Campbell, Rochefort, and Lavoie 2003; Moles and Westoby 2006). There might also be a trade-off between seed weight and species survival ability—

species with small seeds are more likely to colonize new terrain, but can fail to establish and persist because of low tolerance of harsher environmental conditions (Wood and Del Moral 1987; Moles and Westoby 2004). We found no strong indication that different trait states are closely correlated, even if some variables are linked, such as Saxifragaceae having a relatively higher local abundance compared to other families (Figure S3).

Predicted probabilities of colonizing the glacier foreland differed between families and were highest for species within Saxifragaceae, followed by Salicaceae and Asteraceae (Figure S6). Species within these families are characterized by good dispersal ability, mostly having wind-dispersed, light seeds that allow rapid colonization of recently deglaciated terrain. Species within Poaceae had a low probability of occurrence in the glacier forelands even if the most abundant species in the glacier foreland were *Poa alpina*, followed by *Salix herbacea* and *Saxifraga oppositifolia*. These represent species that are very common in arctic communities, with strong adaptations to cold environmental conditions and an ability to occupy recently deglaciated terrain (Alsos et al. 2007; Robbins and Matthews 2009; Muller et al. 2012). For example, the prostrate forms of *S. oppositifolia* have a high capacity for rhizogenesis and can spread vegetatively by shoot fragments—a characteristic that, in addition to good dispersal ability, can be very helpful in harsh environments, facilitating an increase in cover following initial establishment (Kume et al. 1999).

Some plant families, such as Rosacea and Orchidaceae, however, were underrepresented or not present at all in the glacier foreland, despite being present in the surrounding landscape. For Rosaceae, this is probably because of dispersal limitations (e.g., often having large and fleshy fruits), because only the species with high local abundance (*Alchemilla wichurae*, *Dryas octopetala*, *Potentilla crantzii*, and *Sibbaldia procumbens*) were present in the glacier foreland, whereas all other species were found at very low abundances or were absent from deglaciated terrain (see Table S5). For Orchidaceae, establishment limitation is likely, because even orchid species that were locally abundant (such as *Chamorchis alpina*, *Dactylorhiza viridis*, and *Pseudorchis albida*) did not occur on the glacier foreland. Orchid seeds are very small, contain almost no resources, and have to rely on external sources via mycorrhizal fungi for resource acquisition (Eriksson and Kainulainen 2011). The development of a mycorrhizal community requires many years and depends on vegetative history to build up sufficient soil organic matter (Cazares, Trappe, and Jumpponen 2005; McCormick et al. 2012).

While dispersal limitation was shown to be an important factor to reach the recently deglaciated terrain, we detected possible establishment limitation within the terrain that has been exposed since 1898. Species that prefer moister conditions were less successful in their establishment within the glacier foreland than species that prefer drier conditions. This indicates that early successional species may act as nursing plants, facilitating the colonization of later-successional species by adding organic matter to the soil, which increases the availability of both soil moisture and nitrogen (Erschbamer, Niederfriniger Schlag, and Winkler 2008; Anthelme, Cavieres, and Dangles 2014). Chamaephytes were more successful compared with hemicryptophytic forms in colonizing the youngest terrain of the glacier foreland that had been exposed since 1898 (Table 2). Chamaephytes are woody or semi-woody plants (dwarf shrubs) that have overwintering buds close to the ground (Raunkiaer 1934). With adaptations to arctic and alpine conditions, chamaephytes can tolerate various stresses (Illa, Carrillo, and Ninot 2006). In the study area plants might be particularly stressed from the cold winds from the glacier and dramatic shifts in temperature and precipitation. Previously, while observing colonization patterns in younger glacier forelands, a number of studies reported considerable establishment limitation in addition to dispersal limitation (Matthews 1992; Jones and Del Moral 2009). Extreme environmental conditions associated with young terrains, especially drought and soil infertility, have been shown to be unsuitable for species establishment, even when propagules have reached a site (Jumpponen et al. 1999).

Some studies have recognized that abiotic and biotic factors do not have separable effects on species and their interactions (Kraft et al. 2015; Cadotte and Tucker 2017). While experiments can distinguish mechanisms, observational patterns might be especially problematic. We found abundance, seed weight, and plant family to be associated with establishment success, which may hint that these traits are important drivers of establishing species in new terrain. These traits are also associated with early successional species. When the analyses were limited to the terrain that became available since 1898, the trait indicating soil moisture preferences and life forms was associated with colonization patterns, and this might suggest that biotic factors such as competition might also be important. Highly competitive species might even outcompete other species in new terrain (Mori et al. 2008), but our vegetation plots were not totally covered by plants in any case (Figure S7). Possibly other factors such as disturbances and interspecific competition might covary with temperature. We think, however, that competition is not a crucial factor in the study areas, because plant cover is very low in most parts of the former glaciated area (Figure S7).

Additionally, all of the plant species that were present in the youngest terrain were also found in the oldest terrain, indicating that competition is not a dominant driver of succession in the studied glacier forelands. Abiotic and biotic drivers often covary, and this became even more evident in studies that used a chronosequence approach (Johnson and Miyanishi 2008). Indeed, the validity of successional patterns along chronosequences has been criticized (Johnson and Miyanishi 2008; Buma et al. 2017). However, the approach provides an opportunity to study the development of communities on new terrain without relying on the very few rare long-term studies that are available (Buma et al. 2017). Data gathered along a chronosequence should be interpreted with care, but they contribute important new information about how emerging terrain and communities develop. To disentangle the relative importance of biotic and abiotic factors on colonization processes a combination of methods is desired (Crocker and Dickson 1957; Lawrence et al. 1967).

Plant occurrences in relation to temperature increases

We found that species richness increased with more than two species per year in the youngest terrain. Similar increases have been found in other glacier forelands (Kaufmann 2002; Buma et al. 2017). Our results indicate that the successful colonization rates might differ between periods. Selander visited the recently deglaciated terrain surrounding Ålmajallojekna in July 1946 and found only one vascular plant species. The slow colonization rate from 1898 to 1946, according to field observations, is probably because of the limited temperature increase during the period 1898–1946 (only 0.0012°C yearly increase), which could potentially have prevented plants from colonizing the young terrain. In recent decades, temperatures have considerably increased in our study area, potentially benefitting plant colonizations by influencing the length of the growing season (Figure 3). Most of the plant colonizations in the glacier studied have occurred since 1946, and cold periods before 1946 likely hampered earlier plant colonizations. Additionally, the cooling effect of the remaining ice would have been stronger in 1946 compared to 2011–2012. Precipitation might also be an important factor but we could not see any clear pattern in changes of precipitation, including changes in the proportion of rain and snow over time in the study area. However, it is also important to stress that we did not carry out repeated observations between 1946 and the present; thus, our analysis might miss the species that had colonized the area but

went extinct before the survey for this study was carried out in 2012.

During the entire study period of 1898–2012 the temperature increased by 0.01°C per year according to the yearly interpolated temperature grid data, and was surprisingly similar to the temperature differences recorded by the temperature loggers at the location of the glacier edge in 1898 and the glacier edge in 2011, which revealed a difference of 0.96°C (0.008°C per year). Indeed, temperature loggers support the usefulness of the grid data even in topographically highly variable terrains because the temperature difference measured between the loggers was very similar to the temperature change measured over time based on the yearly temperature grid data (0.008°C vs. 0.01°C). We are aware that these results might only be a coincidence and deserve further studies.

Conclusions

Our results show that even after a century of succession, dispersal limitation and, to a lesser extent, establishment limitation still determine the composition of the glacier foreland community. We found that many plant species occupy recently exposed ground. This is probably an effect of rising temperatures in the study area together with developing soils and species-rich vegetation in the surrounding area. Clearly, certain species-specific traits determine whether a plant species will occur on recently exposed terrain. First, dispersal-related characteristics, such as abundance, seed weight, and also taxonomic family, determine whether a species will reach the glacier foreland. Second, characters related to establishment, such as preference for soil moisture and life form, determine where a plant will establish or grow depending on the age of the terrain. Because the decline of the Ålmajallojekna glacier and the observed occurrences of plant species might be representative of numerous glaciers in the Arctic, we assume that under ongoing warming climate conditions, the alpine belt will currently expand its range and the Arctic will subsequently become greener. Therefore, it is important to monitor and study changes in remote areas that traditionally receive little attention.

Disclosure statement

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