Vegetation Recovery Patterns Following Permafrost Disturbance in a Low Arctic Setting: Case Study of Herschel Island, Yukon, Canada

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Abstract

The potential long-term effects of thaw slump disturbances on tundra ecosystems include a significant reorganization of tundra plant communities. In this study, vegetation sucession of stabilized retrogressive thaw slumps was investigated using four age classes: 10, 20, and 250 years old, and undisturbed areas. While still active, slumps are characterized by bare soil, pools of water and liquefied mud, and the initial colonization of graminoids and forbs. Between 0 and 20 years after stabilization, the slump vegetation is characterized by low diversity, grass-dominated vegetation communities with a high percent cover of dry bare ground. This is followed after a few hundred years by a forb, dwarf shrub, and bryophyte-dominated community with a high percent cover of litter. With future warming expected, the presence and areal extent of thaw disturbances are predicted to increase. These findings suggest that the result would be an altered tundra species composition, which remains distinct for at least several centuries.

Introduction

Earth is experiencing climatic changes involving both long-term and seasonal patterns (IPCC, 2007). Even the slightest climatic perturbations trigger a strong response in extreme environments like the Arctic and Antarctic (Svoboda and Henry, 1987; Turner et al., 2007). In the Arctic, past changes have had a profound impact on vegetation (Svoboda and Henry, 1987), and it is not surprising that established tundra vegetation is responding rapidly to currently increasing circumpolar temperatures (Chapin et al., 1995; Stow et al., 2004; Tape et al., 2006; Elmendorf et al., 2012). Within the tundra environment, disturbances in the active layer result in both short- and long-term changes in local vegetation patterns and geomorphology. These changes are most evident when radical physical disturbances like thermokarst (landforms resulting from the melting of ground ice in a region underlain by permafrost) occur, as they completely remove not only large patches of vegetation but the upper layers of soil. Polar ecosystems are especially sensitive to both natural and anthropogenic disturbance, and their resilience in the face of change is largely unknown (Turner et al., 2007; Chapin et al., 2013; Haussmann et al., 2013).

When considering vegetation succession in arctic environments, slow rates of colonization, low temperatures, a short growing season, and slow rates of nutrient turnover limit the potential for the regeneration of vegetation and increase the time scale for regeneration to occur (Forbes and Jefferies, 1999; Brancaleoni et al., 2003). In their study of the relative impacts of disturbance and temperature on persistent changes in the microenvironment and vegetation in retrogressive thaw slumps, Lantz et al. (2009) asserted that disturbance caused by warming has a larger and more immediate impact on Low Arctic ecosystems than temperature increases alone. Activities related to oil and gas exploration, as well as climate change effects associated with rising air temperatures, are also expected to increase permafrost degradation in the western Arctic (Maxwell, 1997). Understanding the vegetation patterns

during succession is therefore an important direction for future research, both for managing the restoration of artificially disturbed sites and for predicting the structure of future vegetation communities since the exposed substrate created by large-scale permafrost disturbance provides unique opportunities for the rapid colonization and northern migration of species from their present geographic ranges (Bartleman et al., 2001; Lantz et al., 2009).

Given that vegetation will change due to climate change even in the absence of disturbance, understanding the current successional dynamics of disturbed areas is crucial for the following reasons: first, vegetation plays an important role in the stabilization of disturbed permafrost systems (both physically and thermally) (Oswald and Senyk, 1977; Forbes et al., 2001); second, vegetation plays a key role in carbon budgets, both as a source and sink; and lastly, the ability of fauna to adapt to both increasing disturbance and a changing climate depends in large part on the availability of suitable forage (Callaghan et al., 1998; IPCC, 2007). Clear baseline knowledge of the existing species and communities, patterns of revegetation, and resiliency of tundra in the Arctic is essential in providing a template for recovery from other disturbances (e.g., industrial activity), including identifying native species that could be used for revegetation efforts.

In this paper, we detail the process of succession following the stabilization of a series of retrogressive thaw slumps on Herschel Island and assess the potential long-term effects of thaw slump disturbances on the tundra ecosystem. The main goals of this research are to address uncertainties in the understanding of the responses of tundra vegetation to disturbance and to establish a baseline vegetation database for future comparison. The specific objectives of this research are to (1) describe the vegetation community of different age classes of landscapes disturbed by retrogressive thaw slumping; (2) determine if these communities are discrete and separable by age class; and (3) outline the broad stages of the revegetation of a stabilized thaw slump and their corresponding indicator species and soil characteristics.

Background

This study was conducted on Herschel Island, 69°36′N; 139°04′W, a territorial park located at the most northern point of the Yukon in the Beaufort Sea, western Canadian Arctic (Fig. 1). Herschel Island is part of the Yukon Coastal Plain physiographic region located within the zone of continuous permafrost (Rampton 1982; Pollard, 1990). Containing no bedrock, the island is composed primarily of deformed, fine-grained marine sediment dredged from the Herschel Basin by the Laurentide ice sheet during the Buckland Stage of the Wisconsinan Glaciation (Mackay, 1959; Lantuit and Pollard, 2008). Up to 70% of the upper 10 to 15 m of the permafrost is ground ice (Pollard, 1990). Shoreline and gully erosion expose ice-rich unconsolidated sediments resulting in numerous active retrogressive thaw slumps along the coast. Also known as retrogressive thaw flow slides (Rampton, 1982), or ground-ice slumps (Mackay, 1966), these geomorphic features are initiated when ice-rich sediments are exposed to above 0 °C temperatures, causing the ground ice to melt. In some cases the annual cycle of thaw activity can remain active for 30 to 50 summers (Burn and Friele, 1989; French, 1996). Retrogressive thaw slumps stabilize when exposed ground ice is either completely consumed or has been covered by an insulating layer of debris (Lantuit and Pollard, 2008). Erosion of the slump floor may result in a new cycle of thaw slump activity within the floor of an existing or stabilized slump, thus this polycyclic nature may lead to a much longer lifespan (Lantuit and Pollard, 2008). Stabilized slump scars are evident even centuries after the original slump has stabilized (Fig. 2). Between 1952 and 2000, the number of retrogressive thaw slumps on Herschel Island has increased both in areal extent and in terms of growth rates (Lantuit and Pollard, 2008). Current retrogressive thaw slump retreat rates are on the order of 10–15

m yr^{-1}, and this is expected to increase with continuing climatic warming in the Arctic (Lantuit and Pollard, 2008). As most previous work on slumps and disturbance has been done in the Mackenzie Delta (Bliss and Wein, 1972; Hernandez, 1973; Lambert, 1976; Johnstone and Kokelj, 2007; Lantz and Kokelj, 2008) or inland at Mayo, Yukon (Burn and Friele, 1989; Bartleman et al., 2001), Herschel Island provides an important opportunity to expand upon disturbance research and provides a better indication of processes along the Yukon and Alaskan coastal plain.

CLIMATE

The climate of Herschel Island is Arctic Maritime, characterized by long, cold winters and brief, cool summers reaching a 2011 maximum daily mean temperature of 16.8 °C in July and a minimum of –39.8 °C in January (Environment Canada, 2012). The mean annual air temperature recorded on the island is approximately –11 °C with a mean annual precipitation of 160 mm (Environment Canada, 2012). Precipitation is strongly skewed toward the summer months when the Beaufort Sea is ice-free, with the highest mean monthly total precipitation (30.6 mm, calculated based on 2004–2012 data) occurring as rainfall in August (Environment Canada, 2012).

VEGETATION

Herschel Island is part of the Northern Mountains and Coastal Plain Ecoregion of the Yukon (Oswald and Senyk, 1977). The vegetation of Herschel Island consists largely of tussock tundra, characterized by a thick, acidic organic layer and the presence of *Eriophorum vaginatum* (Kennedy et al., 2001; Myers-Smith et al., 2011; Sloan and Pollard, 2012). The main vegetation communities are cottongrass/moss, arctic willow/dryas-vetch, and arctic willow/saxifrage-coltsfoot (Smith et al., 1989). Smith et al. (1989) characterize the cottongrass/moss type as a stable community dominated by cottongrass tussocks, commonly referred to as "tussock tundra" with low shrubs such as *Salix reticulata*, *Salix arctica*, and *Salix planifolia* and ericaceous shrubs such as *Vaccinium* spp. present in addition to a variety of forbs including *Pedicularis capitata, Papaver* spp., *Saussurea angustifolia*, and *Valeriana capitata*. This vegetation community also includes a well-developed moss layer and trace amounts of lichens including *Cetraria cucullata, Thamnolia subuliformis*, and *Alectoria ochroleuca*. Smith et al. (1989) asserted that tussock tundra is very stable and likely represents the long-term mature vegetation on most sites where it is established. Based on the Smith et al. (1989) classification, all study sites occurred within the tussock tundra vegetation community.

FIELD METHODS

Five stabilized retrogressive thaw slumps and two undisturbed areas were selected for detailed investigation. Fieldwork was conducted over two field seasons in 2010 and 2011. The age of stabilized areas was established using a combination of a series of differential GPS surveys to monitor recent change, air photos and satellite imagery, stratigraphic analysis, and previous studies (e.g., de Krom, 1990). The stabilized sites represent three age classes: 0–10 years (sites B and C), 10–20 years (sites A and D), and >20–250 years (site E) following stabilization of the slump headwall (Fig. 3). The upper threshold of 250 years was established by dating the oldest known stabilized slump on the island, site E (Figs.
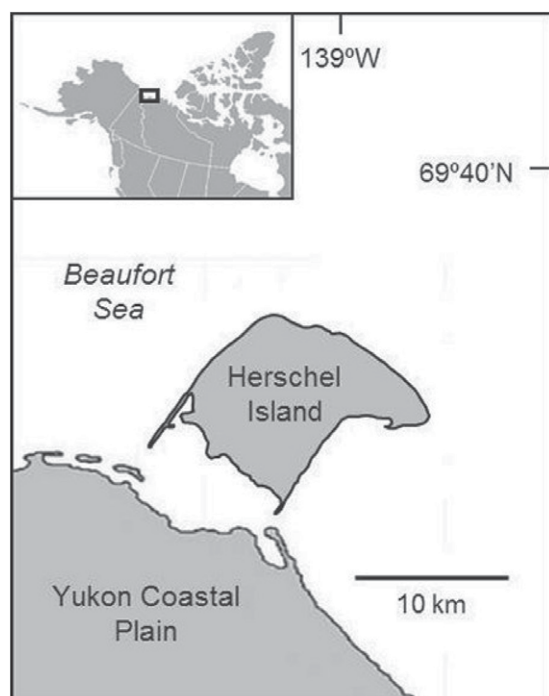

FIGURE 1. **Location map of Herschel Island in the southern Beaufort Sea, Canada.**
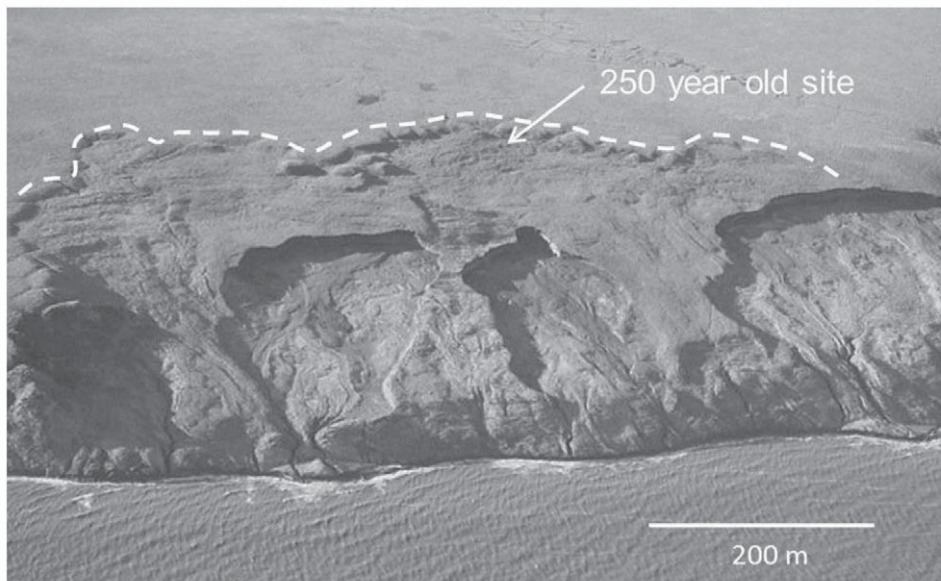
FIGURE 2. A 250-year-old stabilized site illustrating the distinct zonation created by the stabilized area behind the active slumps.

2 and 3). This site was dated by Lantuit et al. (2012) using sedimentological and geochemical analyses in addition to AMS radiocarbon dating. To be conservative, the age of the stabilized site for this study is considered to be 250 years. Two adjacent undisturbed areas (site U1 and U2) were selected based on the lack of observable disturbance in the area evident both from the ground as well as from the 1951 air photos.

The total number of vegetation sample quadrats for each study site was scaled to 1% of the total area of each stabilized retrogressive thaw slump using ArcGIS and differential GPS data from 2010 (Table 1). Within each site, a transect perpendicular to the stabilized headwall was established at the approximate center of the slump; the total of the transect lengths is therefore proportional to the dimensions of each slump. Since all of our study sites were situated within coastal landscape systems, our sample transects ran

the length of the slump floor ending at the point where the slump floor abruptly ended in a coastal bluff. Eighty percent of the sample quadrats in each site were distributed at regular intervals along this transect, with the remaining 20% distributed randomly within the stabilized area using the ArcView extension "MILA Utilities 3.2" and the area boundaries. In the field, transect quadrats were placed at predetermined equidistant points along the transect, and random points were located with a differential GPS unit with 0.5 m accuracy. This method of random quadrat distribution was chosen to effectively remove observer bias in selecting quadrats. To maintain sampling uniformity, undisturbed areas were sampled with both transects and random quadrats in the same way as the other sites, where the median number of sample quadrats and the mean transect length were used for both undisturbed areas and the boundaries were assigned as a rectangle surrounding the transect.
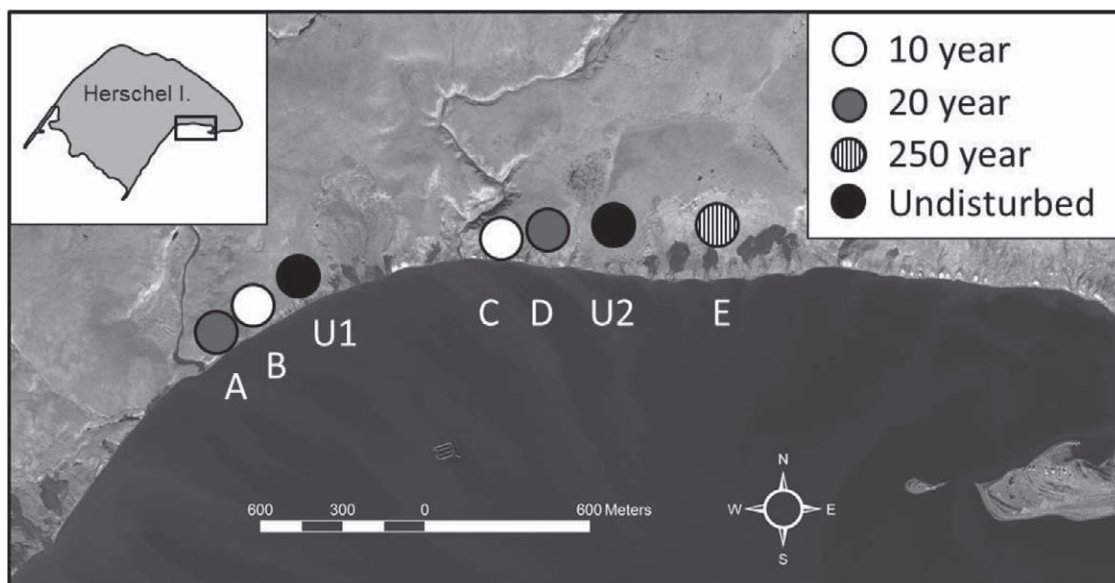

FIGURE 3. Locations of the seven study sites on Herschel Island, Yukon, Canada.

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TABLE 1

Study site quadrat distribution by age class showing the number of vegetation sample quadrats for each study site. Elevation and distance to the coast were measured at the center point of the study site.

Site	Total area (m²)	Total quadrats	Transect quadrats	Random quadrats	Elevation (m a.s.l.)	Distance to coast (m)	Transect length (m)	Total soil samples
B-10	10,030	100	80	20	20	107	165	20
C-10	2360	24	19	5	26	55	45	5
A-20	4370	44	35	9	17	73	65	9
D-20	2330	23	18	5	32	114	85	5
E-250	24,400	244	195	49	26	209	215	49
U1	7200	72	58	14	25	125	145	14
U2	7200	72	58	14	32	148	145	14

Vegetation was sampled in July of 2011 with 1×1 m quadrats using visual percent cover estimates. All cover estimates were performed by the lead author. Cover was estimated separately for each vascular plants species, and three voucher specimens were collected for each species recorded; this voucher specimen collection has been donated to the Canadian Museum of Nature Herbarium. Species nomenclature followed Cody (2000). In addition to vascular plant species, percent cover estimates also included bare ground, bryophyte, litter, and fungi. Litter was dead unattached vegetation on the ground and bare ground consisted of soil without any decaying organic matter (such as peat-hummock islands or willow roots).

Soil samples from the uppermost 10 cm were collected from 20% of the vegetation sample quadrats in each study site. At each site, 80% of the soil samples were collected from transect quadrats (spaced evenly along each transect) and 20% were collected from the site's random quadrats. All soil samples were collected in the same week of July and sampling followed a 24-hour precipitation-free period. Soil samples were sealed in Whirlpak sample bags, stored at or below 2 °C within 4 hours of collection, and kept at this temperature until lab processing. Soil samples were analyzed for pH, gravimetric moisture content, and organic matter content following McKeague (1978). Active-layer depths were determined at each vegetation quadrat by inserting a steel permafrost probe into the soil to the depth of refusal. Active-layer depth measurements were collected in late July and thus likely represent near-maximum depths. These abiotic variables were included in the study based on previous studies, which show that they vary consistently with time since disturbance (Lambert, 1972; Lantz et al., 2009).

DATA ANALYSIS

Diversity in this study was measured by calculating species richness and the Shannon Index of Alpha diversity using the R software packages "vegan" and "ecodist" (Goslee and Urban, 2007; Oksanen et al., 2012; R Development Core Team, 2012). Multi-response Permutation Procedures (MRPP) were calculated using vegan and Bray-Curtis distances to test whether the age classes were distinct and separable. To examine difference in plant community composition among age classes, a nonmetric multidimensional scaling (NMDS) ordination was performed on the species data set using vegan, ecodist, and "labdsv" (Roberts, 2012). NMDS was selected because it is generally able to produce robust and interpretable results even when relationships among variables are nonlinear

(McCune and Grace, 2002). NMDS calculations were performed using Bray-Curtis distances, random starting configurations, and 100 independent, iterative runs with the data. The optimal number of ordination axes was assessed using a scree stress plot and the strength of the ordination was assessed using the final stress and a Shepards plot. To reduce noise in the analysis, species observed in only a single quadrat and species that had less than a 5% total summed cover score (for all quadrats combined) were deleted from the data set. This resulted in 31 species being deleted.

Indicator species analysis was used to identify species that consistently differed in their abundance between age classes (Dufrêne and Legendre, 1997). Indicator species calculations were performed using the R package "indicspecies" (De Caceres and Legendre, 2009) with the command "multipatt" using "indval" (Dufrêne and Legendre, 1997). Indicator values for each species were calculated from the relative abundance and frequency of the species using age class as the associated site grouping combination. Randomization trials with 1000 iterations were used to identify indicator species with a low probability of obtaining an equal or higher indicator value by chance ($p < 0.01$). As calculated in this study, high species indicator values indicate that a species is found mostly in a single age class and is present at most of the sites belonging to that age class. Indicator values range from zero (no indication) to 100 (perfect indication). Perfect indication means that within the calculated data set, the presence of a species points to a particular age class without exception.

Mean thaw depth, organic matter content, pH, and gravimetric water content were compared between sites using Kruskal-Wallis tests. Kruskal-Wallis tests were selected because parametric assumptions of normality and homoscedasticity as assessed by Anderson-Darling and Levene's Tests of model residuals were not met. Kruskal-Wallis tests were conducted in R using the software package "pgirmess" (Giraudoux, 2014). Sites were compared using a multiple comparison post hoc test for Kruskal-Wallis with a Bonferroni correction using the "agricolae" package (de Mendiburu, 2009).

Results

VEGETATION

Vegetation composition was observed to change dramatically across the time series, reflecting stages characterized by predomi-

nantly bare ground and grasses to low continuous vegetation. The most diverse and species-rich age class was the undisturbed class, followed by the 250 year old stabilized site, and then the 20- and 10-year-old stabilized sites (Fig. 4). As illustrated by the indicator species analysis, very few species occurred in every age class, and the overall tendency was for overlapping species to occur in successional age classes (e.g., the 10 and 20 classes; undisturbed and the 250 classes; 20, 250, and undisturbed classes; Tables 2 and 3). Out of a total of 101 species, only 15 occurred in every age class, and the majority of these only infrequently and at low percent cover (Appendix 1). The species that were the most useful indicators of age class groupings ($p < 0.01$) are described in Tables 2 and 3. The lowest number of indicator species was identified in the 10 year age class at 2 species, followed by the 250 year age class at 6, the 20 year class at 12, and the undisturbed sites at 21 indicator species. The 250 and undisturbed sites contain the most shared indicator species.

Pattern analysis of the data set shows that the age classes of the 10/20, 250, and undisturbed are distinct and separable. NMDS ordination of the species cover data resulted in a three-dimensional solution with a linear fit R^2 value of 0.859, and a final stress of 0.154. The NMDS (Fig. 5) revealed clustering around the three major age classes—10/20, 250, and undisturbed. The 10/20 age classes are expressed as one because the NMDS showed them to be similar, suggesting less distinction of discrete communities. The 250 year and undisturbed age classes showed some less obvious overlap. Examination of the NMDS ordination reveals that quadrats that appear anomalous to their site are unusual in their species composition. These quadrats fall into four broad groups: those representing vegetation "islands" where species from the headwall (mainly *Salix arctica*) have survived; quadrats containing a high percent cover of an uncommon species; quadrats that are in close proximity to the undisturbed headwall (e.g., quadrats at the top of the E-250 site) where blocks of the headwall have slid intact into the stabilized zone; and finally, those quadrats with an unusually high percent cover of moss, litter, or bare ground for their age class. Despite intra-site variability, the results of the pattern analysis clearly indicate that the 10/20 year, 250 year, and undisturbed age classes each have a distinct vegetation community and ground cover.

The strength of these differences was demonstrated by the MRPP analysis. We rejected the null hypothesis $H0$ = no differences between age classes. MRPP analysis resulted in $A = 0.1797$. This measures the effect size that is independent of sample size and is formally known as chance-corrected within-group Agreement (within-group homogeneity). McCune and Grace (2002) noted that typically $A < 0.1$ for most communities, hence a value of $A = 0.1797$ indicates a clearly heterogeneous set of age classes. This was confirmed by the statistical outcome of $p < 0.01$.

Considering both frequency and average percent cover, the most commonly occurring species in the undisturbed age class were *Eriophorum vaginatum*, *Salix richardsonii*, *Dryas integrifolia*, *Carex consimilis*, *Salix reticulata*, and *Salix glauca* (Appendix 1). By the same criteria, the most common species recorded in the 250 year class were *Salix arctica*, *Salix pulchra*, *Salix reticulata*, and *Astragalus alpinus*. The 20 year age class sites were dominated by *Arctagrostis latifolia*, *Alopecurus alpinus*, *Salix arctica*, *Matricaria ambigua*, and *Artemisia alaskana*. This is similar to the 10 year stabilized class, for which *Artemisia tilesii*, *Arctagrostis latifolia*, *Salix arctica*, *Alopecurus alpinus*, *Poa arctica* ssp. *arctica*, and *Matricaria ambigua* were the dominant species. Species notable for occurring with a relatively high frequency and percent cover in every age class include *Salix arctica* and *Arctagrostis latifolia*.

SOIL

Study site and age class had a significant effect on the thaw depth (Kruskal-Wallis, $X2 = 265.8$, $p < 0.0001$), soil organic matter (Kruskal-Wallis, $X2 = 75.89$, $p < 0.0001$), soil pH (Kruskal-Wallis, $X2 = 86.38$, $p < 0.0001$), and soil gravimetric water content (Kruskal-Wallis, $X2 = 77.63$, $p < 0.0001$) (Fig. 6). The active layer was thickest at the most recently disturbed sites and steadily decreased in depth with disturbance age (Fig. 6). The high standard error reported reflects the heterogeneity of the landscape, where measurements recorded on transported vegetation islands in stabilized slumps had an active layer as shallow as 20.5 cm and bare areas within the same age class (20 year) were thawed to 82 cm. Within the undisturbed sites, quadrats with dense, insulating tussocks contributed to the low minimum thaw depth, whereas quadrats containing exposed soil or a high proportion of litter were those with the deepest active layer. Mean pH was lowest in undisturbed
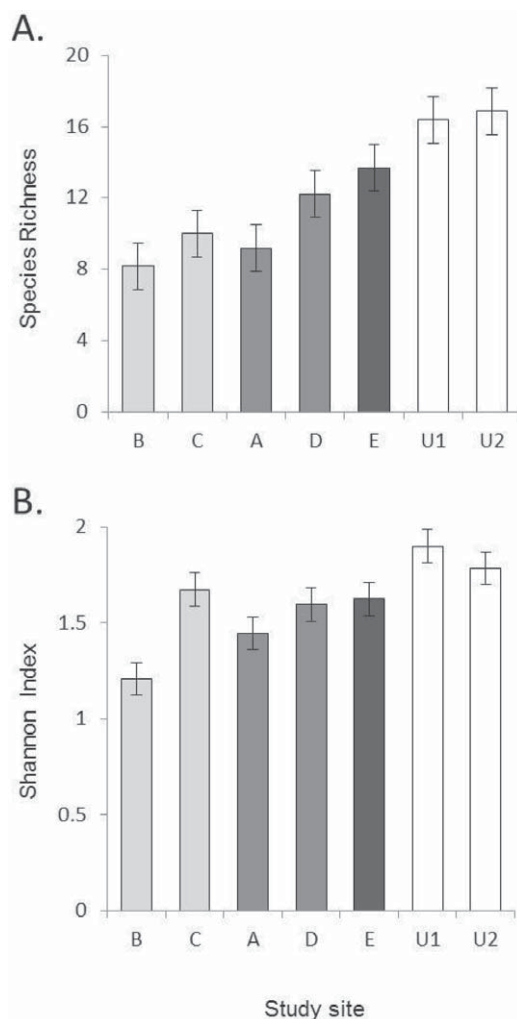

FIGURE 4. **Variations across study sites and age classes in (A) species richness and (B) the Shannon index of alpha diversity (mean ± SE). Bars differentiate the four age classes and study sites: 10 years (light gray), 20 years (medium gray), 250 years (dark gray), undisturbed (white).**

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TABLE 2

Indicator species associated with one age class.

Age class	Indicator species	IV	*p*-value	Obs. in class	Total obs.	Mean %C
10	*Poa arctica* ssp. *arctica*	41	0.001	22	80	8.8
	Trisetum spicatum	24.5	0.003	8	11	3.4
20	*Pedicularis sudetica*	65.7	0.001	43	92	2.7
	Puccinellia arctica	55.8	0.001	21	22	2.9
	Artemisia alaskana	51.6	0.001	18	20	6.1
	Parnassia kotzebuei	45.6	0.001	16	21	1
	Castilleja pallida	44.5	0.001	18	46	3.1
	Lomatogonium rotatum	42.2	0.001	14	19	1
	Oxytropis deflexa	36.4	0.001	11	31	3.9
	Potentilla nivea	32.3	0.001	7	7	0.5
	Achillea millefolium	27	0.001	5	6	1
	Oxytropis campestris	22.1	0.002	6	7	0.6
	Silene involucrata	19.7	0.006	3	4	0.6
	Bupleurum americanum	17.3	0.014	2	2	0.8
250	*Astragalus umbellatus*	78	0.001	176	224	4.1
	Astragalus alpinus	73.6	0.001	132	132	6.4
	Oxytropis maydelliana	66.4	0.001	111	112	2.7
	Pedicularis langsdorfii	54.7	0.001	85	102	1.2
	Myosotis alpestris	42	0.001	57	70	1.1
	Artemisia norvegica	24	0.003	14	14	3.1
U	*Dryas integrifolia*	92	0.001	138	253	10.6
	Carex consimilis	88	0.001	121	182	9.6
	Eriophorum vaginatum	79.8	0.001	92	95	24.2
	Saxifraga nelsoniana	70.8	0.001	90	118	1
	Saussurea angustfolia	70.4	0.001	87	112	1
	Pyrola grandiflora	59.2	0.001	54	59	1.6
	Cassiope tetragona	58.3	0.001	49	49	7.4
	Pedicularis lanata	53.1	0.001	52	70	0.5
	Senecio atropurpureas	50.3	0.001	39	45	0.3
	Lupinus arctica	49.2	0.001	55	65	3
	Lagotis glauca	47.8	0.001	35	39	0.9
	Polygonum plumosa	47.1	0.001	47	78	1.2
	Sagina nivalis	43.3	0.001	28	29	0.6
	Papaver radicatum	43.2	0.001	30	31	0.3
	Luzula confusa	40.1	0.001	37	46	0.4
	Cardamine digitata	30.4	0.001	14	15	0.3
	Salix phlebophylla	27.1	0.002	15	19	1.6
	Vaccinium ulginosum	20.4	0.006	6	6	3.3

Notes: IV = indicator value significant to >0.1 × 10^{-2}; Obs. in class = # of observations in each age class; Total obs. = total # of observations; Mean %C = total mean percent cover within age class.

TABLE 3

Indicator species associated with more than one age class.

Age class	Indicator species	IV	*p*-value	Obs. in class	Total obs.	Mean %C
10 and 20	*Alopecurus alpinus*	89.8	0.001	155	201	17.1
10 and 250	*Matricaria ambigua*	82.5	0.001	130	130	6.3
	Pedicularis verticillata	56.5	0.001	67	101	2.1
	Cochlearia officinalis	53.7	0.001	55	55	2.3
	Artemisia tilesii	48.8	0.001	48	77	7.8
	Castilleja elegans	33.1	0.001	22	27	2.4
	Draba cana	20.8	0.012	9	13	0.4
20 and 250	*Senecio yukonensis*	21.2	0.015	14	14	0.5
20 and U	*Salix glauca*	30.2	0.001	20	24	7.6
250 and U	*Salix reticulata*	79.2	0.001	248	250	8
	Luzula arctica	74.9	0.001	222	225	1.5
	Polygonum viviparum	70	0.001	198	200	0.6
	Petasites frigidus	62.2	0.001	150	150	4
	Salix pulchra	54.7	0.001	116	116	11.8
	Pedicularis capitata	53.7	0.001	130	131	1.4
	Equisetum arvense	42.4	0.001	72	73	1.2
	Parrya nudicaulis	40.1	0.001	69	75	1
	Salix richardsonii	38	0.001	56	56	6.8
	Valeriana capitata	34.4	0.001	46	46	1.3
	Hierchloe alpina	24.3	0.014	23	23	2.1
	Vaccinium vitis-ideae	23.8	0.023	22	22	4.4
10, 20, 250	*Salix arctica*	89.7	0.001	368	445	20.6
	Aconitum delphinifolium	32.5	0.004	46	46	1.1
	Festuca baffinensis	23.5	0.034	24	24	1.2

Notes: IV = indicator value significant to $>0.1 \times 10^{-2}$; Obs. in class = # of observations in each age class group; Total obs. = total # of observations; Mean %C = total mean percent cover within age classes.

tundra, showing acidification with time since disturbance (Fig. 6). Both mean organic matter content and mean moisture content increase over the time series.

Discussion

COMMUNITY COMPOSITION THROUGH TIME

A chronosequence of vegetation patterns were observed at stabilized slumps in this study and at active slumps in previous research in 2009 (Cray, 2010). At active retrogressive thaw slumps, three broad zones are observed: First, the zone of liquefaction, which is actively changing, is typically located directly in front of the slump headwall, and while a slump is active it is an area of standing water and saturated mud. Beyond this zone of liquefied sediment is a compaction zone. This area is usually 1 to 2 years old and considerably drier. The soil surface is often desiccated and incised with runoff channels draining the liquefaction zone. Although the surface of this zone appears dry and stable, viscous and plastic mud underlies a thick crust. Finally, the remainder of

the slump floor is characterized by a zone of transient stability. By far the driest, this is an area of significant dewatering, and runoff can cut meter-deep channels into the dry sediment. Throughout the summer season, the boundary between the liquefaction, compaction, and transient zones changes based on factors such as insolation, rainfall, and the ice content (and rate of melt) of the slump headwall. Despite this transience, grasses, mosses, and forbs actively colonize the mosaic of liquid mud lobes, cracked earth, and standing water pools within these zones (Cray, 2010). Plants that colonize both the liquefaction and compaction zones of an active thaw slump include *Senecio congestus*, *Bryum* sp. moss, and grasses, most notably *Arctagrostis latifolia* (Lambert 1972, 1976; Smith et al., 1989; Cray, 2010; Sloan and Pollard, 2012). *S. congestus* is found on waterlogged mineral substrates and has been noted as a prominent first colonizer of tundra disturbances, such as eroding silty outwash surfaces on Alaska's North Slope (Hok, 1969), in Inuvik (Hernandez, 1973), on Garry Island (Lambert, 1976), and on Herschel Island (Smith et al., 1989). Whereas grasses immediately establish in the moist cracks of an active thaw slump floor (Cray, 2010) and persist within this foothold, *S. congestus* disap-
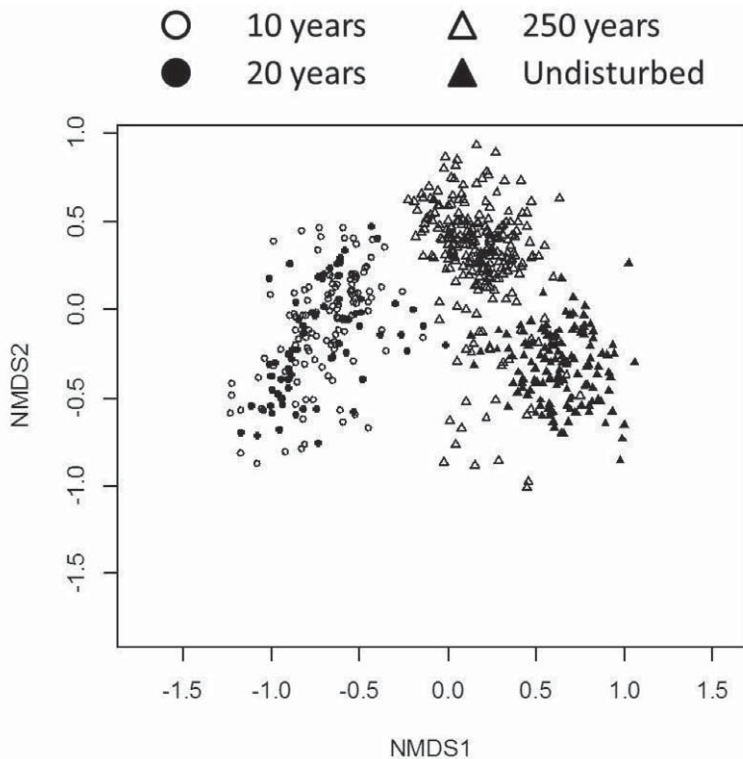
FIGURE 5. Distribution of quadrats of vegetation cover plotted on the first and second axes of a three-dimensional nonmetric multidimensional scaling (NMDS) ordination. The NMDS ordination produces a solution with a final stress of 0.154 and a linear fit R^2 value of 0.859. Symbols indicate the age class of each site: 10 years (open circles), 20 years (closed circles), to 250 years (open triangles) and undisturbed sites (closed triangles).

pears after the stabilization of the slump and was not recorded in either the 10 or 20 year old stabilized sites. This is likely because stabilization of the slump headwall induces a physically significant change in the hydrology of the foot slope as the meltwater supply is terminated, altering soil moisture conditions (Lambert, 1972; Bartleman et al., 2001). Indeed, *S. congestus* was most common in the liquefaction zone of the slump floor and was observed progressively less into the compaction and transient zones (Cray, 2010). Stabilization of a slump headwall also changes the seasonal pattern of water availability for plants—as the slump floor dries out, snowmelt becomes the main source of water. Given that no *S. congestus* individuals were observed in any study site, it is likely that this process takes fewer than 10 years after the stabilization of the thaw slump headwall.

Once a retrogressive thaw slump is stabilized, the liquefaction and compaction zones disappear. Within a few years, the initial slump floor vegetation community shifts to include other grasses such as *Poa arctica*, *Puccinellia* spp., and *Alopecurus alpinus*, all of which were recorded at the 10 and/or 20 year old stabilized sites. Two species of grass were associated exclusively with the 10 year stabilized slump age class: *Poa arctica* ssp. *arctica* and *Trisetum spicatum*. Other grasses and recognized disturbance-colonizing species of the Western Arctic have high indicator value for the 20 year class or the 10 and 20 classes, including *Puccinellia arctica*, *Artemisia alaskana*, *Matricaria ambigua*, *Cochlearia officinalis*, and *Artemisia tilesii*. These species are well-adapted to establish in the bare, compacted soils of a stabilized thaw slump floor. *M. ambigua*, *P. arctica*, *C. officinalis*, and *A. tilesii*, in particular, are known colonizers of freshly exposed mineral soils elsewhere in northwestern Canada and neighboring Alaska (Lambert, 1972; Gill, 1973; Hernandez, 1973; Billings and Peterson, 1980). Smith et al. (1989) consider these species typical of an early successional

stage maintained by the frequent deposition of fine-grained sediment, with flora originating from wind-borne propagules of typical pioneer species (e.g., *Matricaria* spp.), and strongly nitrophilous grasses that thrive on nutrients released from melted headwall material (e.g., *A. alpinus*), in addition to remnants of mature vegetation (e.g., *S. arctica*) that have sloughed off the adjacent terrain and headwall.

Plants colonizing the bare slump floor may either sprout from seeds newly dispersed on to the soil, or they may have survived the disturbance as adult plants or rhizome fragments rooted in surviving vegetation islands transported from the slump headwall (Forbes et al., 2001; Cray, 2010). In most cases, however, the only surviving species recorded on vegetation islands in this study was *Salix arctica*. *Salix* spp. are rapidly growing deciduous shrubs that produce large amounts of seed, often with high viability, and are common in disturbed habitats (Forbes and Jefferies, 1999). This suggests that its presence at the 10 and 20 year old sites is due not only to its capacity to produce copious amounts of seeds, but also to its ability to survive changing soil moisture conditions and re-grow from half-buried adult plants. Certain grasses, the other main colonizer of the 10 and 20 year age classes, are well adapted to the bare, compacted soils of a stabilized thaw slump floor. After stabilization, the dry, fine-grained mud of the slump floor is very dense, and plants root in the moist cracks between hard blocks of bare soil. Compacted soils may limit horizontal and lateral root penetration so that only a few rhizomatous grasses, such as *Alopecurus alpinus* and *Poa* spp. can establish (Forbes et al., 2001). Similarly, although *Arctagrostis latifolia* seedlings remain small in the first year of establishment from seed, they grow rapidly the following season and produce large shoot systems and large and deep penetrating root systems in the second year and thereafter (Bliss and Wein, 1972).
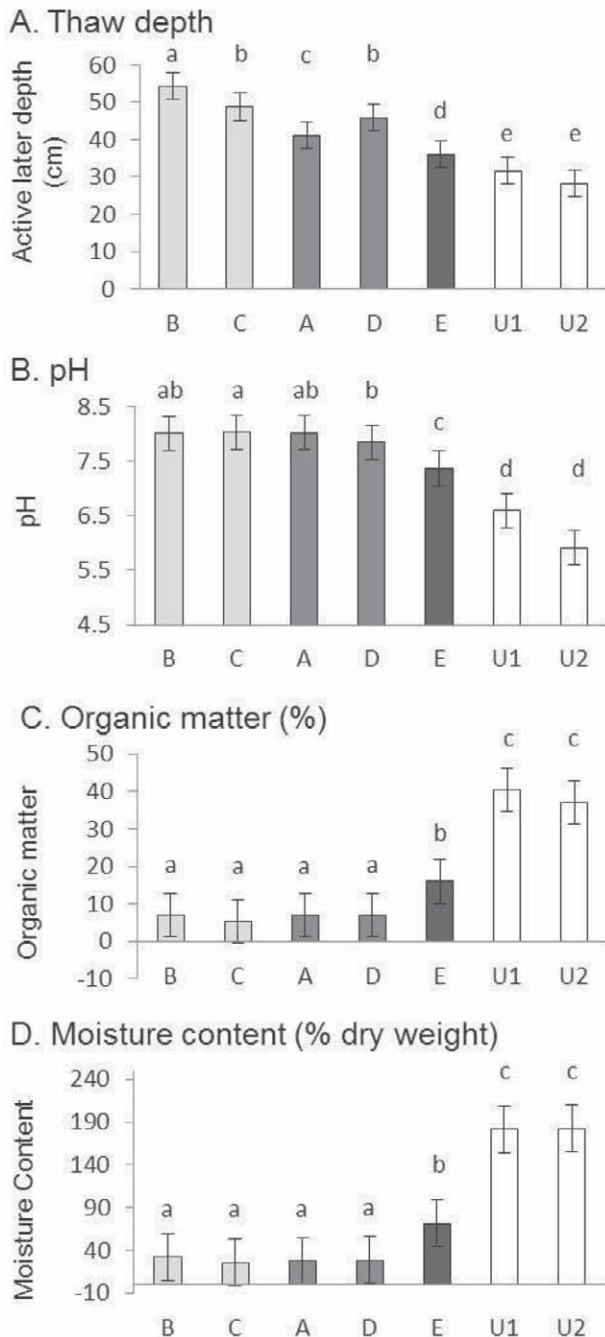
A. Thaw depth

B. pH

C. Organic matter (%)

D. Moisture content (% dry weight)

FIGURE 6. Variation across sites (mean ± SE) in soil characteristics: (A) thaw depth; (B) pH; (C) organic matter content (%); (D) gravimetric moisture content (% dry weight). Bars differentiate the four age classes: 10 years (light gray), 20 years (medium gray), 250 years (dark gray), undisturbed (white). Lower case letters denote the Kruskall-Wallis grouping for each soil characteristic, where shared and overlapping letters denote site values that are not significantly different.

After approximately 250 years of stabilization, site E was considerably more species-rich and diverse than younger age classes, and bare ground was almost entirely absent. The species richness of site E was lower than the undisturbed class, however. This is not surprising, given that the altered physical and chemical soil properties (e.g., pH, moisture, organic matter, active layer, nutri-

ent availability, ground thermal regime) that persist in stable thaw slumps suggest that the effects of disturbance endure for decades to centuries and that vegetation is still developing (Lantz et al., 2009; Sloan and Pollard, 2012). The hummocky microtopography of tussock tundra reflects the interaction between complex geomorphic processes like frost heave, vegetation, and time. Although the length of time needed to form the tussock tundra topography in this setting is not known, it is clearly greater than the approximately 250 years that site E has been stabilized. In the case of thaw slump scars specifically, the residual concave morphology resultant from slumping can likely be sustained for centuries, and hence, elevated snow accumulation (which inhibits ground heat loss and delays freezeback compared to the undisturbed tundra) and distinct abiotic conditions also persist (Lantz et al., 2009).

The dominant species in the 250 year age class were the willows *Salix arctica*, *Salix pulchra*, *Salix reticulata*, and *Astragalus alpinus*. It has been suggested that *S. arctica* is well adapted to areas with drier, older terrain due to its high below- to aboveground biomass ratio (Jones and Henry, 2003). In addition, ectomycorrhizal symbiosis facilitates nutrient transfer in this species (Jones and Henry, 2003; Cripps and Eddington, 2005). Species with high indicator values in the 250 year age class include *Astragalus umbellatus*, *A. alpinus*, *Oxytropis maydelliana*, and *Pedicularis langsdorfii*. Being legumes, the *Astragalus* and *Oxytropis* species may have an advantage in this environment as pioneer herbs that fix nitrogen are known to be common in disturbed habitats in the Low Arctic (Forbes and Jefferies, 1999). Gillett et al. (1999 onwards) described *A. alpinus* as a phenotypically plastic species that is able to occupy a variety of habitats, but noted that it occurs most commonly on dry soils with low organic content and rarely on poorly drained surfaces. It is not surprising then that *A. alpinus* is indicative of the 250 year age class as opposed to the undisturbed age class as the 250 year age class has lower organic matter and better drainage. Similarly, *P. langsdorfii* seems to prefer sloped, imperfectly drained substrates with a low organic content and a sandy or silty soil (Gillett et al., 1999 onwards), which aptly describes the vegetation community characterizing the 250 year age class.

Conclusions

The impact of disturbance on arctic vegetation communities is likely to increase as the Arctic warms further and the frequency of thermokarst increases (French, 1974; Lantz et al., 2009). With an increasing number of retrogressive thaw slumps in the Western Arctic, we can expect to see an increase in low-diversity, grass-dominated vegetation communities in the short-term, both during the active and recently stable stages of a thaw slump. Even after a thaw slump has been stable for centuries, the effect of disturbance on vegetation persists. The results of this research suggest that even after approximately 250 years, the soil and vegetation community characteristics of a disturbed area are still very distinct from neighboring undisturbed tundra, and certain species, most notably *Eriophorum vaginatum*, do not reoccur in this timeframe. The difference between the conditions observed in the 250-year-old stabilized thaw slump compared to the undisturbed tundra suggests that the effects of disturbance will persist for centuries to come. The combination of expected climate change influence on community structure together with the length of time it takes for disturbed area to recover suggests that areas of ice-rich permafrost prone to thermokarst are undergoing a restructuring of vegetating patterns that will have long-term consequences. Logically, where disturbance causes long-term alterations of ground thermal regime, pH, slope, and drainage, changes in plant

community composition may be irreversible. This has important implications for the resiliency of polar ecosystems, as an increase in the number of retrogressive thaw slumps and the area they impact will change the tundra landscape, and plant community types occurring exclusively on undisturbed tundra will be replaced with those characteristic of disturbance.

Acknowledgments

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APPENDIX

TABLE A1

Total species percent frequency (%F), average percent cover (%C), and standard error of percent cover (SE %C) for each study site.

	B-10 (n=100)			C-10 (n=24)			A-20 (n=44)			D-20 (n=23)			E-250 (n=244)			U1 (n=72)			U2 (n=72)		
	%F	%C	SE %C	%F	%C	SE %C	%F	%C	SE %C	%F	%C	SE %C	%F	%C	SE %C	%F	%C	SE %C	%F	%C	SE %C
Bare ground	1	19	2.54	1	24	4.09	1	45	4.45	1	15	4.94	—	1	0.32	—	6	4.64	—	2	1.13
Fungi (fruiting body)													—	1		—	+				
Lichen	—	1	0.28				—	+	0.05	—	1	0.48	1	2	0.15	1	2	0.18	1	1	0.10
Litter	1	21	1.88	1	17	2.89	1	20	3.98	1	34	3.68	2	23	1.04	1	34	1.93	1	29	1.60
Moss	1	10	1.05	1	12	2.16	1	6	1.92	1	10	1.26	2	19	1.15	1	4	0.33	1	5	0.55
Achillea millefolium ssp. borealis							—	1	0.62				—	1							
Aconitum delphiniifolium				—	2	0.46				—	3		—	1	0.09						
Alopecurus alpinus	1	21	2.15	1	8	2.86	1	11	1.87	1	5	1.35	—	1	0.23				—	+	0.05
Androsace chamejasme										—	1										
Antennaria monocephala ssp. angustata																—	+	0.02			
Arctagrostis latifolia	1	18	2.40	1	8	3.43				1	11	3.19	1	3	0.42	1	4	0.62	1	4	0.57
Arctostaphylos alpina																			—	2	0.60
Artemisia alaskana	—	1								1	5	1.50	—	2							
Artemisia norvegica													—	3	0.76						
Artemisia tilesii	—	3	0.94	1	12	2.51	—	2	0.38	—	5	1.00	—	2	0.43						
Astragalus alpinus													1	6	0.78						
Astragalus umbellatus							—	+		—	1		1	4	0.32	—	1	0.21	1	2	0.34
Bupleurum americanum							—	1	0.25												
Cardamine digitata										—	+					—	+	0.10	—	+	0.07
Cardamine pratensis													—	+	0.10	—	+				
Carex consimilis	—	1	0.17							—	1		—	3	0.61	1	10	1.37	1	9	1.12
Cassiope tetragona ssp. tetragona																—	6	1.36	—	9	2.01
Castilleja caudata	—	1	0.30										—	2	0.37				—	2	
Castilleja elegans	—	2	0.34							—	5	3.00	—	1	0.12						

TABLE A1
Continued

Species	B-10 (n = 100)			C-10 (n = 24)			A-20 (n = 44)			D-20 (n = 23)			E-250 (n = 244)			U1 (n = 72)			U2 (n = 72)		
	%F	%C	SE %C	%F	%C	SE %C	%F	%C	SE %C	%F	%C	SE %C	%F	%C	SE %C	%F	%C	SE %C	%F	%C	SE %C
Castilleja pallida	—	2	0.48	—	3	1.01	—	1	0.21	1	4	0.77	—	1	0.33						
Cerastium beeringianum	—	1	0.33				—	2		—	+		—	+		—	4				
Cochlearia officinalis	—	3	0.69	—	1	0.34	1	1	0.33												
Conioselinium cnidiifolium							—	+													
Descurainia sophioides	—	1																			
Draba cana	—	1		—	+	0.13				—	+	0.09	—	+		—	+	0.07			
Draba glabella													—	+	0.08						
Draba juvenalis																—	+	0.15	—	+	0.00
Draba stenoloba				—	1	0.44							—	+	0.13						
Dryas crenulata													—	1							
Dryas integrifolia	—	3	1.22	—	+					—	2		—	3	0.30	1	8	0.99	1	11	1.38
Epilobium angustifolium	—	1																			
Equisetum arvense				—	2								—	1	0.14	—	2	0.43	—	+	0.27
Eriophorum angustifolium																			—	13	
Eriophorum vaginatum										—	2		—	5	3.50	1	24	2.60	—	22	2.57
Festuca baffinensis	—	2	1.55							—	2	0.58	—	1	0.10						
Hierchloe alpina ssp. alpina													—	4	0.72	—	+	0.06			
Kobresia myosuroides																			—	5	1.25
Lagotis glauca							—	1					—	1		—	1	0.07	—	1	0.16
Lloydia serotina				—	+																
Lomatogonium rotatum ssp. rotatum				—	1	0.32	—	1	0.21	—	2	1.04									
Lupinus arcticus	1	6	0.77	1	12	3.56	1	3	0.43				—	16	5.23	—	1	0.12	1	3	0.98
Luzula arctica ssp. latifolia										—	1	0.17	1	2	0.17	1	1	0.08	1	2	0.35
Luzula confusa													—	2	0.57	—	+	0.17	—	+	0.04
Matricaria ambigua										—	4	1.07									
Minuartia arctica	—	1	0.25										—	2	1.95						
Myosotis alpestris				—	1	0.10				—	1	0.35	—	1	0.14				—	+	0.05
Orthilia secunda																			—	+	0.09

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	B-10 (n = 100)			C-10 (n = 24)			A-20 (n = 44)			D-20 (n = 23)			E-250 (n = 244)			U1 (n = 72)			U2 (n = 72)		
	%F	%C	SE %C	%F	%C	SE %C	%F	%C	SE %C	%F	%C	SE %C	%F	%C	SE %C	%F	%C	SE %C	%F	%C	SE %C
Oxytropis campestris ssp. *roaldii*							—	1	0.19				—	11							
Oxytropis deflexa					6						4	1.34	—	1	0.34						
Oxytropis maydelliana											3		1	3	0.28						
Oxytropis nigrescens										—	+		—	1					—	2	
Papaver macounii ssp. *discolor*													—	+							
Papaver radicatum ssp. *polare*							—	+	0.15					2		—	+	0.05	—	+	0.09
Parnassia kotzebuei				—	1	0.39				1	1	0.42	—	+							
Parrya nudicaulis	—	1		—	1	0.12							—	1	0.27	—	1	0.09	—	1	0.22
Pedicularis capitata										—	9		—	2	0.31	—	1	0.12	—	1	0.09
Pedicularis lanata				—	2					—	+		—	1	0.06	—	+	0.05	—	1	0.07
Pedicularis langsdorfii	—	2					—	1	0.35				—	1	0.14	—	+	0.15	—	+	0.04
Pedicularis sudetica	—	3	0.56				1	3	0.36	—	2	0.41	—	2	0.33						
Pedicularis verticillata	—	2	0.29	—	2	0.88	—	1	0.36	—	3	0.54	—	1	0.15				—	1	0.06
Petasites frigidus													—	3	0.51	—	6	2.84	—	8	1.48
Poa alpina													—	+	0.04	—	+				
Poa arctica ssp. *arctica*	—	9	2.02							—	1	0.45	—	+	0.06	—	+	0.03	—	+	0.04
Poa pratensis ssp. *alpigena*				—	16	6.36							—	1	0.08	—	+	0.10			
Polygonum plumosa	—	3											—	1	0.22	—	2	0.36	—	1	0.12
Polygonum viviparum							—	1		—	1		—	1	0.07	1	+	0.04	—	1	0.06
Polymonium boreale										—	2		—	1	0.44						
Potentilla nivea							—	1	0.10												
Potentilla uniflora													—	1							
Puccinellia arctica							—	3	0.66										—	1	
Pyrola grandiflora													—	2	0.80	—	2	0.23	—	1	0.36
Ranunculus turneri	—	1																			
Rumex arcticus	—	1																	—	2	
Sagina nivalis													—	1		—	+	0.11	—	1	0.12
Salix arctica	1	10	1.18	1	6	1.38	1	7	1.66	1	14	2.74	1	27	1.13	—	4	0.73	1	4	0.33

TABLE A1
Continued

	B-10 (n = 100)			C-10 (n = 24)			A-20 (n = 44)			D-20 (n = 23)			E-250 (n = 244)			U1 (n = 72)			U2 (n = 72)		
	%F	%C	SE %C	%F	%C	SE %C	%F	%C	SE %C	%F	%C	SE %C	%F	%C	SE %C	%F	%C	SE %C	%F	%C	SE %C
Salix fuscesens													—	5							
Salix glauca				—	2	1.00				—	4	2.37	—	2	0.50	—	7	1.85			
Salix niphoclada													—	16	11.50						
Salix phlebophylla										—	2		—	3	0.88	1	2	0.25	—	1	
Salix pulchra													1	15	2.01	1	6	0.85	—	6	2.17
Salix reticulata	—	11								—	9		1	8	1.02	1	8	1.25	1	7	0.51
Salix richardsonii													—	5	1.44	—	10	2.57	—	12	3.55
Salix rotundifolia ssp. *rotundifolia*				—									—	20	9.41						
Saussurea angustfolia										—	+		—	1	0.23	1	1	0.07	1	1	0.20
Saxifraga cernua																			—	3	
Saxifraga hieracifolia										—	1		—	1	0.11				—	1	0.25
Saxifraga hirculus													—	1					—	1	0.95
Saxifraga nelsoniana										—	1	0.85	—	1	0.15	1	1	0.05	1	1	0.13
Senecio atropurpureas ssp. *frigidus*													—	+	0.07	—	+	0.02	—	+	0.03
Senecio kjellmanii													—	1							
Senecio lugens													—	+	0.18						
Senecio yukonensis							—	1		—	2		—	+	0.07						
Silene acaulis																—	1	0.25			
Silene involucrata							—	1		—	+	0.10									
Stellaria longipes	1		0.28	—	1	0.35	—	1	0.61	1	3	0.94	1	+	0.05	1	+	0.06	—	+	0.15
Taraxacum ceratophorum							—	1													
Taraxacum lyratum													—	2							
Trisetum spicatum				—	3	0.83	—	+	0.13												
Vaccinium ulginosum																—	5	3.00	—	3	1.17
Vaccinium vitis-ideae													—	3	0.53	—	9	6.51	—	2	0.25
Valeriana capitata													—	2	0.45	—	1	0.33	—	1	0.06

n, number of 1 × 1m quadrats.

%F, percent frequency of occurrence in *n* quadrats, each 1 × 1m; —, a value less than 1%.

%C, average percent cover in *n* quadrats; +, a value less than 1%.

SE %C, standard error of percent cover values; SE less than 0.005 are not reported.

F, number of observations.

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