



Non-stochastic colonization by pioneer plants after deglaciation in a polar oasis of the Canadian High Arctic

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Abstract

Initial plant colonization is critical in determining subsequent ecosystem development. In a High-Arctic oasis showing atypical “directional primary succession”, we quantified the microhabitat characteristics associated with colonization by pioneer vascular plants of a bare moraine. The study moraine, formed during the Little Ice Age, is located within the proglacial area at the southern front of Arklio Glacier, Ellesmere Island, Canada. We established two line-transects on this moraine to quantify microhabitats for vascular species. Microsites favorable for plants were concave depressions, probably increasing the likelihood of colonization. At microsites distant from stable boulders, which probably protect seeds/seedlings from wind desiccation, plant colonization was less likely. Furthermore, favorable microhabitat properties differed depending on topographical location within the moraine, suggesting that, even within a single moraine, microhabitats favorable for plant colonization are heterogeneously-distributed. This moraine was characterized by two major pioneer species, *Epilobium latifolium* and *Salix arctica*. Their species-specific microhabitat requirements highlight the importance of biotic factors in colonization processes. Favorable sites for plants are generally distributed at random in harsh environments. However, we showed that initial plant colonization is a deterministic process rather than random, indicating the possibility of non-stochastic processes even during the early phase of ecosystem development in High-Arctic ecosystems.

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1. Introduction

Primary plant succession and ecosystem development are important aspects of ecology, and have been the subjects of extensive study. Irrespective of ecosystem, region, and succession pattern (primary or secondary), initial plant colonization is the most critical phase in the succession process, determining

subsequent long-term ecosystem development and shaping various ecological processes during each ensuing phase of succession (Cooper et al., 2004; Elmarsdottir et al., 2003; Gill et al., 2006; Jumpponen et al., 1999; Ledger et al., 2006; Matthews and Whittaker, 1987; Mori et al., 2008; Robbins and Matthews, 2009). Knowledge of community ecology also sheds light on the significant role of early events including a priority effect (e.g., Chase, 2010; Fukami and Nakajima, 2011), which can lead to unexpectedly high variability in community structure

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among similar sites. Cutler et al. (2008) noted that even in a subarctic ecosystem characterized by stressful abiotic environments, the initial phase of colonization is of substantial importance for subsequent ecosystem development. The initial phase of primary succession is dominated by stochastic processes (del Moral, 2009; Marteinsdóttir et al., 2010; Robbins and Matthews, 2009), including the random distribution of pioneers relative to the distribution of suitable sites (Cutler et al., 2008). Consequently, identifying the causal factors that determine the colonization success of pioneer plants has major implications for understanding the subsequent shift to a gradual dominance of deterministic processes through succession.

Lévesque (2001) showed that plant recruitment in a High Arctic desert is spatially nonrandom as a result of the limited availability of microhabitats that can trap seeds and favor their germination and subsequent plant growth. This is attributable to the specific succession pattern in the polar region. As a consequence of the overwhelming effects of marginal physical conditions and the lack of biological interactions in the High Arctic, successional patterns differ greatly from those in lower latitude areas (Svoboda and Henry, 1987). In High Arctic deserts the typical succession pattern is generally referred to as ‘non-directional, non-replacement (of species) succession’, which means that a very low number of species survive and maintain their status, while fluctuating in terms of cover, abundance, and productivity (Svoboda and Henry, 1987). Thus, the conceptual models of directional ecosystem development (reviewed by Cutler et al., 2008) may not be applicable to systems in extremely harsh environments, such as those in High Arctic ecosystems.

The High Arctic region is generally characterized by vast expanses of barren or sparsely vegetated terrain without significant populations of land animals, or by ice fields (Freedman et al., 1992). Nevertheless, uncommon well-vegetated areas referred to as “polar oases” (Muc et al., 1992) occasionally occur. In these oases primary plant succession can sometimes exhibit directional succession involving directional addition of species over time (Svoboda and Henry, 1987), although this is very atypical (Breen and Lévesque, 2006; Hodkinson et al., 2003; Jones and Henry, 2003; Mori et al., 2008). Given that biotic factors and processes have a significant effect on vegetation development in the glacier forelands of High Arctic oases (Mori et al., 2008), plant colonization patterns in these areas may differ from those observed in typical polar deserts dominated by marginal abiotic environments. Despite the importance of microscale environmental conditions

for plant occurrence on deglaciated forelands (Jones and del Moral, 2005; Jumpponen et al., 1999), the physical properties of such favorable microsites have not been well quantified for the polar oases of the High Arctic. This study focused on a High Arctic oasis on a relatively new moraine on Ellesmere Island (Canada); this oasis formed during the Little Ice Age (LIA) (Mori et al., 2006, 2008; Okitsu et al., 2004). By characterizing the attributes of microhabitats favorable for the colonization of pioneer plants in the bare terrain, this study aimed to provide information on the initial process of directional succession following glacial retreat in a High Arctic environment.

2. Materials and methods

2.1. Study site

The study site (80°52'N, 82°50'W) is located within the proglacial area at the southern front of Arklio Glacier in the Krieger Mountains near Oobloyah Bay, Ellesmere Island, Nunavut, Canada. Climate data from the nearest weather station (Eureka; 80°00'N, 85°56'W; 130 km south of Oobloyah Bay) show that the study area has a polar climate (Okitsu et al., 2004). The mean temperature in the warmest month (July) is 3.3 °C, and is –38.0 °C in the coldest month (February), while the mean annual temperature is –19.7 °C and the mean annual precipitation (1951–1980) is 64 mm. The geological features of the study site have been described previously (King, 1981; Okitsu et al., 2004).

The Arklio Glacier has glacial moraines that have developed over different periods since the Last Glacial Period (King, 1981). The vegetation characteristics of the deglaciated moraines in this area have been described previously (Mori et al., 2008; Okitsu et al., 2004). Among the moraines formed during different periods of glacial advance, the youngest moraine (located at the front of the glacier) is estimated to have formed during the LIA (400–250 years ago; Mori et al., 2008; Okitsu et al., 2004). Although both the occurrence and abundance of plants are very low, several plant species have colonized and become established on this moraine (Mori et al., 2006).

2.2. Moraine features

A morphological description of the study moraine is provided in Fig. 1. Topographical features within the moraine were categorized as the moraine ridge (Ridge site; Fig. 2); the upper part of the moraine side slope,

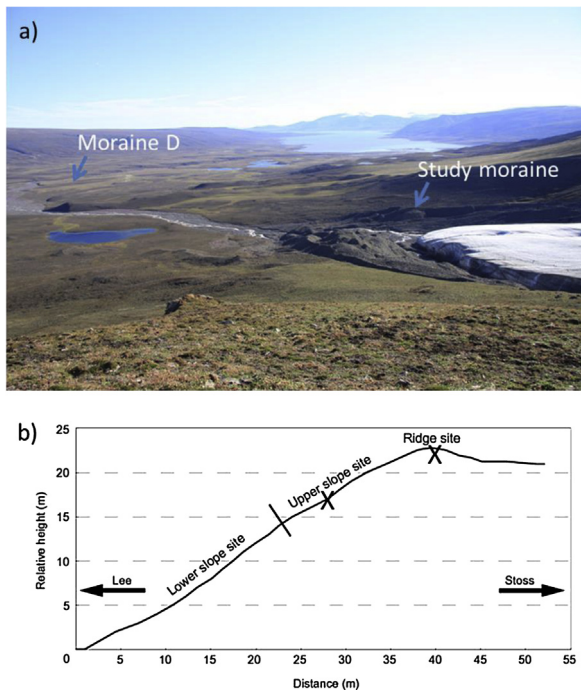


Fig. 1. a) An image of the overall study area taken from the slope adjacent to the Arklio Glacier. The geographical distance from the tongue of the glacier to the oldest moraine (Moraine D of the study by Mori et al. (2008)) is approximately 5 km b) A morphological description of the studied moraine. The solid line connecting the upper and lower slopes is the break line of the moraine side slope. The ridge site was set on the ridge line, and the upper and lower slope sites were set horizontally along the break line. The relative height was measured from the relatively flat terrain where the lower slope of the moraine connects. The locations of the two transects are shown with X. The figure is from Mori et al. (2006).

above the break line of the slope (Upper slope site; Fig. 2); and the lower part of the moraine side slope, below the break line of the slope (Lower slope site; Fig. 2). The mean angle of the moraine ridge was 0° (min–max: $0\text{--}7^\circ$), and thus the substrate at this location was relatively stable. In contrast, substrates on the side slope were unstable and susceptible to movement at any time. The mean angle of the lower slope was 37° (min–max: $30\text{--}42^\circ$), which approached the angle of repose and indicated substantial substrate instability at this location. The mean angle of the upper slope was 30° (min–max: $24\text{--}39^\circ$). Materials including rocks at this location were also unstable and prone to fall, but appeared to be relatively stable relative to those on the lower slope. Mori et al. (2006) therefore considered that the three topographical sites have different substrate stabilities, and reported that among them the lower slope had the lowest abundance of vascular plants in terms of percent cover, frequency



Fig. 2. Images of the studied moraine located at the southern front of the Arklio Glacier. The upper image shows the moraine side slope and the lower image shows the surface of the moraine ridge. The moraine formed during the Little Ice Age, between 250 and 400 years ago.

of occurrence, and species number, demonstrating that it was relatively less suitable for plant colonization. In contrast, the ridge and the upper slope site had higher abundances of vascular plants. Thus, our study focused on the ridge and upper slope sites in characterizing favorable microhabitats for plant colonization.

2.3. Field research

In July 2008 we established a 100-m line transect on the ridge site and a 50-m line transect on the upper slope site of the youngest moraine. Both transects were established on areas representative of the site. Along each transect, 0.5×0.5 m quadrats were established at successive 2-m intervals (in total, 51 quadrats for the ridge site and 26 quadrats for the upper slope site). On each transect there were boulders larger than a quadrat, but no boulder completely occupied the area of any quadrat. Within each quadrat we observed and recorded occurrences of vascular plants. If plants were present we recorded the site attributes characterizing the colonized microhabitat, following the approach of

Jumpponen et al. (1999) who defined a safe microhabitat as a 10×10 cm area centered on a plant. A 10×10 cm square net with a 1 cm mesh size was placed on each plant found within each quadrat: the net center was placed where the plant was estimated to have germinated, following assessment of the root collar and root structure. The surface covered (%) by the target plant (including live and dead matter), substrate particles ($2 \text{ mm} < \text{diameter} \leq 2 \text{ cm}$), and fine substrate ($\text{diameter} \leq 2 \text{ mm}$) were recorded. The distance (cm) from the nearest stable rock/boulder (>20 cm in diameter) to the colonized microhabitat, the topology (elevated, flat or depressed) relative to that of the surrounding 1 m^2 area, and the surface contour (convex, plateau, concave; the surface shape within a 10×10 cm microsite) were also recorded for each colonized microhabitat. Stable rocks and boulders were defined as those that could not be moved when gently pushed with one hand. Control sites were selected following the methodology of Jumpponen et al. (1999). We chose a microsite 50 cm east of each colonized microhabitat. If this microsite was non-vegetated (we found no vegetated microsities 50 cm east of all target plants) it was used as a control site,

and the same attributes described above, except for plant coverage, were recorded. We measured microsite properties for all of the plants observed in each 0.5×0.5 m quadrat.

In the glacier foreland studied here, *Epilobium latifolium* L. and *Salix arctica* Pall. (Porsild and Cody, 1980) are the vascular plant pioneer species that occur most frequently on this relatively young terrain (Mori et al., 2008, Fig. 3). To determine differences in microsite requirements among species we identified 40 colonizing individuals of each of the two species on the ridge site, and recorded the associated microsite characteristics. A non-vegetated control site was established 50 cm to the east of each colonized microhabitat, and the site attributes were recorded. Because these vascular pioneer plants can be multi-stemmed, to accurately count the number of individuals in each 0.5×0.5 m quadrat we were careful to assess whether multiple stems originated from the same root system. Some *S. arctica* individuals were larger than the size of a microsite; however, our description of the physical characteristics centered on the place of germination of these plants was within an area of 10×10 cm.



Fig. 3. Images of the two dominant vascular pioneer plants, *Epilobium latifolium* (right) and *Salix arctica* (left), growing on the moraine ridge. The microhabitats of *E. latifolium* were generally characterized by an abundance of substrate particles with a diameter ranging from 2 mm to 2 cm. The individuals in the images are representative of mature (reproductive) individuals of each species (the height of *E. latifolium* is approximately 5 cm and the longest stem of *S. arctica* is approximately 20 cm). Larger individuals were rarely observed on the moraine.

2.4. Statistical analyses

At the two locations on the moraine we assessed the effect of the presence/absence of vascular plants on the microsite attributes using generalized linear models (GLMs). We evaluated the probability of plant occurrence as a logit function using a binomial error distribution and a logit link function (Crawley, 2007). We first fitted potential models of the probability of plant occurrence using all of the measured variables as explanatory variables. Surface coverage was arcsine-transformed, and the distance from rocks/boulders and the rock/boulder size were log-transformed. Topology and surface contour were treated as categorical variables. We calculated the Akaike information criterion (AIC) for all possible models, and then selected the best models by choosing those with the smallest AIC values (Burnham and Anderson, 2002). Subsequently, we evaluated the characteristics of the microhabitats colonized by vascular plants at the two locations, based on the selected logistic models. The null model was that plant occurrence could not be predicted by any explanatory variable, and was regarded as a random event. The microhabitat characteristics for the *E. latifolium* and *S. arctica* individuals found on the youngest moraine were evaluated using the same procedure. Furthermore, the distance from the nearest rock/boulder was compared between the colonized microhabitats and the control sites. This was evaluated using Wilcoxon signed-ranks tests. All statistical analyses were performed using R software version 2.14.0 (R Foundation for Statistical Computing, Vienna, Austria).

3. Results

Although plant occurrence was quite variable on this young moraine, five pioneer vascular plant species were found at each of the study sites on the moraine. The mean density of vascular plants was 2.2 individuals/m² for the ridge site and 5.4 individuals/m² for the upper slope site (Table 1). The order of relative dominance was the same for both sites: *E. latifolium* was the most abundant and *S. arctica* was the second most abundant.

According to the model selection based on AIC values, on the ridge site plant occurrence was determined by topology, surface contour, distance from the nearest rock/boulder, and size of the nearest rock/boulder (Table 2). In particular, concave microsites probably increased the likelihood of plant colonization, but the likelihood of plant colonization was decreased

Table 1

Density of vascular plant species (no./m²) on the two topographical positions within the moraine studied in Ooblayah Bay, Ellesmere Island, Canada. Mean and standard error values are shown. Nomenclature follows Porsild and Cody (1980).

Vascular plant species	Position	
	Ridge (<i>n</i> = 51)	Upper slope (<i>n</i> = 26)
<i>Epilobium latifolium</i> L.	1.10 ± 0.51	2.92 ± 1.04
<i>Salix arctica</i> Pall.	0.71 ± 0.33	1.08 ± 0.64
<i>Dryas integrifolia</i> Vahl	0.24 ± 0.24	0.31 ± 0.31
<i>Stellaria monantha</i> Hultén	0.08 ± 0.08	0.77 ± 0.39
<i>Papaver radicum</i> Rottb.	0.08 ± 0.08	0.15 ± 0.15
All species	2.20 ± 0.07	5.39 ± 1.49

at microsites that were distant from stable rocks and boulders. On the upper slope the same microsite variables (with the exception of topology) were important for plant colonization, and the microhabitats of vascular plants were characterized by concave microsites near stable rocks/boulders (Table 2). In addition to these two variables, larger stable boulders increased the probability of plant occurrence on the upper slope site (Table 2). The distance from the nearest rock/boulder was less for colonized microhabitats than the control sites (Fig. 4), indicating that colonized plants were preferentially distributed near stable rocks/boulders.

Microhabitat characteristics differed slightly for the dominant vascular plant species *E. latifolium* and *S. arctica*. Consistent with the above results, concave microsites located near stable rocks/boulders were important for both species (Table 3), but for *E. latifolium* the proportion of substrate particles having a diameter of 2 mm to 2 cm was also important (Table 3). A high percentage cover of substrate particles greatly increased the likelihood of *E. latifolium* occurrence.

4. Discussion

The High Arctic environment is a marginal area for plant growth and survival because of the short and cold growing season, extremely low winter temperatures, nutrient-poor soil, low levels of precipitation, and the occurrence of drought, all of which contribute to quite low net production and sparse ground cover (Chapin, 1987; Jones and Henry, 2003; Lévesque, 2001; Lévesque and Svoboda, 1999; Svoboda and Henry, 1987). Nevertheless, biologically driven directional succession, atypical of vegetation development in the High Arctic, can occur in the study area at latitudes higher than 80°N (Mori et al., 2008). In the studied

Table 2
 Logistic regression models characterizing the microhabitats favorable for vascular plant colonization at each site within the studied moraine in Ooblayah Bay, Ellesmere Island, Canada.

Position	Variables	Odds-ratio	P-value
Ridge n = 28	Model ^a (AIC = 46.81)		
	Topology (reference: Flat)		
	Depressed	0.035	0.031
	Surface (reference: Plateau)		
	Concave	66.954	<0.0001
	Convex	–	0.993
	Distance from nearest boulder/rock	0.185	0.005
	Size of nearest boulder/rock	–	0.106
Upper slope n = 35	Model ^a (AIC = 26.94)	–	<0.0001
	Surface (reference: Plateau)	–	<0.0001
	Concave	17049726508.669	<0.0001
	Convex	–	0.998
	Distance from nearest boulder/rock	0.110	0.0150
	Size of nearest boulder/rock	1638.604	0.0340

^a Results of the logistic regression model using the parameters listed below.

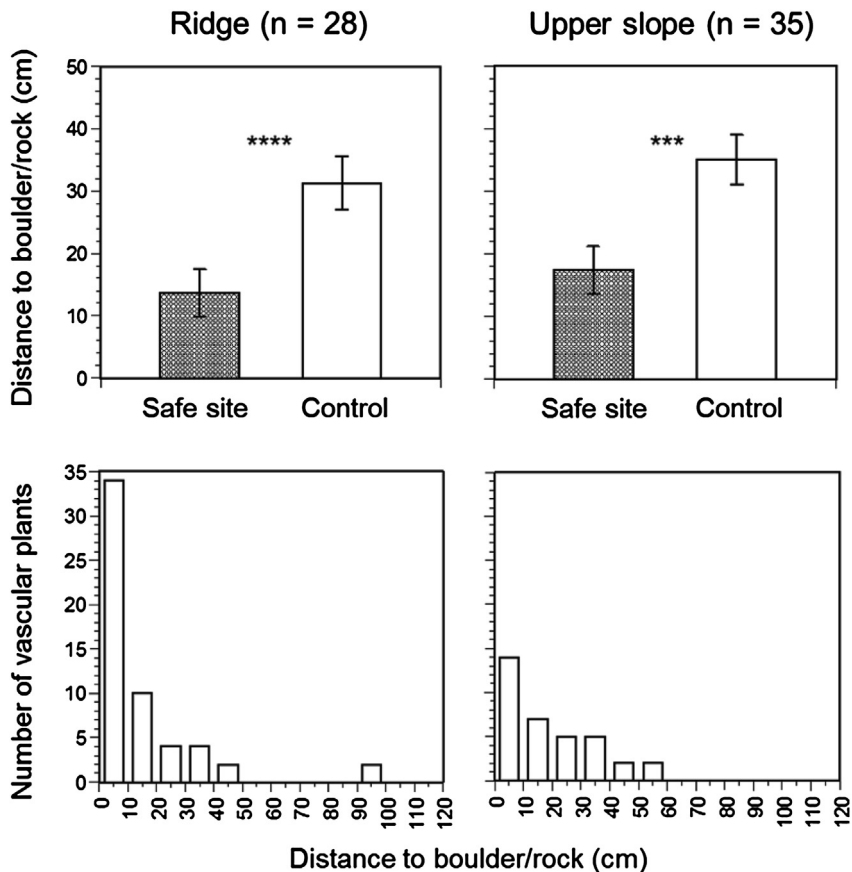


Fig. 4. Distance of nearby stable boulders and rocks from the microhabitats at each location on the moraine. The upper figures show mean values and the vertical bars are standard errors. The lower figures show the total number of vascular plants according to distance from stable boulders and rocks at each location on the moraine.

Table 3

Logistic regression models characterizing the microhabitats favorable for vascular plant colonization in the studied moraine in Ooblayah Bay, Ellesmere Island, Canada.

Species	Variables	Odds-ratio	P-value
<i>Epilobium latifolium</i> n = 40	Model ^a (AIC = 40.60)		
	Surface (reference: Plateau)		
	Concave	48.192	0.001
	Convex	–	0.995
	Distance from nearest boulder/rock	0.142	0.003
<i>Salix arctica</i> n = 40	Model ^a (AIC = 67.19)		
	Surface (reference: Plateau)		
	Concave	65.301	<0.001
	Convex	–	0.344
	Distance from nearest boulder/rock	0.413	0.014

^a Results of the logistic regression model using the parameters listed below.

glacier foreland, pioneer vascular plants have a significant role in modifying microsite environments through litter input and surface coverage, thus facilitating subsequent plant invasion and consequently contributing to directional succession (Mori et al., 2008). Successful colonization by vascular pioneer plants in the initial phase of succession is likely to be one of the most important processes in the relatively long-term course of ecosystem development in this High Arctic glacier foreland.

The moraine in this study formed during the LIA, and is characterized by abundant unstable boulders and sharp rocks, little organic matter on the moraine surface, and sparse distribution of plants (Mori et al., 2006), resulting in limited microsite availability for plants. Nevertheless, some vascular plant species successfully became established on this young moraine. The microhabitats favorable for plant occurrence are generally characterized by concave microsites near stable rocks and boulders, irrespective of their topographical position within the moraine (Table 2). This is because small concave microsites are effective in trapping seeds, and can probably provide greater water availability relative to surrounding microsites (Jumpponen et al., 1999). The results showed that the effectiveness of the favorable sites was reduced if the microsites were located away from stable rocks/boulders (Fig. 4), which provide shelter and protection for seeds and seedlings from wind desiccation (Anderson and Bliss, 1998; Fowler, 1986; Lévesque and Svoboda, 1999; Walker et al., 2006) as well as micro-watersheds for the plants (Livingston, 1972). Another possibility is that snow conditions (accumulation and timing of melt) change according to the presence of rocks (Jumpponen et al., 1999), which affects moisture availability for plants. It is well known

that, irrespective of the type of ecosystem and region, drought is the major factor causing plant mortality during the initial stage of a plant's life (Cutler, 2011; Gimenez-Benavides et al., 2007; Hamrick and Lee, 1987; Mori and Mizumachi, 2005). Microhabitats that enhance moisture availability and reduce wind desiccation are thus crucial for successful plant establishment on the bare terrain in this High Arctic area.

In addition to the fundamental importance of microhabitats favoring plant growth by reducing the likelihood of drought, the results imply that the factors determining successful plant establishment differ depending on location, even within one moraine. Compared with the moraine ridge, plants occurred relatively abundantly on the upper slope of the moraine (Table 1). The slopes of young moraines on which there is little vegetation are generally unstable and susceptible to mass movement, such as rock falls (Matthews, 1992). Because substrate instability can greatly limit plant establishment and survival (Heilbronn and Walton, 1984), the ridge site appears to be a relatively more favorable location for plant colonization. However, Mori et al. (2006) showed that on this moraine, every attribute measured in relation to vascular plants indicated a greater probability of vascular plant emergence on the upper part of the side slope, which was expected to be less stable than the ridge site. Specifically, the depth of accumulated organic matter (an indicator of the duration of plant establishment) was greater on the upper slope, suggesting that gradual but relatively successful plant establishment has occurred on this site (Mori et al., 2006). This may be attributable to the microhabitat properties of the upper slope. Mori et al. (2006) showed that relatively stable boulders remaining on the upper slope of the moraine have an important role in retaining finer moist sediments that favor plant survival. Boulder gravels often contain finer sediment particles sourced

from the passive transport of material, including wind-blown sand and silt (Benn et al., 2003). The present results further demonstrate the importance of such boulders for pioneer plants, because larger boulders are more stable (Mori et al., 2006). In addition to microsite concavity and proximity to boulders, the size of nearby stable boulders greatly affected the probability of plant colonization on this steep slope (Table 2). This emphasizes that, in addition to the shelter effects of proximal boulders for plant establishment and survival (Lévesque, 2001; Elmarsdottir et al., 2003), microhabitat stability also has a significant effect on plant colonization on generally unstable recently deglaciated terrain.

Plant colonization in High Arctic environments is related to extrinsic factors (environmental conditions), but also to intrinsic biological factors (Lévesque, 2001). One such factor potentially affecting the distribution patterns of plants is seed limitation. However, we observed that the two species successfully reproduced on this moraine (Fig. 3), suggesting that this has less effect on plant establishment than micro-environmental factors. Another possible factor is related to interspecific differences in microhabitat requirements. On this glacier foreland the successional pattern is directional succession without species replacement, but only *E. latifolium* disappears during the long process of vegetation development (Mori et al., 2008). On the other hand, *S. arctica* is a major species that dominates all phases of primary succession in this area (Mori et al., 2008). These two dominant pioneer species had different microsite requirements for colonization in the very early phases of succession. On the moraine ridge, both species colonized concave microsites near stable boulders, but only *E. latifolium* was associated with high surface coverage of substrate particles 2 mm to 2 cm in diameter (Table 3). This species is generally found in habitats with undeveloped soils, such as the margins of streams, riverbanks and floodplains. Therefore, the greater density of *E. latifolium* on the upper slope site (Table 1) may reflect such species-specific requirements for establishment on bare terrain (Fig. 3), because abundant large stable boulders on the upper slope help to retain finer substrates, which increases moisture availability for the plants (as noted above). In contrast, *S. arctica* occurs in a wide range of habitats throughout much of the circumpolar Arctic. The differences in favorable microhabitat requirements between the two dominant pioneer species probably reflects their respective life-history traits (Flinn, 2007), and supports the importance of intrinsic factors in plant colonization processes, as suggested by Lévesque (2001).

The results of this study suggest that the two pioneer species function as environmental engineers, probably through the addition of organic matter to the mineral sediments and stabilization of loose substrates. This contributes to the facilitative effects of pioneer plants in harsh environments including tundra (Brooker et al., 2008), although such effects do not occur in all cases (Nakatsubo et al., 2010). The interaction of substrate quality with pioneer plant expansion to create gradients of suitability for later stage plant species was explained in the geocological model of Matthews (1992) (reviewed in Cutler et al., 2008). The impacts on later stages of a community can include priority effects, whereby a species that arrived early at a site can have disproportionately large effects on subsequent community development; these vary across localities (Chase, 2003). Priority effects have generally been found to be more prominent in high productivity environments (Chase, 2010), but we suspect that the studied oasis, which is unusually productive for a polar climate, may provide a rare opportunity to understand the role of community history in plant succession in the High Arctic.

The observed pioneer colonization associated with favorable microsites is the critical initial phase of directional succession, and leaves significant imprints on subsequent biological processes, both stochastically and non-stochastically. Elucidating how historical contingency effects influence the rate and direction of plant community development is an unsolved ecological problem (Gotzenberger et al., 2012; Kardol et al., 2007). The present study suggests that this issue can also potentially be discussed in relation to polar oases in high latitude regions. Specifically, favorable sites for pioneer plants on bare terrain are generally distributed at random in harsh and stressful environments (Cutler et al., 2008; Lévesque, 2001), and stochastic processes predominate in the initial phase of primary succession (del Moral, 2009; Robbins and Matthews, 2009). Nevertheless, the present study shows that initial plant colonization is not necessarily structured by a stochastic process, and reflects significant plant–microsite associations (habitat filtering). We thus suspect that the interaction between stochastic and deterministic processes can be substantial even in marginal High Arctic environments, with profound implications for ecosystem development and community assembly.

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