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Succession in tundra landscapes and its implications for polar restoration efforts: case study of Herschel Island, YT, Canada

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ABSTRACT
This research investigates natural revegetation patterns following permafrost disturbance by retrogressive thaw slumps on Herschel Island, YT. Seven sites were chosen, representing undisturbed areas in addition to 250, 20, and 10 year old stabilized thaw slumps. Species diversity and percent cover of different plant functional groups are presented. Results indicate that distinct vegetation assemblages are associated with each age class, and that changes persist for centuries. Using the natural successional plant communities presented here as a guideline, ecological restoration methods using propagule addition which targets effective natural initial colonizers are suggested. If our goal is to control erosion, create habitat, and enhance freezeback in these landscapes at an accelerated pace, this type of restoration intervention may be necessary and is thus a promising direction for future research.

RÉSUMÉ
Cette recherche examine les modèles de revégétalisation naturelle à la suite de perturbations du pergélisol par glissement régressif dû au dégel sur l'île Herschel, YT. Sept sites représentant des zones non perturbées, ainsi que des zones de glissements dus au dégel stabilisées de 250, 20, et 10 ans, ont été choisis pour l'étude. L'abondance proportionnelle de la diversité des espèces et le pourcentage de couverture de plusieurs groupes fonctionnels de plantes sont présentés. Les résultats indiquent que des assemblages de végétation distincts sont associés à chaque classe d'âge et que les changements persistent pendant des siècles. En utilisant les communautés végétales naturelles et successives présentées ici en tant que ligne directrice, les méthodes de restauration écologique qui utilisent l'ajout de propagules, qui ont pour cible les premiers colonisateurs naturels efficaces, sont suggérées. Si l'objectif est de lutter contre l'érosion, de créer des habitats, et d'améliorer le regel dans ces paysages, et ce, à un rythme accéléré, ce type d'intervention de restauration peut être nécessaire et représente une voie prometteuse pour des recherches futures.

1 INTRODUCTION

The Arctic is experiencing considerable geomorphological and ecological changes due to acute and rapid warming in air and permafrost temperatures (ACIA 2005; Anisimov et al. 2007; IPCC 2007). Excluding glaciers and ice sheets, permafrost (perennially frozen ground) underlies 23.9% of the northern hemisphere (Zhang et al. 2008). Since permafrost is a thermal condition, its occurrence reflects the complex interaction between climate, ground surface, and subsurface thermal properties. Furthermore, its temperature, distribution, and thickness respond to natural environmental changes and anthropogenic disturbances that disrupt ground thermal regimes. Thermokarst is the process by which characteristic landforms result from the thawing of ice-rich permafrost and or melting of massive ice (van Everdingen 1998). Naturally occurring thermokarst represents one of the most dynamic processes modifying arctic and subarctic landscapes (French 1974).

With future warming and resource extraction activities, the presence and areal extent of thaw subsidence in the circumpolar Arctic are predicted to increase. In the context of restoration, these rapidly and dramatically changing conditions present unique challenges for mitigating ecosystem change and developing effective restoration strategies for environmentally sensitive areas and derelict lands. While the need for restoration applies to any permafrost environment, the sub-Arctic and low Arctic are particularly vulnerable as the permafrost in this zone is already close to destabilization temperatures and small changes in temperature will likely support more rapid northerly migration of southern species (Bartleman et al. 2001). To date, restoration activities in arctic ecosystems have been limited in number and extent and have often proceeded with little consideration for long-term ecosystem impact. If we aim to actively restore disturbed arctic landscapes, we first must understand their natural successional patterns and use that knowledge to guide restoration strategies. The aim of this paper is to establish the general pattern of community succession following large-scale thermokarst disturbance on Herschel Island and suggest options for directed restoration.

1.1 Study Site

This research investigated natural revegetation patterns following permafrost and terrain disturbance by retrogressive thaw slumps on Herschel Island (69°36′N; 139°04′W), Yukon, Canada (Figure 1). The vegetation of Herschel Island consists largely of tussock tundra, characterized by a thick organic layer and the presence of *Eriophorum vaginatum* (Kennedy et al. 2001; Myers-Smith et al. 2011), which is representative of the long-term mature vegetation on most sites where it is established (Smith et al. 1989).

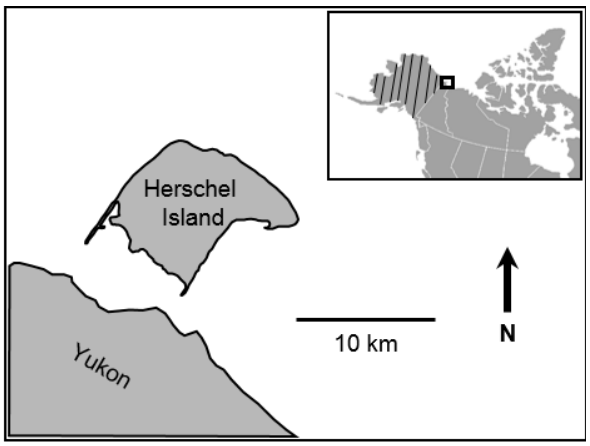

Figure 1. Location map of Herschel Island in the southern Beaufort Sea, Yukon, Canada

Ground ice is widespread on Herschel Island; up to 70% of the upper 10 to 15 m of the permafrost is ground ice (Pollard 1990). As the island contains no bedrock, the ice-rich sediments are easily eroded following any geomorphic disturbance. The Island is therefore subject to high rates of surface and coastal erosion, as evidenced by the more than 100 active retrogressive thaw slumps on the island (Lantuit and Pollard 2008). This makes the site an ideal location to study the natural revegetation processes following thaw slump stabilization.

Retrogressive thaw slumps are a particularly dynamic type of thaw subsidence in permafrost environments and are highly active and influential agents of landscape modification in these ecosystems (French 1996). In the Western Canadian Arctic, retrogressive thaw slumps are numerous and individual disturbances may be several hectares in area (Figure 2). The total number, growth rates, and areal extent of retrogressive thaw slumps have increased significantly over the past 50 years (Lantuit and Pollard 2008; Lantz and Kokelj 2008; Lantz et al. 2009). With these increases comes the potential for disturbance regimes to increase the intensity and extent of warming temperature effects on vegetation. These changes can, in turn, create positive warming feedbacks as vegetation affects material and energy exchange, provides structure and energy for other trophic levels, and affects soil erosion and geomorphic processes. Retrogressive thaw slumps are initiated when ice-rich soil is exposed by disturbance and generally become stabilized within 30 to 50 summers, although they tend to go through cycles of activity and may reactivate repeatedly (Burn and Friele 1989; French 1996).

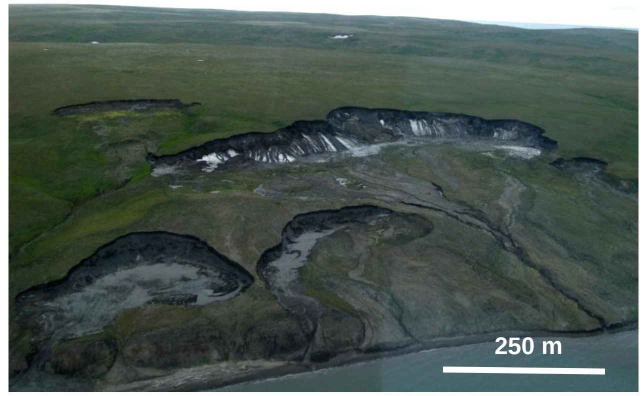

Figure 2. Active retrogressive thaw slump complex on Herschel Island illustrating the scale of disturbance

2 METHODOLOGY

Seven study sites were selected for investigation representing four age classes: 10 year old, 20 year old, and 250 year old stabilized thaw slumps, as well as undisturbed areas. Fieldwork was conducted over two field seasons in 2010 and 2011. At each site, 1% of the total area was sampled using 1x1m vegetation plots for a total of 579 plots. 80% of the plots were distributed along a transect perpendicular to the stabilized slump headwall; the remaining 20% of plots were distributed randomly using ArcGIS. At each sample plot, vegetation data collected included the percent cover of each vascular plant species and ground cover class, and species nomenclature followed Cody (2000). Field methods are described in greater detail in Cray and Pollard (2015). Vegetation data from stabilizing slumps is taken from Cray (2010).

Species diversity was calculated using the Shannon Index and the Simpson Index of diversity (α-diversity). The Simpson Index takes into consideration both the number of species present and the relative abundance of each species, and thus expresses the probability of two randomly selected individuals belonging to different species (Brower et al. 1997). The Shannon Index expresses the average uncertainty in predicting which species a randomly selected organism will belong to (Nagendra 2002).

3 RESULTS

3.1 Community Diversity

The most diverse age class by every alpha diversity measure calculated in this study is the Undisturbed class, followed by the 250 year old stabilized site, and then the 10 and 20 year stabilized sites depending on the metric assessed (Table 1). Mean species richness follows the same pattern; it is greatest at 16.6 in the Undisturbed age class, followed by 13.7 at the 250 year site, and 9.2 and 8.5 at the 20 and 10 year old age classes, respectively. There is also a positive association between diversity (as measured by both the Simpson Index and the Shannon Index) and time since disturbance, where the average index values are highest in the undisturbed age class, followed by a decrease in the 10 year class following disturbance, a further decrease in the 20 year class, and a "recovery" increase in the 250 year stabilized class.

Table 1. Mean species richness, Simpson Index and Shannon Index value by age class

Index value	10	20	250	Undisturbed
Species richness	8.5	9.2	13.7	16.6
Simpson	0.7	0.6	0.7	0.8
Shannon	1.5	1.2	1.6	1.8

3.2 Ground cover

The ground cover distribution varies dramatically through the successional sequence (Figure 3). The percent cover of bare ground is highest in the 20 year age class, followed by the 10 year age class, and is virtually zero in the 250 year and Undisturbed classes. At ten years following slump stabilization, the cover of vascular plants is 49.6%, then decreases at 20 years to 34.2% before increasing once again at the 250 mark. Compared to the undisturbed sites, vascular plant cover remains almost 7% lower after 250 years. Litter increases over time, although 250 years following stabilization of the litter cover on the slump floor is not as high as for the undisturbed sites (24.5% versus 31.7%). Litter cover is lowest at 10 years at 20.5%, and increases at 20 years (29.3%).

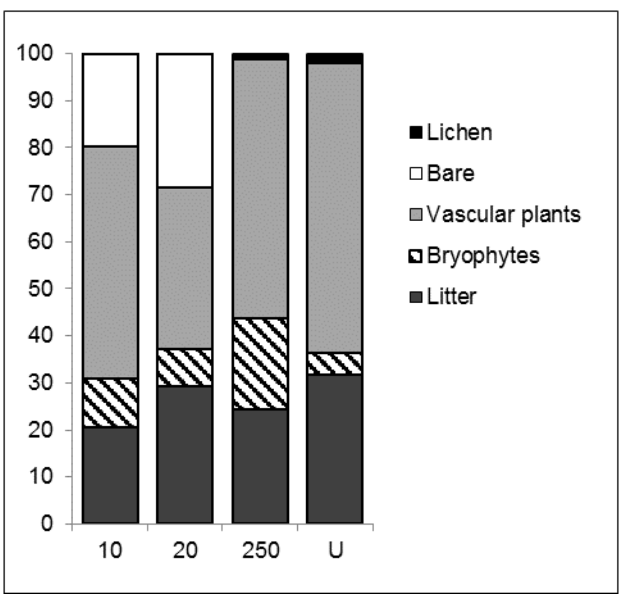

Figure 3. Proportional abundance of ground cover by age class (10, 20, 250 year old and undisturbed sites)

3.3 Vegetation Cover

A total of 101 species were observed in this study, representing 60 genera and 25 plant families. The functional group distribution varied dramatically through the successional sequence (Figures 4 and 5). Grasses dominated the 10 and 20 year age classes, whereas deciduous shrubs made up almost 50% of the 250 year class. Sedges, rushes, lichens, and evergreen shrubs occurred almost exclusively in undisturbed tundra.

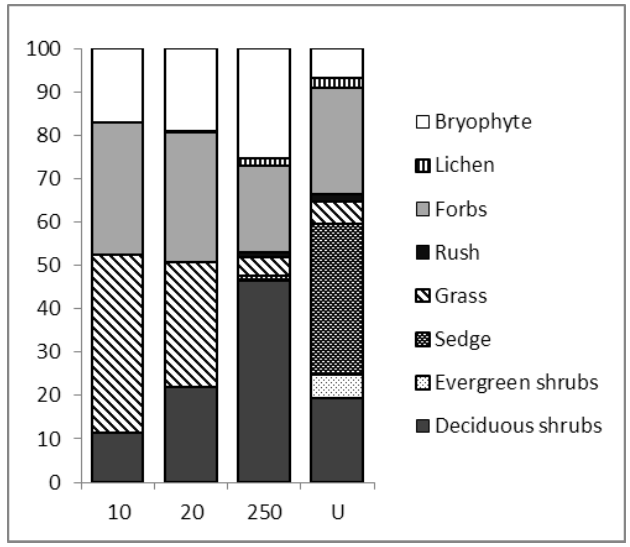

Figure 4. Variations in percent cover of different plant functional groups and cover classes across age site ages (10, 20, and 250 year old stabilized sites in addition to undisturbed sites)

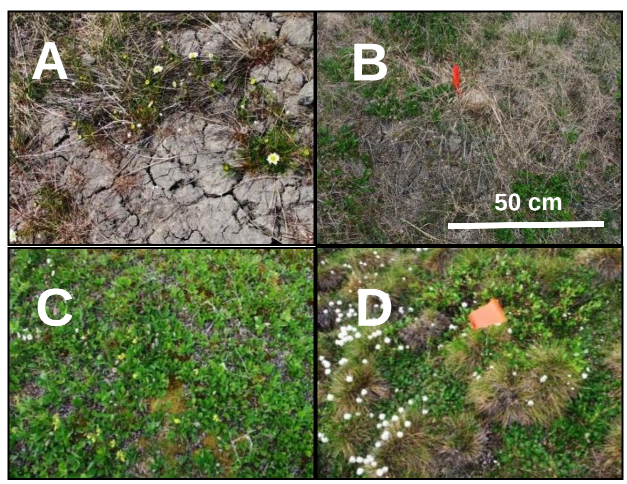

Figure 5. Vegetation colonization and coverage change significantly with time since stabilization, from grass-dominated and partly barren ground (10 years, A, 20 years, B) to low continuous vegetation (250 years, C) compared with adjacent undisturbed tussock tundra (D)

3.4 Colonizing Species

Early colonizing species with the highest percent cover in active and recently stabilized slumps include *Arctagrostis latifolia*, *Alopecurus alpinus*, *Salix arctica*, and *Matricaria ambigua* (Table 2). One species, *Senecio congestus*, was only found within active thaw slumps. Whereas the cover of *Castilleja elegans* increases slightly over time, the cover of *Pedicularis verticillata* remains stable and that of *Artemisia tilesii* peaks at 10 years.

Table 2. Commonly observed early colonizing species and their associated average percent cover (%C) recorded at stabilizing and stable retrogressive thaw slumps

Species	<10	10	20
Arctagrostis latifolia	17	16	11
Alopecurus alpinus	12	19	10
Salix arctica	7	10	10
Matricaria ambigua	4	7	4
Castilleja elegans	2	2	5
Pedicularis verticillata	2	2	2
Senecio congestus	2	-	-
Artemisia tilesii	1	10	3
Poa arctica ssp. arctica		9	1
Pedicularis sudetica		3	3
Trisetum spicatum		3	<1
Cochlearia officinalis		3	1
Achillea millefolium	1		1

4 DISCUSSION

Floristic composition is strongly related to the time since disturbance. The dominant vegetation type at retrogressive thaw slumps which have been stable between 10 and 20 years is grass, followed by forbs and bryophytes, although bare ground and litter combined cover over 40% of these sites. Interestingly, both litter and bare ground are more prevalent 20 years following stabilization than 10 years. This is due to a die-off effect resulting when individual plants which survive the initial stabilization of the thaw slump floor, typically on an unusually intact "vegetation island" clump from the headwall, dehydrate as the clump dries out and the loose organic matter is washed away. Whereas surviving islands of vegetation in the 10 year age class may still have up to 50% of their original vegetation community intact, by the 20 year mark few, if any, of these species remain alive. The partial exception to this is *Salix arctica*, which often survives the dewatering period following stabilization and colonizes *in situ* from fragments (Figure 6).

The fact that stabilized slump surfaces that are a few decades old have distinct vegetation communities has also been documented in the nearby Mackenzie Delta. Between 29 and 73 years following stabilization, thaw slumps still had significantly different species composition than controls (Lantz et al. 2009). Lantz et al. (2009) also found that plant communities on the same site type (i.e., active slump, stabilized, undisturbed) were virtually indistinguishable from one another. Certainly for this study, there was little intra-site difference observed between the two 10 year sites, the paired 20 year sites, and the undisturbed site vegetation communities. This suggests that due to the paucity of colonizing tundra species, the sequential pattern of revegetation and for Herschel Island likely holds true for other slumps in the Western Canadian and Alaskan arctic.

Clearly, the stabilized slump floor is not the ideal environment for many species which thrive in undisturbed tundra. This is not surprising, given that the pH, thaw depth, organic matter content, and gravimetric water content are significantly different between the age classes (Cray and Pollard 2015). Plants characteristic of acidic soils are often slow to establish and are dependent on the build-up of an acidic organic layer of relatively low status which may take centuries or more to develop (Forbes and Jeffries 1999; Cray 2010). However, the slump floor does provide conditions that favour the colonization of early successional species. These conditions include a comparatively warm, nutrient-rich substrate and absence of immediate competition, and at least for the first year or so, high soil moisture content.

Figure 6. Partially buried *Salix arctica,* having survived the slumping action, is a common feature of the stabilized thaw slump floor and recolonizes quickly in the early stages of succession

4.1 Active Restoration

While these results provide evidence of the natural recovery potential of disturbed tundra ecosystems, findings suggest that this process requires a substantial amount of time. While the structural attributes of the 250 year old sites sampled in this study did more closely resemble undisturbed tundra than the recently disturbed sites in terms of vegetation diversity and cover, there remained notable differences from the undisturbed sites following two and a half centuries of successional development. Without further study and access to sites characterized by even longer periods of recovery since disturbance, it is difficult to determine the future successional trajectories of these ecosystems. Under warming conditions, it remains unclear whether the community composition of these disturbed sites will ever return to that found in undisturbed tundra; how long it may take for these communities to reach any potential state is similarly uncertain.

While degraded tundra is potentially subject to on-going and undesirable ecological change, later-stage successional states are generally more resistant to further degradation. Notably, increased cover and complexity of the vegetation community is associated with a shallower active layer and decreased erosion (Lantz et al. 2009; Cray and Pollard 2015). However, given the dramatic and persistent environmental stressors of current and future global climate change and the comparatively slow process of natural recovery in these ecosystems, human-led active restoration may be a necessary and, thus far, under-exploited intervention. Given the unique conditions and limiting factors to growth in the arctic environment, propagule pressure is likely a key limiting factor in the rate and success of vegetation and recovery; by augmenting lower naturally-occurring propagule pressure and slow rates of natural ecosystem recovery, restoration may be able to better mitigate the persistent negative impacts of global climate change effects and aid in the preservation of these vulnerable ecosystems.

Despite the many potential benefits, however, only limited attention has been given to consideration and implementation of arctic restoration programs. While efforts to re-vegetate disturbed tundra using various exotic species such as Engmo timothy, Nugget Kentucky bluegrass, and Arctared creeping red fescue (ARCO 1972; Hernandez 1973; Younkin 1976; Bliss 1979) have demonstrated success in increasing individual parameters such as soil stability and ground cover, the ultimate success of these approaches in achieving states which are structurally and functionally comparable to undisturbed or naturally-recovered tundra is debatable. Despite short-term benefits, it is likely that these interventions will generate oversimplified vegetation communities with little resemblance to the natural vegetation communities which might have otherwise developed *in situ* over a greater time period. Complications from this may include inadequate support of key interspecific interactions such as habitat and food provisioning. In addition, with no suitable reference condition, the future behaviour of these no-analog systems is inherently difficult to predict. In particular, it is uncertain how isolated patches of restored but atypical and uncharacteristic vegetation will integrate with the broader natural landscape.

As an alternative to pursuing short-term restoration benefits at the expense of highly uncertain future risk, ecologically-informed restoration which takes into consideration the natural successional trajectories of recovering tundra systems may offer greater promise. Given that the natural revegetation of these degraded ecosystems appears to proceed through identifiable successional stages, it may be possible to use this understanding to assemble an appropriate long-term restoration scheme which mirrors and supplements this natural trajectory. For example, the earliest stages of restoration will likely benefit from the deliberate reseeding of effective natural initial colonizing species such as *Senecio congestusl, Arctagrostis latifolia*, *Alopecurus alpinus*, *Salix arctica*, and *Matricaria ambigua.* Based on the findings of on-going monitoring, it may be possible to then proceed to the introduction of vegetation characteristic of later successional stages (for example, *Artemisia tilesii* and *Poa arctica ssp. arctica*) on an advanced time schedule and thus accelerate the natural rate of ecosystem recovery. By introducing additional vegetation propagules through direct seeding or seedling planting, this form of active restoration may accelerate the rate of ecosystem recovery while generating a more predictable community composition over time capable of a more seamless integration into the broader natural landscape.

5 CONCLUSIONS

This study represents one of the first detailed descriptions of the successional stages of revegetation following disturbance in the western Arctic tundra environment. Results indicate that distinct vegetation assemblages are associated with each age class, and that substantial differences between undisturbed and stabilized tundra persist for centuries. This has important implications for the stability of these landscapes, as the long time scale of natural recovery limits our ability to mitigate the effects of these disturbances on the surrounding environment. While thinking about active restoration as a method of accelerating revegetation of disturbed surfaces in arctic environments is not new, relatively little work has been done to detail native species regrowth and little directed restoration has been attempted. With accelerated climate warming, we can expect the area and number of large-scale disturbances to increase, and so new research which tests methods of restoration are essential steps for future study. It is hoped that studies such as this will be helpful in addressing the knowledge gap which has likely impeded further exploration of effective restoration options in these ecosystems.

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