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Development of Antarctic herb tundra vegetation near Arctowski station, King George Island

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Abstract

We studied the development of the Antarctic herb tundra vegetation formation in relation to the history of deglaciation across a range of habitats near H. Arctowski Research Station (King George Island, South Shetland Islands). Across the three identified environmental zones (coastal, intermediate, periglacial), we quantified the total vegetation cover, cover of the two indigenous flowering plants and bryophytes, age structure and reproductive features of the two flowering plants, and species diversity of mosses and liverworts. Analysis of these data supported the recognition of the three environmental zones; however, there were few indications of systematic differences in biological features of the two higher plants across the three zones, generally supporting the view that these, and the grass *Deschampsia antarctica* in particular, are effective primary colonists of recently deglaciated ground in this region.

Keywords: Flowering plants; Colonization; Maritime Antarctic; Deglaciation

1. Introduction

Only two species of vascular plants are present in the indigenous flora of the maritime Antarctic: *Deschampsia antarctica* Desv. (Poaceae) and *Colobanthus quitensis* (Kunth) Bartl. (Caryophyllaceae) (Alberdi et al., 2002; Greene and Holtom, 1971), contributing to a vegetation community known as the 'Antarctic herb tundra formation' (Longton, 1988; Smith, 1972). These species and the communities of which they form a part have received considerable research attention in recent years in the context of being indicators of biological responses to rapid environmental change in this region (Fowbert and Smith, 1994; Gerighausen et al., 2003; Parnikoza et al., 2009; Smith, 1994, 1996). However, little attention has been paid to ecological processes such as colonization, succession, and vegetation change, either as part of normal ecological processes or in the context of regional climate change and associated recession of previously permanent ice and snow, thereby exposing new ice-free ground for colonization in the western Antarctic Peninsula region (Convey, 2003; Smith, 1996, 2003).

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Alternating periods of glacial expansion and warmer interglacials have characterized the Antarctic environment throughout the Pleistocene and earlier geological epochs. Dynamic fluctuations in glacial extent result in changes in the area of ground available for colonization and the development of vegetation communities. In recent decades, ice recession in the Antarctic Peninsula region has accelerated under the influence of well-documented and rapid rates of regional warming that are exceptional on a global scale (Convey, 2003; Cook et al., 2005; Smith, 1990). Indigenous vegetation communities in this region have therefore had the opportunity to colonize newly exposed areas of bare ground, thereby expanding their distribution locally (Fowbert and Smith, 1994; Gerighausen et al., 2003; Parnikoza et al., 2009).

During the process of colonization, plants would have been challenged by a gradient of environmental conditions from those already experienced in established communities, to presumably more extreme and/or variable conditions near the margins of retreating ice and snow. In detail, the challenges or stresses associated with this gradient would be related to small-scale features of topographical relief and microclimate that control variations in soil, water, and nutrient conditions. This might lead to the expectation of a 'zone' in which environmental conditions are suitable for the development of this vegetation community, whose boundaries would change in concert with changes in regional macroclimate. However, although zonation of plant species has been reported in relation to nutrient input gradients from vertebrate colonies such as penguin rookeries (Barcikowski et al., 2001; Smykla et al., 2006, 2007), no previous study has addressed the development of a vegetation community in association with recent glacial recession in this region.

Therefore, the aim of the present study is to describe vegetation colonization zones across a transect from the coast to the receding glacial margin of the Ecology Glacier, near the H. Arctowski Research Station (King George Island, South Shetland Islands). We hypothesize that this transect provides a proxy for both the exposure age of ice-free ground at this location, and environmental stress at the microclimatic scale.

2. Materials and methods

2.1. Study areas

Ice-free ground in the vicinity of H. Arctowski Station constitutes the largest oasis of this type in the Admiralty Bay region (Marsz, 2001). The apparently favorable conditions of this area have promoted the development of the largest discontinuous stand of *D. antarctica* in the maritime Antarctic (Barcikowski et al., 2001, 2003a). Water supply to the majority of the ice-free area ground in the study area is provided by thawing permafrost and snow-melt. The complex topographical relief of this area results in the formation of six local watersheds (Rakusa-Suszczewski, 2003), each draining toward the coast. Water accumulates at the bottom of the 'quadrangle' (Fig. 1), providing favorable conditions for the development of the Antarctic herb tundra formation, which also benefits here from aerosol input of nutrients from the neighboring sea (Rakusa-Suszczewski, 2003; see also Bokhorst et al., 2007).

During the 30th Polish and 10th Ukrainian Antarctic expeditions (9 November 2005–9 February 2006), we established nine study plots near H. Arctowski Research Station (King George Island, South Shetland Islands) (Fig. 1). Individual plot sizes varied from 9 m^2 (plots 1, 4, 5, 8, 9) to 4 m^2 (plots 2, 3) and 1 m^2 (plots 6, 7), as constrained by local topography. The major criterion in site selection for each plot was the presence of at least one of the two species of vascular plant that define the Antarctic herb tundra formation. The presence of this formation was initially determined in the vicinity of Arctowski Station by Zarzycki (1993), with further description of the distribution provided by De Carvalho et al. (2005).

Plots were established at different distances between the current glacial margin and the coast (Fig. 1) to cover the gradient in environmental conditions experienced in terrestrial habitats of this area. Five plots (1–5) were located near the coast (<10 m a.s.l.), three plots (6–8) in intermediate ground between the coast and the glacier margin (10–50 m a.s.l.), and one plot (9) adjacent to the Ecology Glacier (approximately 10 m a.s.l.). The latter plot (9) is located in an area recently (post-1979) exposed by glacial recession (Pudełko, 2005). Guano input from vertebrate colonies was not a confounding factor at these study locations, although as with much of the maritime Antarctic, the entire study area is likely to experience a low level of incidental vertebrate influence (cf. Bokhorst et al., 2007). The location of each plot was recorded using hand-held GPS (Garmin eTrex H); brief descriptions of the plots are given in Table 1.

A satellite photograph of the vicinity of Arctowski Station and a topographic map (scale 1:12.500; Pudełko, 2005) were used for analysis of relief, description of hydrological (drainage) features, and other factors likely to influence the vegetation.

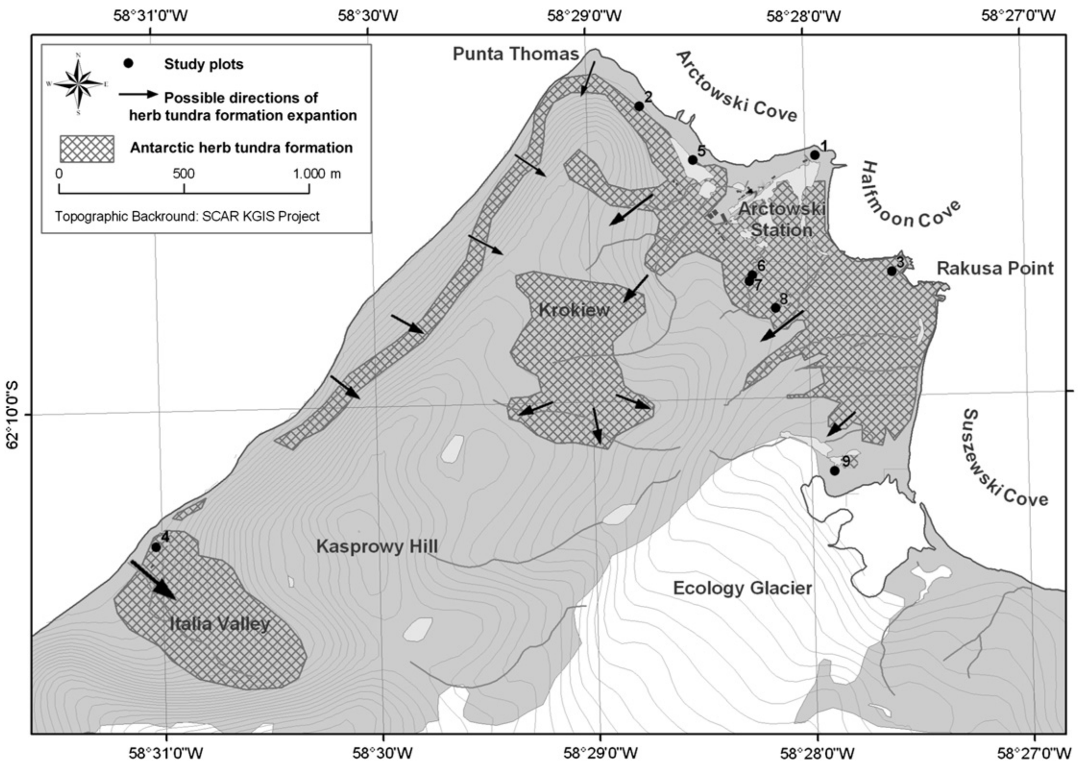

Fig. 1. General distribution of the Antarctic herb tundra formation, and the selected study sites near H. Arctowski Station, King George Island, South Shetland Islands (combining data from the current study with that of De Carvalho et al. (2005)).

2.2. Description of vegetation

Detailed vegetation surveys were made for each study plot. Species diversity of bryophytes (mosses and liverworts) and macroscopic algae were recorded, in addition to the two vascular plants. Lichens are not considered a component of the Antarctic herb tundra formation (Lindsay, 1971), and were therefore not recorded as part of this study. Bryophytes were identified following Bednarek-Ochyra et al. (2000), Ochyra (1998), and Putzke and Pereira (1990). Total cover of the two vascular plants was recorded. The age structures of the populations of both vascular plants were described to allow classification of individual plants as pre-reproductive (seedlings and the early stages of multiple tiller or rosette production), mature (plants of a size including reproductive structures), or moribund/dying (plants with component tillers dead or dying back), following the schemes shown in Fig. 2.

To evaluate reproductive effort, a range of biometric parameters was measured in a set of 20 reproductively active plants of each species (where available) in each plot. Parameters included, for *D. antarctica*: (i) length of the inflorescence, (ii) maximum number of flowers per inflorescence, (iii) quantity of flowers, and (iv) length of the longest leaf; and for *C. quitensis*: (i) diameter of the plant, (ii) length of flower and flower stem for each rosette, (iii) diameter, and (iv) quantity of rosettes per plant.

Data obtained from coastal, intermediate, and periglacial study plots were then compared using non-parametric Kruskal–Wallis and post-hoc multi-comparison tests between treatments (Siegel and Castellan, 1988).

2.3. Soil analysis

Soil samples were collected at each study plot for evaluation of soil characteristics and chemistry. One soil sample was collected from each plot, with dimensions 10 × 10 × 5 (depth) cm, from an area without stones. Soil analytical techniques followed standard procedures (Bulygin et al., 1999). Soil pH was measured after extraction with potassium chloride solution. Nitrogen, phosphorus, and potassium contents were determined after wet ashing of the substrate in the presence of concentrated sulfuric and hydrochloric acids. We also determined hydrolyzed nitrogen and mobile phosphorus, potassium, and

Table 1
Summary features of the study plots.

Plot	GPS position, height above sea level	Inclination and orientation	Distance to shore, m	Substrata	Orientation	Brief notes
1	S62°09.480′ W58°27.953′ 2 m a.s.l.	5°, East	20	Rock	East	4 m from Wujka freshwater lake; sloping toward the sea; intermittent bird guano supply
2	S62°09.366′ W58°28.757′ 4 m a.s.l.	5–10°, East	14	Rock	East	Between station oil tank and freshwater lake; intermittent bird guano supply
3	S62°09.734′ W58°27.611′ 6 m a.s.l.	5°, West	7	Rock	West	Shallow hollow on Rakusa Point; close to source of penguin colony guano
4	S62°10.483′ W58°31.020 10 m a.s.l.	5°, North	15	Rock	North	In Italia Valley at the foot of a scree slope; intermittent bird guano supply
5	S62°09.485′ W58°28.516′ 1 m a.s.l.	Level	13	Gravel	Not applicable	Coastal location below rock face, close to a freshwater lake, surrounding ground can flood; intermittent bird guano supply
6	S62°09.735′ W58°28.253′ 20 m a.s.l.	5–10°, North-east	350	Gravel	North-east	Sloping location including small glacial melt stream; intermittent bird guano supply
7	S62°09.748′ W58°28.267′ 21 m a.s.l.	5–10°, North-east	350	Gravel	North-east	Sloping location including small glacial melt stream; intermittent bird guano supply
8	S62°09.807′ W58°28.15′ 50 m a.s.l.	5°, East	350	Rock	Eastern	Close to the Pukhalski memorial, at the foot of a scree slope; intermittent bird guano supply
9	S62°10.161′, W58°27.893′ 10 m a.s.l.	Level	360	Gravel	Not applicable	North-east of Ecology Glacier, on flat summit of a small hill, exposed from ice after 1979; minimal bird guano supply

sodium contents. Exchangeable calcium and magnesium were evaluated by atomic absorption after pretreatment in ammonium acetate (pH 4.5). Humus content was measured by the oxidation of organic carbon with potassium dichromate in an acidic environment and subsequent titration of residual potassium dichromate by Mohr's salt solution. Total contents of trace elements and microelements were determined by atomic absorption after dry ashing of the soil in a muffle furnace.

3. Results

Both vascular plants and Bryophyta were present across all study plots, although *C. quitensis* was generally scarce in comparison with *D. antarctica* (Table 2), contributing much lower ground cover.

The coastal zone is typically moist and experiences periods of inundation. In agreement with the findings of previous studies (Barcikowski et al., 2003b; Lindsay, 1971), we found that vegetation development in this area is not strongly influenced by the steepness and inclination of local topography. Total vegetation cover in the coastal study plots varied from 63 to 98% (Table 2). The foliose alga *Prasiola crispa* (Lightf.) Menegh was also present.

The intermediate zone is also characterized by considerable water availability, and total vegetation cover was 100% in all study plots. Total vegetation cover in the periglacial zone was 56%, the majority of this contributed by bryophytes (Table 2). Thus, considerable vegetation cover has developed in this zone in the relatively short period (maximum of 26 years) since deglaciation, indicating the effective ability of both bryophytes and the two flowering plants to act as primary colonists. Overall, vegetation cover data for the two vascular plants provides no indication of a difference in colonization patterns across the study plots and zones (Table 2). The highest species diversity of Bryophyta was present in the intermediate zone (Table 3), and liverworts were only recorded in study plots in this zone. The intermediate zone features particularly strong development of the *D. antarctica–Polytrichum piliferum* association of the Antarctic herb tundra formation. Analysis of the age structure of the *D. antarctica* and *C. quitensis*

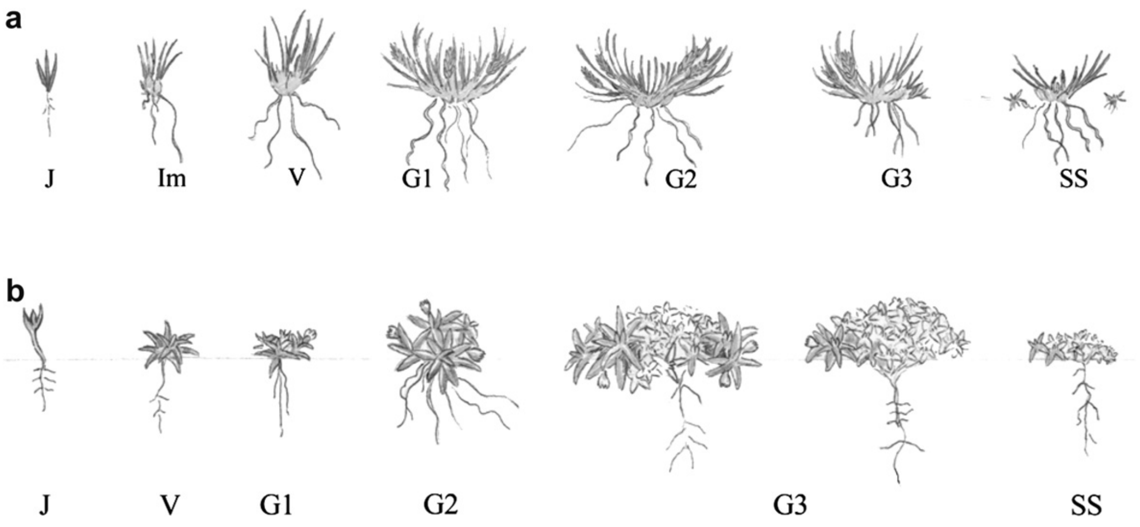

Fig. 2. (a) Schematic representation of the developmental stages of *D. antarctica* used to describe population age profiles. Pre-reproductive stages: juveniles (J) have 3 or more leaves (seed-leaves die off) and no rhizome; Immatures (Im) have a few short rhizomes and form thin turf; Virgin (V) have many short rhizomes and form thick turf; mature stages: young generative (G_1), middle-aged generative (G_2), old generative (G_3), subsenile plants (SS). (b) Schematic representation of the developmental stages of *C. quitensis* used to describe population age profiles: Pre-reproductive stages: juveniles (J) have 2–3 pointed leaves and a single stem, and Virgin (V) a dense rosette without flowers or remnants of flowering stalks from the previous season; mature stages: young generative (G_1), middle-aged generative (G_2), old generative (G_3), subsenile plants (SS).

populations indicated that they were numerically dominated by mature and senescent plants (G_2, G_3; see Fig. 2a, b, Tables 4a and b).

In contrast, in the periglacial zone (site 9), *D. antarctica* populations contained more pre-reproductive plants (J, Im, and V stages), as did those of *C. quitensis,* at both periglacial site 9 and the nearest site within the intermediate zone (site 8).

As shown in Table 5a, morphological (size) and reproductive (number of flowers) features differed significantly across the three zones for both *D. antarctica* and *C. quitensis* (Kruskal–Wallis, $p < 0.05$). Post-hoc multiple-comparison tests (Table 5b) revealed the greatest difference to be between the coastal and intermediate zones, where four of five parameters showed statistically significant differences. Significant differences in three parameters were identified between the intermediate and periglacial zones and between the coastal and periglacial zones. The most sensitive biological indicator of the different conditions across zones was the number of flowers of *D. antarctica*, while the number of rosettes of *C. quitensis* was least affected.

Vegetation community development across the three zones did not appear to be closely linked with the measured characteristics of soil chemistry, although the limited sample sizes and apparent variability between study plots precludes any robust statistical

Table 2
Total vegetation cover, and cover of *D. antarctica* and *C. quitensis*, in the study plots.

Vegetation zone	Study plot	Total vegetation cover, %	Cover of *D. antarctica*, %	Cover of *C. quitensis*, %
I. Coastal	1	63	30	3
	2	58	5	3
	3	80	25	25
	4	100	65	30
	5	98	95	–
II. Intermediate	6	100	50	10
	7	100	90	10
	8	100	25	5
III. Periglacial	9	56	3	3

Table 3
Moss and liverwort species present in the study plots in each vegetation zone.

Species	Vegetation zone		
	I	II	III
Sanionia georgico-uncinata (Müll.Hal.) Ochyra & Hedenäs	+	+	
Polytrichum piliferum Hedw.		+	
Polytrichastrum alpinum (Hedw.) G.L.Sm.		+	
Pohlia nutans (Hedw.) Lindb.	+	+	
Pohlia drummondii (Müll.Hal.) A.L.Andrews			+
Ceratodon purpureus (Hedw.) Brid.			+
Syntrichia princeps (De Not.) Mitt.	+		+
Cephaloziella varians (Gottsche) Steph.		+	
Barbilophozia hatcheri (A.Evans) Loeske		+	

Table 4a
Population age distribution (see Fig. 2) of *Deschampsia antarctica* in study plots in each vegetation zone.

Vegetation zone	Study plot	Juvenile, %	Mature, %	Senescent, %	Dead, %
I	1	–	13	–	87
	2	10	33	57	–
	3	–	100		
	4	30	70	–	–
	5	–	100	–	–
II	6	–	100	–	–
	7	–	100	–	–
	8	5	82	3	10
III	9	25	69	6	–

Table 4b
Population age distribution (see Fig. 2) of *Colobanthus quitensis* in study plots in each vegetation zone.

Vegetation zone	Study plot	Juvenile, %	Mature, %	Senescent, %	Dead, %
I	1	–	5	95	–
	2	19	71	5	5
	3	–	100	–	–
	4	10	90	–	–
	5	–	100	–	–
II	6	–	100	–	–
	7	–	100	–	–
	8	36	60	4	–
III	9	59	41	–	–

analyses (Table 6). The low pH of soils in the intermediate zone is likely to reflect humic acid input from partially decomposed plant remains. Likewise, trace element presence varied widely between different study plots across the three zones, and showed no clear relation with vegetation development (Table 7).

4. Discussion

The current study found significant differences between the characteristics of vegetation development across the three vegetation zones, even though the zones were initially arbitrarily defined. The coastal zone is intuitively likely to have been ice-free for the longest period, although no explicit estimates of exposure age are available for this location. However, proximity to the marine environment may itself lead to environmental stresses on developing vegetation, in particular as a result of salt spray and marine vertebrate activity, which may serve to limit vegetation extent and diversity. By reducing these stresses, the intermediate zone appears to provide the environment most conducive to vegetation development, underlying the greater diversity and cover recorded in this zone.

Table 5a
Comparisons of biological parameters using Kruskal–Wallis analysis of variance for reproductive specimens of *D. antarctica* and *C. quitensis* from the three environmental zones.

D. antarctica	
Inflorescence length	$\chi^2 = 12.99, n = 171, \mathrm{df} = 2, p = 0.002$
Longest leaf	$\chi^2 = 74.21, n = 199, \mathrm{df} = 2, p < 0.001$
Number of flowers	$\chi^2 = 30.13, n = 171, \mathrm{df} = 2, p < 0.001$
C. quitensis	
Diameter of cushions	$\chi^2 = 8.86, n = 126, \mathrm{df} = 2, p = 0.012$
Number of rosettes	$\chi^2 = 8.42, n = 113, \mathrm{df} = 2, p = 0.015$

df = $k - 1$, provided that the sample sizes of the k samples are not too small.

Table 5b
Post-hoc multiple-comparison tests between treatments (Siegel and Castellan, 1988) for biological parameters of reproductive specimens of *D. antarctica* and *C. quitensis* from the three environmental zones, by a given probability of $p = 0.05$.

	Zone 1 vs. zone 2	Zone 1 vs. zone 3	Zone 2 vs. zone 3
D. antarctica			
Inflorescence length	$p < 0.05$	$p < 0.05$	ns
Longest leaf	$p < 0.05$	ns	$p < 0.05$
Number of flowers	$p < 0.05$	$p < 0.05$	$p < 0.05$
C. quitensis			
Diameter of cushions	ns	$p < 0.05$	$p < 0.05$
Number of rosettes	$p < 0.05$	ns	ns

We found no indication that soil chemistry (including trace element levels) had a strong influence on vegetation development across the three zones, although this influence may have been obscured by the high variability in concentrations measured within each zone. Other *Deschampsia* species are known to show high tolerance to such variability (Nkongolo et al., 2001), while *D. antarctica* tolerates high trace element concentrations in soils at the Argentine Islands (Parnikoza et al., 2007).

The periglacial zone, although represented by only a single study plot in the current study, has been ice free for at most 26 years, yet it already shows considerable vegetation cover, plant size, and diversity, indicating the effectiveness of the species involved as primary colonizers (Smith, 2001, 2003). The high investment in reproductive structures by both flowering plants in this zone is consistent with plants that exist in relatively stressful environments (see the discussion in Convey, 1996). Given the small physical distances separating the periglacial zone from the more developed vegetation of the intermediate zone, the magnitude of microclimatic differences leading to increased environmental stresses is likely to be small, leading to

Table 6
Ion content and pH of soil samples from each study plot.

Vegetation zone	Study plot	N alkaline hydrolized mg/100 g	General forms, %		Mobile forms, mg/100 g			Exchangeable Ca^{2+} and Mg^{2+} (combined), meq/100 g of soil	pH	Humus, %
			N, %	P_2O_5, %	P_2O_5, %,	K_2O, %	Na_2O, %			
I	1	15.8	0.13	0.72	43.8	32.5	172.5	10.4	5.7	2.84
	2	4.9	0.06	0.10	36.6	15.9	23.3	14.5	5.8	0.32
	4	32.8	0.18	0.30	60.0	45.0	478.8	12.1	4.6	2.26
II	6	10.8	0.15	0.57	74.0	68.8	50.0	26.8	3.4	4.93
	7	5.2	0.06	0.72	78.0	27.8	66.0	41.5	3.3	1.82
III	9	3.9	0.03	0.26	18.8	16.5	146.0	32.6	6.6	0.38

No soil samples were obtained from plots 3, 5, 8.

Table 7
Trace element content (mg/kg air-dried mass) of trace elements in soil samples from each study plot.

Vegetation zone	Study plot	Trace element content, mg/kg						
		Cu	Zn	Fe	Mn	Pb	Cd	Ni
I	1	37.2	60.6	242.2	5.6	27.2	1.1	4.3
	2	27.2	5.5	30.0	2.2	5.6	0.5	3.5
	4	21.0	9.7	14.4	1.2	5.4	0.6	2.8
II	6	46.3	19.3	249.7	15.5	7.7	0.6	10.7
	7	47.1	15.9	346.3	10.4	7.1	0.3	7.6
III	9	58.0	10.7	212.2	53.7	3.7	0.5	5.3

No soil samples were obtained from plots 3, 5, 8.

an expectation that this recently colonized vegetation will develop rapidly toward that of the more established zones, particularly if rapid recession of the glacier margin continues its recent trend.

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