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Investigating primary succession following the retreat of the Breiðamerkurjökull glacier, Iceland

Ella Roelofs
SIT Iceland: Climate Change in the Arctic (Fall 2022)
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Abstract

The accelerating rates of glacier retreat around the world as a result of climate change make the study of primary succession in expanding forefields increasingly important. While this is a well studied topic in many parts of the world, little data exists specific to Iceland. This study investigated vegetation development along a chronosequence of eight time periods in the Breiðamerkurjökull outwash plain. Data was collected on percent vegetation cover, dominant species, the number of unique plant groups, and percent cover of five substrate types at 10 plots (0.55 x 0.55 m quadrats) per time period. Important findings include the fact that both vegetation cover and plant diversity increased with time since glaciation and mosses dominated cover in the majority of plots. A comparison to similar studies from around the world demonstrated that, while some patterns are consistent, local factors have important impacts on the rates, processes, and outcomes of processes of primary succession.

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Introduction

Glaciers around the world are melting at rapid and accelerating rates due to anthropogenic global warming (Hugonnet et al., 2021). The retreat of glaciers exposes barren landscapes void of life, providing a unique opportunity to study primary succession, the process of ecosystem development on surfaces lacking previous biological activity (Walker & del Moral, 2003). Ever-growing glacier forelands create chronosequences that allow succession to be studied across long time scales by substituting space (distance from the glacier) for time (Erschbamer & Caccianiga, 2017; Walker et al., 2010). Deglaciated land farthest from the glacier has been undergoing succession for the longest, while succession is just beginning at the newly ice-free areas closest to the glacier.

While many studies have used this method to examine the vegetation development in succession at glacier forelands around the world (including in the European Alps, Alaska, and the Andes) (Dolezal et al., 2008; Erschbamer & Caccianiga, 2017; Fastie, 1995; Fickert, 2020; Frenot et al., 1998; Llambí et al., 2021; Matthews & Whittaker, 1987), fewer studies have been conducted in Iceland (Glausen & Tanner, 2019; van Leeuwen et al., 2018; Vilmundardóttir et al., 2015). Iceland's glaciers currently cover about 10% of the country and are retreating at some of the fastest rates in the world (Hannesdóttir et al., 2020; Hugonnet et al., 2021). Since the end of the 19th century, Iceland's glaciers have lost 18% of their area (2200 km^2), exposing new land that is now at various stages of primary succession (Hannesdóttir et al., 2020). Given the importance of local conditions in determining successional processes (Dolezal et al., 2008; Erschbamer & Caccianiga, 2017; Fastie, 1995; Garibotti et al., 2011; Walker & del Moral, 2003) and Iceland's uniquely harsh climate and low biodiversity (Ministry of the Environment & Icelandic Institute of Natural History, 2001), studies specific to Iceland are important for understanding how these exposed landscapes are developing and will continue to change. Even within Iceland, local factors can lead to differences in succession between the country's many forelands.

Breiðamerkurjökull is the fastest-retreating outlet glacier of Iceland's largest ice cap, Vatnajökull, and its historical retreat is well-documented, providing a chronosequence of accurately dated time periods (Hannesdóttir et al., 2020). Although one 2012 study investigated vegetation succession and soil development at the Breiðamerkurjökull foreland to the southeast of the Jökulsárlón lagoon (Vilmundardóttir et al., 2015), this study aimed to expand on this limited existing knowledge by investigating successional processes a decade later and at the area of Breiðamerkursandur to northwest of the lagoon. By collecting data on and analyzing differences in vegetation cover, species composition and diversity, and substrate types along a chronosequence of 8 dated time periods, this study sought to 1) document successional communities and timelines for this specific foreland, 2) examine how the impact of site-specific conditions such as substrate type may affect primary succession, and 3) compare relative rates and processes of succession in this area to other forelands in Iceland and around the world.

Methods

Study area

The study was conducted within Breiðamerkursandur (N64.10°−64.13°, W16.09°−16.24°), the outwash plain of the Breiðamerkurjökull outlet glacier that extends from the Vatnajökull ice cap. The study area (black box in Figure 1) was selected in the glacial foreland to avoid the Jökulsárlón lagoon to the southwest and the mountains to the northeast. The area has a maritime climate with cool summers and mild winters (Einarsson, 1984). The mean annual temperature is ~5℃ and mean annual precipitation is ~1400-1800 mm, as measured at 3 nearby weather stations (Skaftafell, Kirkjubæjarklaustur, and Höfn í Hornafirði). Both temperature and precipitation have increased since the 1900s (Table 1) (*Climatological Data*, 2012). The area is part of the Vatnajökull National Park, and land use is limited to travel associated with glacier guiding tours, all of which are confined to a dirt road and path along the northeast side of the study area.

Breiðamerkurjökull reached its maximum extent in the 1890s and began to slowly retreat until the 1930s, when it began retreating more rapidly although with some re-advancing and stationary periods (Guðmundsson et al., 2017). Rates of retreat have been highest since 2000, and the current rate of retreat is 200-300 m/yr, one of the fastest rates for glaciers in Iceland (Hannesdóttir et al., 2020; Icelandic Meteorological Office, 2018). In the study area, the glacial terminus had retreated ~5.9 km by 2019, exposing new land (Icelandic Meteorological Office, 2018).

Table 1. General information on climate near Breiðamerkursandur in the 20th and 21st centuries at 3 nearby weather stations in Skaftafell, Kirkjubæjarklaustur, and Höfn í Hornafirði. Data is from the Icelandic Meteorological Office (*Climatological Data*, 2012).

	Skaftafell		**Kirkjubæjarklaustur**		**Höfn í Hornafirði**	
	1965-1999	2000-2021	1932-1999	2000-2012	1966-1984	2007-2017
Mean annual T (℃)	*NA*	*NA*	4.8	5.4	4.1	5.5
Mean daily max T (℃)	*NA*	*NA*	7.7	8.5	6.5	8.2
Mean daily min T (℃)	*NA*	*NA*	1.9	2.7	2.0	3.0
Mean annual precipitation (mm)	1502	1684	1683	1883	1308	1524 *(2007-2021)*

Plot selection

The Icelandic Meteorological Office's glacier outline data was used to map the extent of Breiðamerkurjökull at eight different time periods: 1890, 1945-46, 1970-80, 1998-2004, 2007-2013, 2014, 2017, and 2019 (Icelandic Meteorological Office, 2019). In ArcGIS, consecutive GPS points were made along each outline within the study area. Ten points for each time period were then randomly selected as sample plots. If the point fell within 1 m of a walking path, 5 m of a road, or contained more than 5% water (determined in the field), another randomly selected point was selected. See Figure 1 for a map of plots.

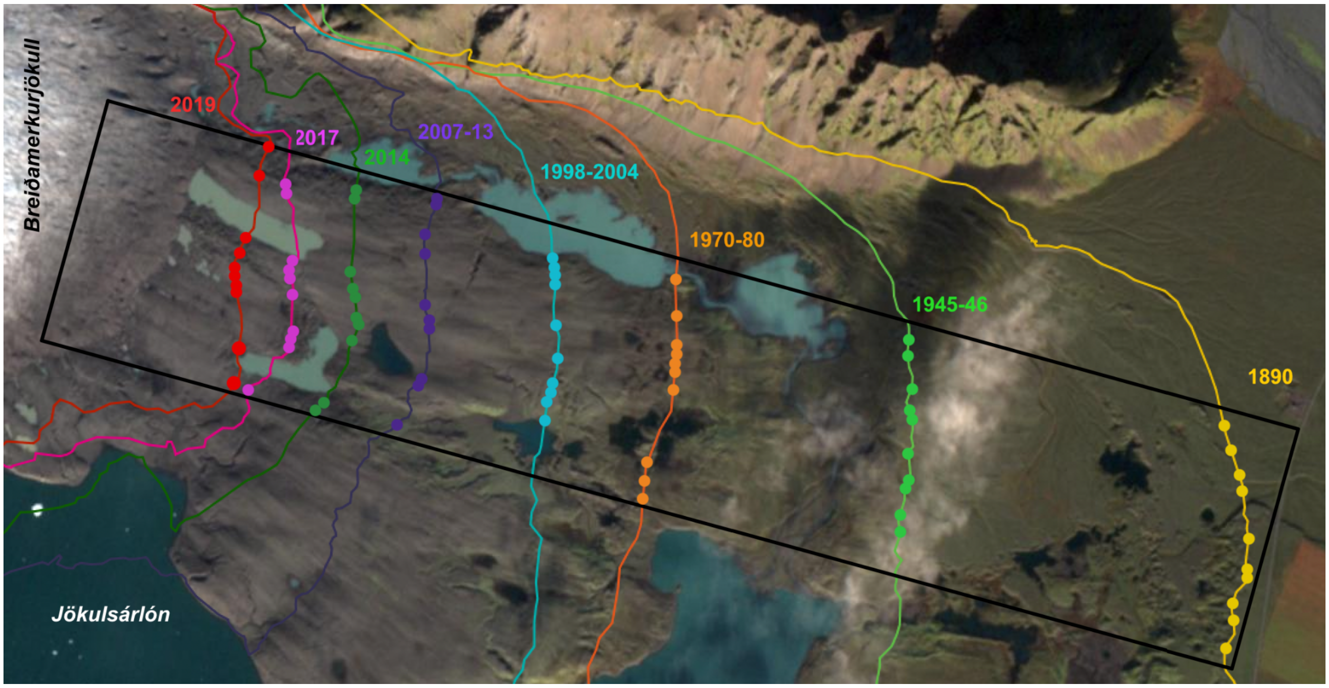

Figure 1. Study area, historical glacial extent outlines, and plot locations. The black box represents the study area, each line represents the location of the glacier at eight different time periods in history, and dots along the lines show the locations of the 10 randomly selected plots sampled for each time period. The glacier was at the right side of the image in 1890 and has since retreated to the far left. Map created in ArcGIS with outline data provided by the Icelandic Meteorological Office.

Data collection

Data collection occurred in the last week of October 2022. Data was collected for each plot within a 0.55 x 0.55 m (0.3025 m^2) quadrat segmented into 25 even squares. Percent cover of vegetation was documented in the field by visually estimating cover within the quadrat's squares. Following the Wentworth scale classifications, the percent cover of each of five substrate classes (boulder, cobble, pebble, granule, and sand or smaller) were also recorded in the field (Wentworth, 1922). To avoid disturbing vegetation, data was not recorded on substrate covered by vegetation. Percent vegetation and substrate cover estimates were both grouped into 5% intervals (i.e., 0 = 0%, 5 = 1-5%, 10 = 6-10%, 15 = 11-15%... 100 = 96-100%). Observations were recorded on the plot's slope, proximity to water, and moraine topography (i.e., whether the plot was on the top, side, at the base, or not on a moraine at all). Photographs of the full quadrat and each plant species within it were taken for later identification. Plants were identified to the nearest taxonomic group possible (species, genus, or family) using pictures and descriptions from several online resources and papers (*Flóra Íslands*, 2019; *Plants of Iceland*, n.d.; Glausen

& Tanner, 2019; Ian Atherton et al., 2010; van Leeuwen et al., 2018). Plants that could not be identified to a taxonomic group but were determined to be the same in several plots were grouped into the same unknown category. Therefore, each unknown category (i.e., unknown 1, unknown 2, etc) is most likely the same plant species or genus, with the exception of unknown group 11 which includes miscellaneous plants that were often too dead to be recognized and categorized. This allowed for measures of plant richness despite the uncertainty of species name (unknown 11 was not included in richness and diversity measurements).

Data analysis

The differences in percent cover of vegetation across the different time periods since glaciation were analyzed with the nonparametric Kruskal–Wallis test. The parametric ANOVA test could not be used because the data did not meet the assumption of equal variances and was not continuous. The nonparametric Wilcoxon pairwise post-hoc test with the Benjamini-Hochberg (BH) p-adjustment method was then used to determine which time periods differed significantly. Additionally, the dominant species in each plot with >5% vegetation cover was determined by the species with the highest percent cover from a full quadrat photograph.

Several different measures were used to compare diversity across the time periods. The number of unique plant groups per plot for each period were compared with the nonparametric Kruskal–Wallis and Wilcoxon pairwise tests to estimate differences in species richness. Diversity was also analyzed using sample size-based incidence (presence-absence) data with the 10 quadrats per period as the sampling units (Colwell et al., 2012). Rarefaction and extrapolation diversity curves were constructed with Hill numbers for species richness ($q = 0$), Hill-Shannon diversity ($q = 1$), and Hill-Simpson diversity ($q = 2$) using the iNEXT package in R (Chao et al., 2014; Hsieh et al., 2016; Roswell et al., 2021). This method allows a comparison of 3 measures of diversity that weigh rare and common species differently: species richness is most impacted by rare species, Simpson emphasizes common species, and Shannon falls in between (Chao et al., 2014; Roswell et al., 2021). Hill numbers were estimated with the mean of 50 bootstrap replicates to generate 95% confidence intervals, and extrapolations were extended to a sample size of 20. Differences in diversity were determined where confidence intervals do not overlap.

Dominant substrate type for each plot was determined, excluding plots that were 100% vegetated (which had no substrate data). The differences in percent cover and number of plant groups for different dominant substrate types were analyzed with Kruskal–Wallis and Wilcoxon pairwise tests.

Ethics

The study area was located within Vatnajökull National Park, and the park granted a research permit. No samples were needed or taken, and substrate data excluded areas fully covered by vegetation to avoid disturbance. Vegetation trampling was minimized as much as possible when walking to sites and handling the quadrat. Plants were identified as accurately as possible, but it is important to recognize the lack of previous experience, the difficulties of identifying plants in the fall/winter (some plants were dead or dormant), and the fact that identification relied on photographs.

Results

Vegetation cover

There were significant differences in vegetation cover between time periods (χ^2 = 62.374, df = 7, $p < 0.001$), and cover increased with time since glaciation (see Figure 2). Time periods farthest apart more often differed significantly in cover, and the four most recent periods (2007-13, 2014, 2017, 2019) did not significantly differ from each other (Figure 2). Plots closest to the glacier had no or very little (<5%) vegetation, while those farthest from the glacier were up to 100% vegetated (Figure 2). However, as Figure 2 shows, there was high variability in cover for the later four time periods (periods with >10% mean cover), and standard deviations were ± 20.1, 22.7, 33.8, and 32.5% for 1998-2004, 1970-80, 1945-56, and 1890, respectively.

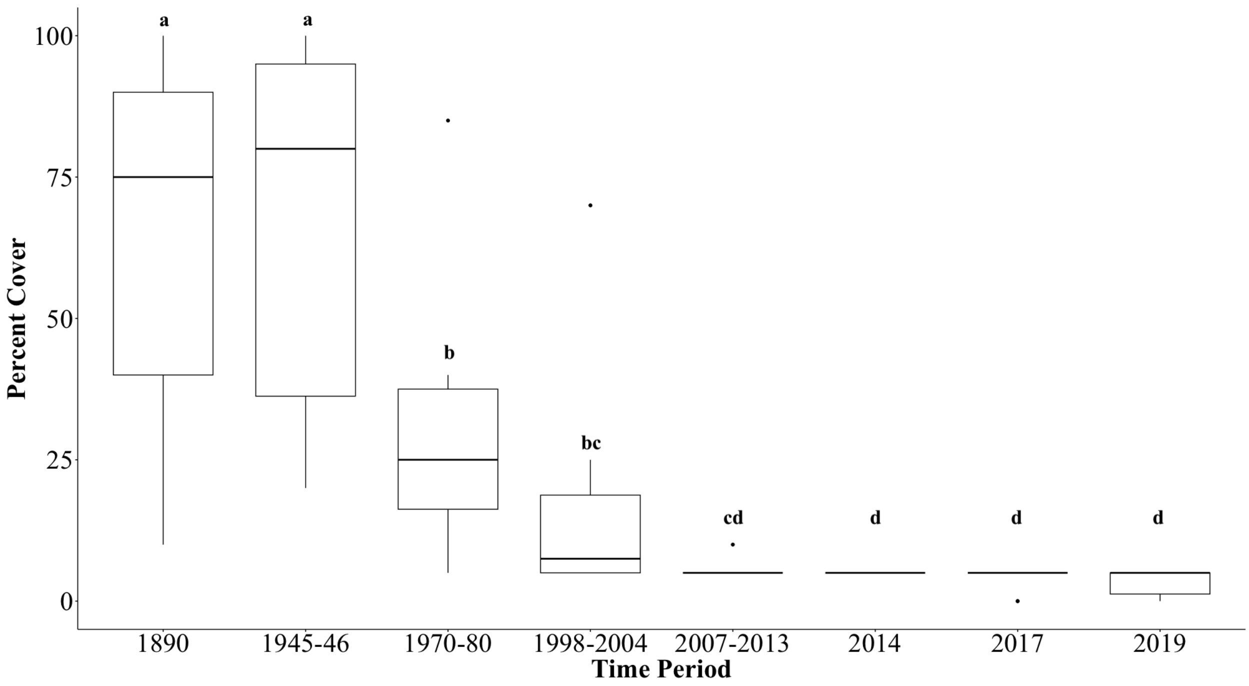

Figure 2. Box plot of percent cover of vegetation in quadrats for the different time periods (n = 10 for each). Significant differences ($p < 0.05$) are detonated with letters: cover differed significantly for time periods that do not share a letter.

Plant diversity

There were significant differences in richness (number of unique plant groups) between time periods ($\chi^2 = 57.048$, df = 7, $p < 0.001$). Significant differences are denoted with letters in Figure 3: time periods that share none of the same letters significantly differed in their richness. Richness increased with time since glaciation, with 2019 having the lowest mean number of plant groups per plot (1.8 groups) and 1890 having the highest (12.7 groups).

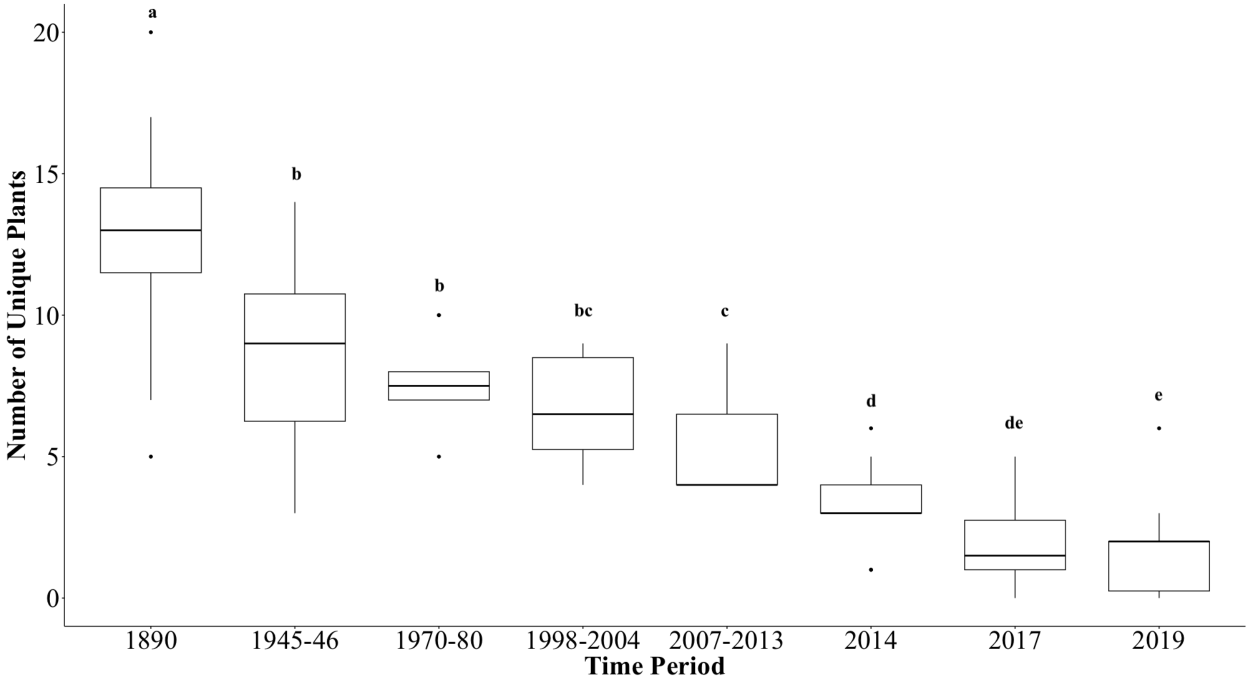

Figure 3. Box plot of the number of unique plants in quadrats for the different time periods (n = 10 for each). Significant differences exist between time periods that do not share a letter ($p < 0.05$).

Species diversity curves demonstrate a clear trend in increasing plant diversity from more recently deglaciated areas to areas exposed several decades ago, and differences are more pronounced when abundance is taken into account (Figure 4). While confidence intervals often overlap for adjacent time periods, this pattern as a whole holds. For example, confidence intervals for 2014, 2017, and 2019 overlap for all curves but never overlap with the 1890 intervals, nor the intervals for the latest 4 time periods when abundance is accounted for ($q = 1$, $q = 2$). The 1890 species richness intervals ($q = 0$) do not overlap with the 4 most recent time periods, and, when abundance is accounted for, only overlap only with those of 1945-46 (Figure 4).

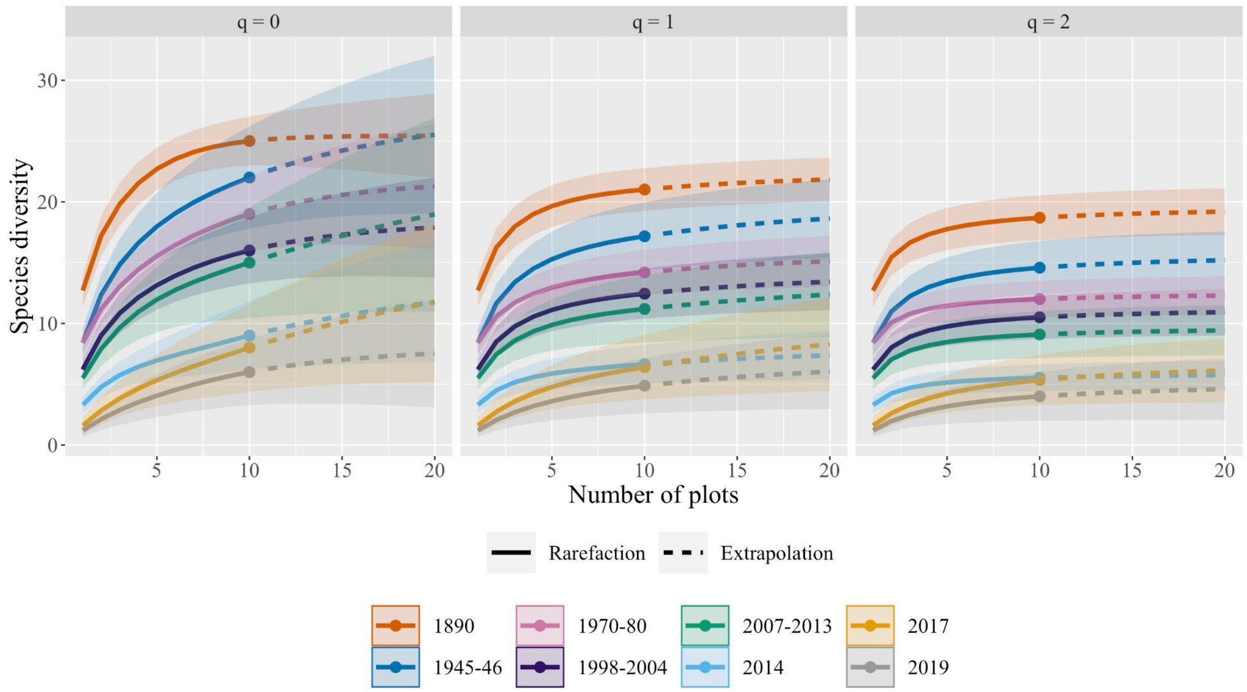

Figure 4. Sample-size based rarefaction and extrapolation species diversity curves constructed from 3 Hill numbers (q = 0, q =1, q = 2) for the different time periods since glaciation. The 95% confidence intervals (shaded areas) were obtained with 50 bootstrap replications.

Plant composition

A total of 31 unique plant groups were identified in the 80 plots, including 5 bryophyte groups, 7 graminoid groups, and 19 forbs (including 3 woody plants). Four plots had no vegetation (3 quadrats in 2019, 1 in 2017). The moss genus *Racomitrium* was present in 89% of the plots with vegetation and dominated vegetation cover in 55% of those. When *Racomitrium* was not dominant (although it was sometimes co-dominant), grasses and small forbs (often *Arenaria norvegica*) dominated in more recent time periods and dwarf shrubs (*Calluna vulgaris* and *Empetrum nigrum*) or the forb *Alchemilla alpina* dominated in later time periods. Woody plants (dwarf shrubs *Calluna vulgaris* and *Empetrum nigrum* and one unknown) were present in 9 of the 1890 plots, 7 of the 1945-46 plots, 6 of the 1970-80 plots, 1 of the 1998-2004 plots, and none of the plots for the other time periods. See Table 2 for a complete list of plant groups present in the plots.

Table 2. List of all plant groups identified showing how many plots per time period and the percentage of the 80 total plots the group was found in. Woody plants are marked with an asterisk. Unknown 11 includes dead and unidentifiable plants of various types, while all other unknown groups include one type of unidentifiable plant that was found at several time periods.

Category	Plant Group	Time Period	Number of Plots (of 10)	Presence in Total Plots (%)
Bryophytes				
	Racomitrium spp.	1890	10	85.0%
		1945-46	10	
		1970-80	10	
		1998-2004	10	
		2007-13	10	
		2014	10	
		2017	3	
		2019	5	
	Polytrichum spp. (most likely *piliferum*)	1890	9	46.3%
		1945-46	7	
		1970-80	10	
		1998-2004	7	
		2007-13	3	
		2014	1	
	Ptilidium ciliare	1890	4	8.8%
		1945-46	3	
	Trichostomum crispulum (most likely)	1945-46	1	1.3%
	Unknown 1: order Hypnales (feather mosses)	1890	5	13.8%
		1945-46	3	
		2014	1	
		2017	1	
		2019	1	
Graminoids				
	Poa spp. (most likely *annua*)	2007-13	2	6.3%
		2017	1	
		2019	2	
	Festuca spp.	1890	8	31.3%
		1945-46	3	
		1998-2004	9	
		2007-13	4	
		2017	1	
			1	
	Festuca vivipara	1945-46	1	2.5%
		1970-80	1	
	Juncus spp.	1890	3	6.3%
		1945-46	1	
		1970-80	1	
	Luzula spicata	1890	6	32.5%
		1945-46	4	
		1970-80	7	
		1998-2004	6	
		2007-13	3	

Unknown 2: order Poales	1890	1	6.3%
	1998-2004	1	
	2007-13	3	
Unknown 3: order Poales	1890	10	71.3%
	1945-46	9	
	1970-80	10	
	1998-2004	9	
	2007-13	10	
	2014	6	
	2017	1	
	2019	2	
Forbs			
*Calluna vulgaris**	1890	3	17.5%
	1945-46	6	
	1970-80	4	
	1998-2004	1	
*Empetrum nigrum**	1890	3	15.0%
	1945-46	5	
	1970-80	4	
Erophila verna	1890	3	7.5%
	1945-46	2	
	2007-13	1	
Plantago spp. (*maritima or tubulosa*)	1890	2	3.8%
	2019	1	
Alchemilla alpina	1890	5	30.0%
	1945-46	7	
	1970-80	8	
	1998-2004	3	
	2014	1	
Sedum spp. (villosum or annum)	1998-2004	2	3.8%
	2007-13	1	
Erigeron boreale	1890	1	1.3%
Arenaria norvegica	1998-2004	2	18.8%
	2007-13	7	
	2014	5	
	2017	1	
Honckenya peploides	1890	10	31.3%
	1945-46	7	
	1970-80	2	
	1998-2004	5	
	2007-13	1	
Rumex acetosella	1890	2	10.0%
	1970-80	2	
	1998-2004	3	
	2007-13	1	
Galium spp. (*normanii* or *verum*)	1890	8	20.0%
	1945-46	2	
	1970-80	4	
	1998-2004	1	
	2007-13	1	

Unknown 4 (maybe *Cardamine hirsuta*)	1890	2	8.8%
	1945-46	3	
	1970-80	1	
	1998-2004	1	
Unknown 5 (maybe *Bistorta vivipara*)	1890	4	7.5%
	1945-46	1	
	1970-80	1	
Unknown 6 (maybe *Salix spp.*)	1890	9	15.0%
	1945-46	1	
	1970-80	2	
Unknown 7	1945-46	1	16.3%
	1998-2004	2	
	2007-13	4	
	2014	1	
	2017	5	
Unknown 8	1890	4	7.5%
	1970-80	2	
Unknown 9	1890	2	25.0%
	1945-46	2	
	1998-2004	4	
	2007-13	4	
	2014	4	
	2017	3	
	2019	1	
Unknown 10 *	1890	6	7.5%
Unknown 11 (dead, misc.)	1890	7	33.8%
	1945-46	5	
	1970-80	5	
	1998-2004	5	
	2007-13	1	
	2014	4	

Plot conditions

Plots varied in their proximity to water and topography. The landscape was characterized by glacial streams and small pools; a few plots appeared to have been recently underwater or in depressions where rain or melt water may collect. Some plots were on the top, middle, or base of a moraine while others were not located on moraines at all. Some plots were on flat terrain while others were on slopes facing various directions. There were no clear differences in substrate cover between time periods other than that data for older periods showed <100% total cover since vegetation more often concealed the underlying surface. Pebble had the highest mean percent cover for all time periods and dominated in the majority of plots, most commonly followed by cobble. However, variability within time periods was high. Standard deviations in substrate class cover were up to ± 32% within a period, and there were 3 outliers dominated by sand and 1 by boulder. There were no significant differences in percent cover ($\chi2 = 9.417$, df = 6, $p > 0.05$) or number of plant groups ($\chi2 = 6.600$, df = 6, $p > 0.05$) with different dominant substrate types.

Discussion

Primary succession following glacial retreat at forelands around the world is a widely studied topic (Erschbamer & Caccianiga, 2017). However, succession has been found to be highly dependent on local conditions, including climate, parent material, topography, moisture levels, nutrient availability, distance to and composition of seed sources, fauna impacts, and more (Dolezal et al., 2008; Erschbamer & Caccianiga, 2017; Fastie, 1995; Garibotti et al., 2011; Walker & del Moral, 2003). Therefore, the process can vary greatly both on small scales (e.g., between the top and bottom of a moraine) and larger scales (e.g., between glacial forelands of different countries) (Dolezal et al., 2008; Erschbamer & Caccianiga, 2017; Fastie, 1995; Garibotti et al., 2011; Walker & del Moral, 2003). While some general patterns found in this study are consistent with those in previous studies, others differ, demonstrating the importance of site-specific research. Additionally, comparisons to other studies can provide a way of estimating the stages and rate of succession at Breiðamerkursandur, although no conclusions can be made with certainty.

Vegetation cover

Vegetation cover increased with time since glaciation, a pattern consistent with primary succession following glacial retreat in other areas in Iceland (Glausen & Tanner, 2019; van Leeuwen et al., 2018) and around the world (Dolezal et al., 2008; Fickert, 2020; Garibotti et al., 2011; Knoflach et al., 2021; Llambí et al., 2021; Raffl et al., 2006). A similar study conducted on the Breiðamerkurjökull foreland to the southwest of Jökulsárlón in 2012 also found an increase from almost no vegetation on the youngest moraines to up to 100% cover on the oldest moraines (Vilmundardóttir et al., 2015). The mechanisms that transform a newly exposed surface void of biological activity to a fully vegetated community, including seed dispersal, plant growth and reproduction, soil formation, and nutrient accumulation inherently take time to occur, so it makes sense that older areas are further along in the process of primary succession (Dolezal et al., 2008; Erschbamer & Caccianiga, 2017). While species compositions and the rate of succession are location-specific, these long-term processes form the basis of succession in all landscapes (Erschbamer & Caccianiga, 2017; Walker & del Moral, 2003).

Plant diversity

Plant diversity increased with time since deglaciation in this study. While this trend is supported in some studies (Fickert, 2020; Llambí et al., 2021), other studies have found diversity to increase in early successional stages, reach a maximum in middle stages, and then decline or stabilize at later stages along a chronosequence as time since deglaciation increases (Dolezal et al., 2008; Garibotti et al., 2011; Prach & Walker, 2019; Sommerville et al., 1982). The Skaftafellsjökull foreland provides an example of this: species diversity increased until a peak in mid-1900s sites and then declined at older sites (Glausen & Tanner, 2019). This pattern is explained by the fact that species accumulate early in succession as pioneers arrive and then diversity begins to level off and decline as later successional species (generally more stress-tolerant and stronger competitors for resources) outcompete pioneers and prevent new colonizers from establishing (Erschbamer & Caccianiga, 2017; Fickert, 2020; Frenot et al., 1998; Whittaker, 1972). Therefore, the consistent increase in diversity from most recent to latest time periods at Breiðamerkursandur may indicate that communities are further from reaching an equilibrium or climax stage.

Plant composition

Bryophytes dominated vegetation cover in this study, a finding that is consistent with other studies. Bryophytes dominated at all moraines in Vilmundardóttir et al.'s Breiðamerkursandur study and all sites in Glausen and Tanner's chronosequence study on the Skaftafellsjökull foreland (Glausen & Tanner, 2019; Vilmundardóttir et al., 2015). The abundance of *Racomitrium* spp. is unsurprising given that they are pioneer species commonly found in successional communities around the world, as well as the most common moss genus in Iceland (Cutler et al., 2008; Glausen & Tanner, 2019; Ingimundardóttir et al., 2014; Knoflach et al., 2021; Llambí et al., 2021; Ministry of the Environment & Icelandic Institute of Natural History, 2001; van Leeuwen et al., 2018; Vilmundardóttir et al., 2015). Many species found in this study overlapped with those found in Vilmundardóttir et al.'s, including *Poa* spp. in earlier years and *Empetrum nigrum* in later ones, likely due to the largely similar conditions in the two adjacent areas (Vilmundardóttir et al., 2015). While exact species in Iceland's forelands may be different than those found around the world, families and genus often overlapped, especially at earlier stages, which may be due to the importance of certain functional strategies for colonizing barren landscapes (Erschbamer & Caccianiga, 2017; Fickert, 2020). Pioneer species often have light, wind-dispersed seeds, are fast-growing, produce large numbers of seeds, and may have asexual clonal propagation strategies (Erschbamer & Caccianiga, 2017). For instance, grasses including *Poa* spp. exemplify these traits and have been found to colonize forelands across the world (Erschbamer & Caccianiga, 2017; Fickert, 2020; Glausen & Tanner, 2019; Llambí et al., 2021; van Leeuwen et al., 2018). As succession progresses, soil development, nutrient accumulation, and facilitation from pioneer species allow species with different functional strategies to colonize. This includes more forbs, dwarf shrubs, shrubs, and trees that are more stress-tolerant, have larger and fewer seeds, and are slower growing) (Erschbamer & Caccianiga, 2017; Llambí et al., 2021). The increase in forbs and dwarf shrubs in this study exemplifies this pattern and is consistent across many locations (Cutler et al., 2008; Erschbamer et al., 2008; Erschbamer & Caccianiga, 2017; Frenot et al., 1998; Llambí et al., 2021; van Leeuwen et al., 2018).

Despite some increase in functional diversity, no true shrubs or trees were identified in this study after 130 years of succession. Vilmundardóttir et al. also noted an absence of these typical later successional species and attributed it the long distance from seed banks (Vilmundardóttir et al., 2015). This is not the only location with seemingly slow succession: in the Patagonian Andes, shrubs took over after 140 years to dominate with forests not appearing until after 260 years (Garibotti et al., 2011). That being said, many locations exhibit faster succession with late successional shrubs and trees present less than a century after deglaciation (Dolezal et al., 2008; Fickert, 2020; Glausen & Tanner, 2019). The study at Skaftafellsjökull, which has also been retreating since 1890, had many overlapping species but found more tree and shrub species (willows and birch) likely due to the site's proximity to a birch woodland (Glausen & Tanner, 2019). Interestingly, however, this study's findings indicated that a low shrub-moss heath may be the climax community in this area: dwarf shrub and moss cover was highest at the oldest two sites and increased from 2007 and 2014 (Glausen & Tanner, 2019). Given that forests cover only about 1% of Iceland, and heath lands of moss, grass, and dwarf shrubs are more common, it makes sense that succession may never reach the forested climax stage that is typical in other areas (Ministry for the Environment and Natural Resources, 2014). Thus, this comparison of successional stages, based on community composition, highlights the difficulties of predicting successional stages and the importance of understanding local contexts (Walker & del Moral, 2003).

Small-scale variability

In addition to successional rates varying widely across the world's glacial forelands, the process can vary at a smaller scale. Within a single foreland, patterns of succession vary even between sites that have been deglaciated for the same amount of time, again speaking to the importance of site-specific conditions. In this study, there was high variability in percent cover between plots of the same age (standard deviations of ± 20.1–32.5% for time periods with >10% mean cover). Studies have shown that substrate texture and topography are important environmental factors influencing the course of succession and plant community composition (Dolezal et al., 2008; Garibotti et al., 2011; Marteinsdóttir et al., 2013). For example, a study on the Glacier Seco foreland in Argentina found that total cover and species richness was higher at the base of moraines than the crest or mid-slope, which was attributed to the consequent more favorable wind exposure, moisture, sunlight, soil development, and organic matter and nutrient conditions as well as effects of erosion-type disturbances on moraines (Garibotti et al., 2011; Schaller et al., 2010). While further study on the effects of moraine topography would be necessary to determine if a similar pattern exists for Breiðamerkursandur, the observed differences in moraine location, substrate type, slope, and proximity to water of plots likely explains some of the variability in vegetation cover. Although cover and diversity were not found to differ significantly with dominant substrate type, the study was not set up to specifically investigate the effect of this factor.

Further study

Further studies would be necessary to determine how small-scale conditions affect vegetation patterns within this succeeding foreland and others. The effect of substrate type could be better investigated by having an equal number of plots with each dominant substrate type. Moraine placement could be studied by having plots on the top, sides, and bottom of a moraine for each selected location. Other variable conditions such as wind, sunlight, and moisture levels could be regularly monitored to investigate their effects on vegetation development.

Many studies have investigated soil development along chronosequences of glacier retreat, including for some areas in Iceland (van Leeuwen et al., 2018; Vilmundardóttir et al., 2015), but this has yet to be done for this study's area of interest. Soil formation and nutrient and carbon accumulation allow more species to colonize and thus are essential for the development of more complex communities. Some studies have already shown that this process may be slow under Iceland's climatic conditions (over a century), and it would be interesting to further investigate this potential explanation for the seemingly slow succession at Breiðamerkursandur (van Leeuwen et al., 2018).

This study did not collect data on lichen cover, nor the presence of algae, fungi, or microorganisms that also may play important roles in primary succession, especially in the earliest stages (Garibotti et al., 2011; Garrido-Benavent et al., 2020). Fauna was also not considered, but the arrival of invertebrates has been found in many places to help facilitate soil formation (Hågvar et al., 2020). Birds and other animals may aid in seed dispersal and contribute nutrients, as has been found in other areas (Turner-Meservy et al., 2022). While this study did not investigate seed sources, dispersal methods, or surrounding vegetation, these factors may help explain the species composition that was found and give insight into what a potential stable climax community may look like in this area.

There are many receding glaciers in Iceland, and primary succession at each of their forelands is largely understudied. More work would be necessary to better understand the process in Iceland, where the cool climate and low biodiversity may impact the rates and characteristics of succession at different stages. Further study would allow a more comprehensive comparison to primary succession in other forelands around the world. Additionally, Iceland is unique in that it provides an opportunity to study and compare primary succession in two different types of new landscapes: newly exposed glacial forelands and fresh volcanic lava fields (or new volcanic islands, i.e., Surtsey). It would be interesting to compare existing (and future) studies conducted in these landscapes that have very different geologies but similar climate conditions and seed sources.

Finally, climate change is both indirectly the cause of and may have an impact on the primary succession that is currently occurring with glacial retreat. Although this is a newer area of study, some early findings suggest that rising temperatures, changing precipitation patterns, and elevated CO_2 levels may affect successional rates and processes, and further research is necessary (Erschbamer & Caccianiga, 2017; Kaufmann, 2002).

Limitations

As suggested by the further study section, this study was limited in scope. It was confined to a single glacier foreland and collected data on only a few aspects of succession (vegetation cover and plant species), leaving many variables uninvestigated. While data analysis with this sample size did produce significant differences, more plots would have been included had time allowed. One of the main limitations of this study was the high uncertainty in species identification. The time of year (late fall) meant that many plants were dead or dormant. This difficulty was compounded with a lack of previous experience with identifying Icelandic flora, especially bryophytes. Therefore, many plants could not be identified or could only be identified to the family or genus level, and even these identifications have not been confirmed. Identifying plants to different taxonomic levels and grouping unknown but like plants allowed for data on the number of "unique plant groups," but it is important to note that the groups contained varying levels of similarity amongst their members. This grouping strategy also helps to explain why this study found fewer distinct plants than other studies that identified the species level (Glausen & Tanner, 2019; Vilmundardóttir et al., 2015). The data on the number of unique plant groups were used to calculate "species" diversity measures, but it is important to recognize the improper use of these indices and remember that the results do not actually refer to species.

Conclusion

This study used a chronosequence approach to investigate vegetation patterns of primary succession following glacial retreat at the Breiðamerkurjökull foreland. The data showed that both vegetation cover and plant diversity increased with time since deglaciation, findings consistent with other similar studies and the existing understanding of the succession process. A comparison of these patterns and plant composition data to studies in other glacial forelands in Iceland and around the world demonstrated the importance of local conditions. While this comparison allowed some inferences to be made about rate and stages of succession at Breiðamerkursandur, nothing could be concluded with certainty. Small-scale variability within the data also highlighted the importance of site-specific conditions (such as moraine topography) to vegetation development, prompting ideas for future research.

The accelerating rates of glacier retreat around the world make the study of primary succession at growing forefields an increasingly important topic. As new land emerges, so do new questions. What factors affect how these landscapes develop over time? Do climate changes affect processes of primary succession? How long does it take for these barren landscapes to become productive, carbon sequestering ecosystems? How will these new areas of land be used by organisms and humans? Therefore, while glacier forelands present unique opportunities for studying succession, it will also be important to consider how humans will use, impact, and interact with these new landscapes and ecosystems.

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