

Thermo-erosion gullies boost the transition from wet to mesic vegetation

Perreault, N., Lévesque, E., Fortier, D. and Lamarque, L. J.

Response to reviewers #1 and #2

We are grateful to the two reviewers for their thorough comments that improved the manuscript, which was revised following their suggestions. We particularly tried to better highlight our results and strengthen our message in the Abstract and the Discussion.

We have responded to all comments as detailed below using blue colour.

Reviewer #1

The authors strongly revised the manuscript and virtually responded to all my concerns and requests from the first submitted version. The methods, results and overall message of the study appear now clearly and I am confident this paper will significantly contribute to our better understanding of arctic ecosystem functioning and of the consequence of ongoing environmental changes.

However I still have a small problem with the presentation of the difference in polygon habitat responses to summer rainfall: the author still claim that intact and disturbed polygons responded positively to summer rainfall (reversely to mesic polygons, I guess) and justify it by no significant habitat x date interaction, both in the results (L196-197) and the discussion (L274-276). But it is a non-sense, if the no significant interaction showed something it should be the similar response among the polygon types. I clearly understand that the variability can avoid the detection of such difference apparently demonstrated in a companion paper, but the data here does not support that idea. Did the authors try within polygon type date effect analyses? If there was a difference, it should be visible in F and p values of independent tests and could be an easy way out.

Thanks you for this comment. Yes, we also tested the date effect per habitat type, and the difference was significant for each of them. We agree that the non-significant habitat x date interaction shows the similar response to rainfall among habitats, and we do not wish to over-interpret this result. We therefore tried to clarify the presentation of this result by rephrasing the sentences both in the Results and the Discussion.

Eventually, I also have some minor comments:

There still is some redundancy in the statistical results presentation between the text and figures and unnecessary specification: To me, the brackets L197, L206-206 and L232-233 (with the end of the sentence: and independently of the sampling location) can be deleted. We deleted the three brackets.

Throughout the manuscript, some items are described using various denomination and even if it was a detail, it could lead to ask why the author used different words: ‘wet’ and ‘intact’ polygons, ‘site’ and ‘polygons’.

Thanks for pointing this out. We agree that we should have been more precise by using one single word for a given meaning. We thus replaced “intact” by “wet” throughout the manuscript. As for the use of “site” and “polygon”, the 197 sites were not all polygons since some mesic habitats were polygon rims but others were in zones not clearly defined as

polygons; we thus used “polygons” only when referring to intact (and wet) or disturbed (recently or not) sites. We tried to clarify this throughout the manuscript.

Sentences L141-142 and 146-147 could be pooled for clarity.
We agree and rephrased the sentence L141-142.

L131: Add a space between gully and RN08
We made the change.

L142: ‘70 x 70 cm’ instead of ‘70 cm x 70 cm’ (same in the figure legend)
We preferred to keep “70 cm x 70 cm” because “70 x 70 cm” does not necessarily mean a cm² surface.

L231: delete one ‘;’
We made the change.

Reviewer #2

Review of the “Thermoerosion gullies boost the transition from wet to mesic vegetation” by Perreault et al.

This is my second review of the manuscript and I only have some very minor suggestions that I think will make the manuscript and its main story even stronger and more clear. The suggested references should help the authors to more clearly interpret their observations and to more effectively describe how their contribution complement and expand upon the existing literature.

L11-12: Clarify which sub-polygon feature the soil moisture and thaw depth observation was made (I assume the center of the polygon?) as the variability within a single polygon can be substantial due to presence of raised or depressed center, rims and/or troughs.
Indeed, we made the observations in the center of wet and disturbed polygons and in the representative central part of the mesic sites. We added the information in the sentence.

L16: Delete “therefore”
We made the change.

L17-18: Define/clarify “short period of time”
We clarified by adding “5 to 10 years” in brackets.

L132: Centimeters (spelling error)
We made the change.

L133: “..driven into..”
We made the change.

L125-: If I understand the authors correctly, all the authors’ measurements refer to the center of polygons. If so, it needs to be clearly stated in the paper (perhaps even in the title?) due to the large spatial variability that otherwise can be found between center, troughs and rims. I would actually encourage the authors to include “polygon centers” in the title, because of this. Especially considering recent literature that address ice wedge degradation and/or polygon

types (see Lara, Mark J., et al. "Polygonal tundra geomorphological change in response to warming alters future CO₂ and CH₄ flux on the Barrow Peninsula." *Global change biology* 21.4 (2015): 1634-1651; and also Jorgenson, M. T., et al. "Role of ground ice dynamics and ecological feedbacks in recent ice wedge degradation and stabilization." *Journal of Geophysical Research: Earth Surface* (2015)). Changes in hydrology, vegetation and carbon fluxes can be completely different in troughs than in centers with ice wedge degradation. We agree that the exact location of the measurements has to be clearly stated, and that is what we had done after the first reviews (see L128 and L132). We now added this information also in the Abstract. However, we feel that doing so in the title would change the focus of readers, and thus we have left the title as it is.

Thanks for pointing these papers out. We referred to them in the Introduction and Discussion.

L188-208: I would add the observation that soil moisture and thaw was similar (same?) between the two disturbed sites, despite the time since disturbance. Because this observation together with the clear difference in above ground biomass in figure 5 highlights a lag-time in vegetation response to the altered physical environment – a finding to be mentioned in both abstract and discussion/conclusion.

Thanks you for this comment. We added the comparison between the two types of disturbed polygons in the Results and highlighted it in both the Abstract and the Discussion.

L197-200: Awkward sentence. I think the use of the word “driven” is what makes it confusing. Please find another word/rewrite.

We replaced “driven” by “associated to”.

L207-208: Unclear sentence. Please clarify/expand. Is the location of the “)” off? We rephrased the sentence.

I think the authors can increase their emphasis in the abstract about their finding that the observed changes occurred across a relatively short time frame (<5yrs after initialization of ice wedge degradation) and also expand/highlight (in the discussion/conclusion) on the observation about their finding of a gradual vegetation transition along the time since disturbance.

Thanks for pointing this out. We highlighted the gradual and relatively rapid vegetation transition in the Abstract and Discussion.

L231: Duplication of “;”

We deleted one “;”.

L251-253: I would not describe the soil moisture (nor the thaw) to have a gradient from the young and old disturbed site –they are the same! The biomass on the other hand shows a clear gradient (see my comment earlier about a lag in vegetation response).

Thanks you for this comment. We rephrased the sentence.

L281: Delete “(see below)”

We made the change.

L282-287: This contradiction can also be explained by subsidence of the ground surface as ice rich permafrost thawed (see Shiklomanov, Nikolay I., et al. "Isotropic thaw subsidence in undisturbed permafrost landscapes." *Geophysical Research Letters* 40.24 (2013): 6356-6361.) I would recommend adding this reference as a complementary explanation to the existing

references.

I would also like to alert the authors on another relevant publication: Jorgenson, Janet C., et al. "Twenty-five year record of changes in plant cover on tundra of northeastern Alaska." *Arctic, Antarctic, and Alpine Research* 47.4 (2015): 785-806.

Thanks for pointing these papers out. We referred to them in the Discussion.

L393-403: As I mentioned earlier, I think the abstract and the conclusion can be strengthened, because in their current form, they do not provide justice to the presented results. For example, emphasize that the moisture and thaw is a relatively immediate change as they are similar between the old and young disturbed sites, while the vegetation response was slower. Also highlight the exact time scale (5 and 10 years, respectively). I would also like to see in the discussion and conclusion the authors commenting on whether the site (10 years after disturbance) is still undergoing a transition in the vegetation, ie has the vegetation at the old disturbed site yet reached an equilibrium with the hydrology and thaw regimes (which appears to have stabilized due to the similar values between the old and younger disturbed site)?

Thanks for pointing this out. As mentioned above, we better emphasized the relative short time scale and the comparison between recently and old disturbed polygons in the Abstract and the Discussion. We highlighted in the Conclusion the current hydrological and thermal regimes and vegetation state, and called for long-term monitoring of permafrost-vegetation dynamics.

Thermo-erosion gullies boost the transition from wet to mesic vegetation

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Abstract

Continuous permafrost zones with well-developed polygonal ice-wedge networks are particularly vulnerable to climate change. Thermo-mechanical erosion can initiate the development of gullies that lead to substantial drainage of adjacent wet habitats. How vegetation responds to this particular disturbance is currently unknown but has the potential to strongly disrupt function and structure of Arctic ecosystems. Focusing on three major gullies of Bylot Island, Nunavut, we aimed at estimating the effects-impacts of thermo-erosion ~~in-on~~ ~~shaping~~ plant community changes. We explored over two years the influence of environmental factors on plant species richness, abundance and biomass ~~studying in 197 sites~~ 62 low-centered wet polygons, 87 low-centered disturbed polygons and 48 mesic environment sites including 62 in intact low-centered polygons, 87 in polygons disturbed by thermo-erosion and 48 in mesic environments. Gullying decreased soil moisture by 40 % and thaw-front depth by 10 cm in the center of breached polygons within less than five years after the inception of ice wedge degradation, which has entailed-entailing a gradual yet marked vegetation shift from wet to mesic plant communities within five to ten years ~~with mesic habitat plant species such as *Arctagrostis latifolia* and *Salix arctica* replacing wet habitat dominant *Carex aquatilis* and *Dupontia fisheri*~~. This transition was accompanied by a five times decrease in graminoid above-ground biomass ~~in mesic environments~~. Soil moisture and thaw-front depth changed almost immediately following gullying initiation as they were of similar magnitude between older (> 5 years) and recently (< 5 years) disturbed polygons. In contrast, there was a lag-time in vegetation response to the altered physical environment with plant species richness and biomass differing between the two types of disturbed polygons. To date (ten years after disturbance), the stable mesic environment cover has still to be reached. Our results ~~therefore~~ illustrate that wetlands are highly vulnerable to the process of thermo-erosion, which can drive landscape transformation on a relative short period of time for High

26 | Arctic perennial plant communities (five to ten years). ~~The~~ Such succession towards mesic
27 | plant communities can have substantial consequences on the food availability for herbivores
28 | and methane emissions of Arctic ecosystems.

1 Introduction

Warming in the Arctic is occurring twice as fast as the global average (USGCRP, 2009; New et al., 2011; NOAA, 2014). Perennially frozen ground (permafrost) has consequently warmed by 2 °C over the last 20 to 30 years (Christiansen et al., 2010; Romanovsky et al., 2010), and there is now evidence of a decrease in both permafrost area extent across the northern hemisphere and permafrost thickness at the local scale (Beilman and Robinson, 2003; Payette et al., 2004; Couture and Pollard, 2007; Smith, 2011).

Permafrost is tightly associated with biophysical components such as air temperatures, soil conditions, surface water, groundwater, snow cover and vegetation (Jorgenson et al., 2010; Sjöberg, 2015). Permafrost impedes water to drain to deeper soil layers and maintains a perched water table and saturated soils which favors the existence of wetlands (Woo, 2012; Natali et al., 2015). Permafrost degradation that would increase subsurface drainage and reduce the extent of lakes and wetlands at high latitudes (Avis et al., 2011; Jorgenson et al., 2013; Beck et al., 2015) would thus have major consequences on ecosystem structure and function (Collins et al., 2013; Jorgenson et al., 2013). It would also strongly influence variations of active layer depths (Wright et al., 2009; Shiklomanov et al., 2010; Gangodagamage et al., 2014), as illustrated by long-term monitoring sites throughout the circumpolar North (Tarnocai et al., 2004; Nelson et al., 2008; Smith et al., 2009; Shiklomanov et al., 2010).

Several forms of ground and massive ice can be found within permafrost (Rowland et al., 2010), especially ice wedges in regions where winter temperatures enable thermal contraction cracking (Fortier and Allard, 2005; Ewertowski, 2009; Kokelj et al., 2014; [Jorgenson et al., 2015b](#); [Sarrazin and Alard, 2015](#)). Continuous permafrost zones with well-developed polygonal ice-wedge networks are particularly vulnerable to climate change because ice wedges are usually found near the top of permafrost (Smith et al., 2005;

Jorgenson et al., 2006; Woo et al., 2008; Vonk et al., 2013). In these regions, thawing permafrost can result in ground ice erosion and displacement of sediments, carbon and nutrients by drainage (Rowland et al., 2010; Godin et al., 2014; Harms et al., 2014). This thermo-erosion process has especially been observed across North-America (Grosse et al., 2011), in Siberia (Günther et al., 2013) and in the Antarctic Dry Valleys (Levy et al., 2008). On Bylot Island in Nunavut, thermo-mechanical erosion by water has initiated ~~internal~~ permafrost tunneling and the development of gully networks in ~~aeolian~~ aeolian, ~~and~~ and colluvial depositional environments ~~which cover about~~ of nearly 158 000 m² (Fortier et al., 2007; Godin and Fortier, 2012a; Godin et al., 2014; Veillette et al., 2015). A fine-scale spatio-temporal monitoring ~~study~~ of the six largest gullies showed that their development rate ranged from 14 to 25 m.yr⁻¹ going up to 80 m.yr⁻¹ during their inception (Godin and Fortier, 2012b), leading to substantial changes in the drainage network and ~~increased~~ increasing eroded area throughout the valley (Godin et al., 2014). To date, the contribution of thermal-erosion and lateral erosion processes in permafrost feedbacks to climate is still poorly documented (Turetsky et al, 2015; Fortier et al., 2015).

Many observational and experimental studies have documented shifts in tundra plant community structure and plant species productivity in response to warming temperatures (Jonsdottir et al., 2005; Hudson and Henry, 2010; Epstein et al., 2013; Naito and Cairns, 2015). Substantial work has also been devoted to the vegetation response to disturbances such as landslides associated with permafrost degradation (Ukrainitseva et al., 2003; Walker et al., 2009; Cannone et al., 2010). In contrast, little is known about how thermo-erosion gullying affects plant community structure and plant species abundance. Yet, this information is urgently needed as vegetation plays an important role in structuring Arctic ecosystems and regulating permafrost response to climate change (Jorgenson et al., 2010; Gauthier et al., 2011; Legagneux et al., 2012). Wetlands serve as preferred grounds for Arctic herbivores

such as snow geese (Gauthier et al., 1996; Massé et al., 2001; Doiron et al., 2014). They are also expected to produce more methane compared to shrub-dominated areas (Olefeldt et al., 2013; Nauta et al. 2015; Treat et al., 2015).

The present study aimed at examining plant community patterns following thermo-erosion gullyng. Bylot Island, where geomorphological and ecological processes in response to climate change have been monitored for over two decades (Allard, 1996; Fortier and Allard, 2004; Gauthier et al., 2013), offered a unique opportunity to specifically assess the response of wetlands to gullyng. The following questions were addressed: (1) to what extent thermo-erosion gullyng modifies environmental conditions of low-centered wetland polygons? (2) how do plant communities cope with these geomorphological changes, i.e. do we observe shifts in plant diversity, abundance and productivity?

2 Methods

2.1 Study area

This study took place in the Qarlikturvik valley of Bylot Island, Nunavut, Canada (73°09'N, 79°57'W; Fig. 1a). Bound to the North and South by plateaus < 500 m asl, it connects C-79 and C-93 glaciers to the Navy Board Inlet sea via a proglacial river ~~that passes through the plain~~. The sampling sites were specifically located in the valley floor (ca 65 km²), which is characterized by a low-centered polygon landscape that has resulted from ice wedge development and sediment accumulation during the late Holocene (Ellis and Rochefort, 2004; Fortier and Allard, 2004; Ellis et al., 2008). Two baseline ~~plant communities~~vegetation types can be recognized. Wetlands, often associated with intact low-centered polygons, represent ca 23 % of the valley area (Hughes et al., 1994) and are dominated by sedges (*Carex aquatilis*, *Eriophorum angustifolium*, *Eriophorum scheuchzeri*), grasses (*Dupontia fisheri*, *Pleuropogon sabinei*; Gauthier et al., 1995) and fen mosses (*Drepanocladus* spp.; Ellis et al.,

2008; Pouliot et al., 2009). Mesic environments, such as low-centered polygon rims, gently
sloping terrain and hummocky tundra, support individuals-a more diverse group of species
including *Salix* spp., *Vaccinium uliginosum*, *Arctagrostis latifolia*, *Poa arctica* and *Luzula*
confusa with *Aulocomnium* spp. as dominant moss species (Zoltai et al., 1983). As a result,
the valley houses many herbivores during summer, in particular such as snow geese (in
summer), and brown and collared lemmings (Gauthier et al., 1995; Gruyer et al., 2008), and
thus representing a critical environment for tundra food web (Gauthier et al., 2011;
Legagneux et al., 2012).

2.2 Field sites

Our work was specifically conducted around three gullies that were selected among the 36
identified in the valley (Godin and Fortier, 2012b). These gully networks have originated
from snowmelt water infiltration into thermal-contraction cracks cavities of the frozen active
layer and the subsequent formation of underground tunnels that have ended up collapsing
(Fortier et al., 2007; Godin and Fortier, 2010). The gullies R08p and R06, respectively 835
and 717 m long, are characterized by ongoing thermo-erosion (Fortier et al., 2007; Godin and
Fortier, 2012b) whilst the gully RN08, 180 m long, has not been active in recent years. A total
of 197 polygons (i.e. sampling sites) were randomly selected around the three gullies (Table
1; Fig. 1b) and classified into one of four categories (referred hereafter as habitats) that
represented the two baseline plant communities vegetation types (wet and mesic) as well as
increasing levels of disturbance related to thermo-erosion related disturbance. The disturbed
habitats were sorted via a visual assessment of the low-centered polygon rim integrity coupled
with a recent close monitoring of drainage system development along the gullies (Fortier et
al., 2007; Godin and Fortier, 2012a,b). The habitats were defined as follows: (i) intact low-
centered wet polygons (n = 62) that were not affected by gullyng. Their elevated rims enclose

a central depression that retains snow cover during winter and is flooded by snowmelt water during spring (Woo and Young, 2006; Minke et al., 2007). These ~~intact~~-polygons are hydrologically independent, with their water content representing the balance between precipitation inputs (snow and rain) and evapotranspiration outputs (Fortier et al., 2006)-; (ii) ~~recently~~-(less than ~~five-five-years~~) (recently) disturbed polygons (n = 44), located along the most recent sections of the gullies, with partially degraded rims, incomplete drainage and heterogeneous water content; (iii) more than five-year (older) disturbed polygons (n = 43), with heavily breached rims adjacent to the gullies and substantial or complete drainage; (iv) mesic environments (n = 48), with distinct heterogeneous mesic vegetation. They are found ~~throughout the valley on the rim of polygons and in adjacent areas~~ and are ~~thus generally~~ not ~~necessarily~~-induced by thermo-erosion gullying but rather dependent of local sedimentary and hydrological dynamics.

2.3 Environmental condition monitoring

Daily precipitation was recorded with a manual rain gauge throughout summer 2010 at the base camp, located 700 m west of the gully R08p (Gauthier et al., 2010). Soil (top 10 cm) moisture was recorded at the center of each ~~polygon-sampling site~~ using ECH₂O EC-5 moisture sensors (accuracy of ± 3 % VWC, resolution of ± 0.1 % VWC) connected to Em5b dataloggers (Decagon Devices, WA, USA). Measurements were carried out in 2010, both July 5 (early season) and July 30 (late season) ~~in the polygons located~~ along the gullies R08p and R06, and July 30 only ~~in the polygons of along~~ the gully_RN08. Thaw-front depth was recorded at the ~~center of each sampling site~~~~polygon-centers~~ using a graduated steel rod ~~graduated in centimetre and~~ driven ~~into~~ the thawed active layer. The data collection spanned two years with measurements in July 2009 and 2010 in the polygons of the gullies R08p and R06 and in July 2010 in those situated along the gully RN08. One measure was taken ~~per~~

~~polygon in each of the wet and disturbed sampled polygons, except for the mesic environments where~~ whereas three random measurements were ~~randomly~~ conducted in each mesic environment site because of the heterogeneity of this type of habitat. In this case, a means per site ~~were~~ was calculated prior to analyses.

2.4 Plant community characterization

Species richness and abundance were determined ~~in at~~ each ~~polygon site~~ in July 2009 or 2010 using three randomly placed 70 cm x 70 cm quadrats ~~within areas that were representative of the site~~ that were vertically photographed at ca 1.3 m from the ground (see detailed protocols in Chen et al., 2010 and the IPY CiCAT, 2012; Fig. 2). Abundances of vascular plants, lichens, mosses, *Nostoc* spp., fungi, cryptogamic crust, bare ground, litter, vascular plant standing dead, standing water, signs of grubbing and goose feces were evaluated as cover percentages using photography analyses (Perreault, 2012). ~~Three quadrats were vertically photographed at each site at ca 1.3 m from the ground (see detailed protocols in Chen et al., 2010 and the IPY CiCAT, 2012).~~ Daubenmire cover abundance classes (Daubenmire, 1959) were used on each quadrat picture overlain by a 7-cm grid to evaluate species cover as the projection on the ground of all species above-ground parts.

Five ~~polygons sampling sites~~ per habitat were also randomly selected along the gullies R08p and R06 to measure above-ground biomass of graminoid species. At each site, an enclosure of 1 m x 1 m was made of chicken wire 30 cm high and supported by wooden stakes at each corner (see Gauthier et al., 1995). Enclosures were set up in early July 2012 to avoid any significant grazing by geese. Above-ground biomass was harvested inside the enclosures near peak production in early August 2012 using ~~imaginary random~~ grids of 25 cm x 25 cm for wet and recently disturbed polygons and of 50 cm x 20 cm for ~~long-time~~ older disturbed polygons and mesic environments. Two different grid sizes were used because of

the difference in structure of the vegetation (herbaceous vs. shrubs) associated with the habitat heterogeneity (Legagneux et al., 2012). All graminoids present in the ~~exlosures-random grids~~ were cut to a standard height, i.e. at an average of 1 cm below the moss surface (Gauthier et al., 1995; Doiron et al., 2014), and live biomass was sorted as follows: *Carex aquatilis*, *Eriophorum angustifolium* and *Eriophorum scheuchzeri* (Cyperaceae); *Luzula arctica* and *Luzula confusa* (Juncaceae); *Anthoxanthum arcticum*, *Arctagrostis latifolia*, *Dupontia fisheri* and *Festuca brachyphylla* (Poaceae). Biomass was then oven-dried at 65°C until constant dry weight and further weighed to ± 0.0001 g using an electronic weighing scale.

2.5 Statistical analyses

Differences in soil moisture, thaw-front depth and graminoid above-ground biomass among habitats were tested with a generalized linear mixed model (procedure MIXED, REML method in SAS, version 9.4, SAS Institute, Cary, NC, USA). Soil moisture, thaw-front depth as well as date or year of measurements and the interaction terms were treated as fixed factors and gully as a random factor. Type III sums of squares were used for the calculation of fixed effect *F* statistics while random effects were assessed using a log likelihood ratio test from the full and reduced models (Littell et al., 2006). Post hoc contrasts were performed to ascertain specific differences between habitats at $\alpha < 0.05$ using the LSMEANS statement and Bonferroni adjustment. Canonical Correspondence Analyses (CCA) were conducted to test unimodal relationships between habitats and environmental variables (ter Braak, 1986; Zuur et al., 2007) using the ‘vegan’ package (Oksanen et al., 2015) in R 3.1.3 (R development core team, 2015). Two matrices were elaborated: one of 197 sites x 65 taxa using their mean cover per site (~~i.e. polygon~~), and another of 197 sites x 8 environmental characteristics comprising the following continuous variables: soil moisture, thaw-front depth, litter cover, bare ground,

grubbing, vascular plant standing dead, standing water and goose feces. Soil moisture measurements obtained on July 30 2010 were used in the analyses.

3 Results

3.1 Environmental conditions

In 2009, above-average spring temperatures led to a rapid snowmelt (June 16) while summer was one of the driest on record (Gauthier et al. 2009). In 2010, despite a relatively warm spring (0.26°C above normal), the high snow pack at the end of the winter (41.6 cm on May 31) delayed the snowmelt in the lowlands to June 28, which was a week later than normal. Summer was characterized by warm and sunny conditions as well as below-average precipitations (cumulative rain of 84 mm vs long-time average of 92 mm; Gauthier et al. 2010). However, the 36 mm received in only five days in mid-July 2010 significantly increased soil moisture between the two monitoring dates in all habitats (significant date effect: $df = 1$, $F = 88.99$, $P < .001$; Fig. 3) ~~and represented an important water input for both intact and disturbed polygons (non-significant habitat x date effect: $df = 3$, $F = 0.51$, $P = 0.68$)~~. There was overall a significant difference in soil moisture among habitats ($df = 3$, $F = 79.86$, $P < .001$), which was ~~driven associated to both in early and late July by~~ differences between wet polygons and the other habitats (5 July: $df = 3$, $F = 33.41$, $P < .001$, 30 July: $df = 3$, $F = 47.36$, $P < .001$; Fig. 3, Table A1). Throughout the summer, soil moisture was approximately 40 % higher in wet sites-polygons compared to disturbed polygons and mesic environments. We also found a significant difference in thaw-front depth between wet polygons and the other habitats (2009: $df = 3$, $F = 21.30$, $P < .001$, 2010: $df = 3$, $F = 33.86$, $P < .001$; Fig. 4, Table A1). Thaw-front depth of wet polygons was approximately 10 cm deeper than in disturbed polygons and mesic sites-environments ~~(35-36 vs 25-27 cm)~~ for both years of monitoring ~~(35-36 vs 25-27 cm) (non-significant year effect: $df = 1$, $F = 1.52$, $P = 0.22$,~~

~~non-significant habitat x year effect: $df = 3$, $F = 0.12$, $P = 0.95$). We did not find any gully effect.~~ The two types of disturbed polygons thus showed similar soil moisture and thaw-front depth despite their differing time since disturbance inception. Results on the environmental conditions of the 197 sampling sites were obtained regardless of the gully location (non-significant gully effect: $df = 2$, $LLR = 1.6$, $P = 0.21$ for soil moisture, $df = 2$, $LLR = 0.0$, $P = 1.0$ for thaw-front depth).

3.2 Plant community characterization

A total of 18 vascular plant families encompassing 59 species were sampled throughout the study (Table A2). The greatest species richness was found in polygons that were disturbed at least five years ago and where both hydrophilic and mesic species were present (Table 2). The transition from wet polygons to mesic environments was accompanied by significant changes in vascular plant community composition, especially with the decline in Cyperaceae and Poaceae cover and the emergence of Salicaceae species (Table 2). *Carex aquatilis* and *Dupontia fisheri* were respectively present in 100 % and 93 % of the wet polygons sampled where they accounted for 52 % and 26 % of the total vascular plant cover. They were found in only 47 % and 16 % of mesic environments accounting for 9 % and 0.45 % of the total vascular plant cover. In contrast, *Salix arctica* and *Arctagrostis latifolia*, which were found in approximately half of the wet polygons accounting for 3 % of the total vascular plant cover, were present in 98 % of the mesic environments where they respectively accounted for 50 % and 14 % of the total vascular plant cover. Differences among habitats were also noted in non-vascular taxa. Abundance of lichens such as *Cladonia* spp., *Stereocaulon* spp. and *Peltigera* spp. increased in polygons disturbed for at least five years and mesic environments (Table 2). Mosses were mostly found ~~live-living~~ in wet polygons and mesic environments and dried (i.e. dead) in disturbed sites-polygons (Table 2), while a significant species turn-over

was observed between habitats with wetland-dominant *Drepanocladus* spp-species replaced by *Aulocomnium* spp-species in mesic environments.

Moreover, we observed vegetation changes through the decline of graminoid above-ground biomass which varied significantly among habitats ($df = 3$, $F = 11.59$, $P < 0.001$; Fig. 5a; Table A1) ~~and independently of the sampling location (non-significant gully effect: $df = 1$, $LLR = 0.0$, $P = 1.0$).~~ Graminoid biomass was nearly five times greater in wet than in mesic environments (29.2 vs 5.9 $g.m^{-2}$; Fig. 2 and 5a) ~~and decreased twofold between < 5-year disturbed and > 5-year disturbed polygons (22.3 vs 9.3 g^{-2} ; Fig. 2 and 5a).~~ Differences were mainly driven by the decline of hydrophilic species, i.e. *Carex aquatilis*, *Eriophorum scheuchzeri*, *Anthoxanthum arcticum* and *Dupontia fisheri*, between wet and mesic habitats (28.8, 19.7, 3.6 and 2.5 $g.m^{-2}$ in wet, < 5-year disturbed, > 5-year disturbed and mesic sitespolygons, respectively; Fig. 5b). Above-ground biomass of *Luzula* spp., *Arctagrostis latifolia* and *Festuca brachyphylla* was contrastingly nine times greater in mesic than in wet habitats (3.30 vs 0.35 $g.m^{-2}$) ~~and twenty-four times greater in > 5-year disturbed than in < 5-year disturbed polygons (5.61 vs 0.23 $g.m^{-2}$).~~

3.3 Relationships between plant communities and environmental variables

The first two axes of the Canonical Correspondence Analysis retained 14 % of the vegetation data variance and 80 % of the vegetation-environment relationship variance (Table 3). Five of the eight environmental variables tested were significant within the canonical model ($P < .05$, 999 permutations), but only three – litter cover, thaw-front depth and soil moisture - showed high correlations with the canonical axes (Table 4). Thaw-front depth and soil moisture were strongly related to the first axis, while litter cover was mainly associated with the second axis (Table 4). Altogether, these variables discriminated well the four studied habitats of the Qarlikturvik valley. Wet polygons were mainly related to high soil moisture and substantial

thaw-front depth whilst mesic environments were associated with greater litter cover (Fig. 6).
A-The gradual vegetation transition was also observed from < 5-year to > 5-year disturbed polygons ~~was also observed along following~~ the soil moisture ~~gradient shift in these habitats from the polygons disturbed less than five years ago to the ones that have been~~ disturbed for a longer period of time (Fig. 6).

4 Discussion

Sustainability of wetlands at high latitudes essentially relies on perennial frozen ground that prevents drainage and allows wet soil ~~moisture~~ conditions (Woo and Young, 2006; Ellis et al., 2008). However, snowmelt water run-off through ice-wedge polygon landscapes can initiate ~~permafrost thermo-~~al erosion of the permafrost and the development of gullies (Fortier et al., 2007; Godin and Fortier, 2014). We showed here that ~~thermo-erosion~~permafrost gullying significantly ~~alters~~altered wetlands by changing the original polygons' microtopography, and decreasing soil moisture and thaw-front depth of ~~low-centered~~disturbed polygons ~~adjacent to~~along the gullies. Vegetation ~~is~~was sensitive to this process, and mesic ~~habitat~~environment plant species gradually replaced hydrophilic species within five to ten years, although the full transition hasn't been reached yet. This vegetation turn-over can have substantial consequences on wildlife biology, permafrost stabilization and ecosystem-level greenhouse gas emissions (Blok et al., 2010; Doiron et al., 2014; Jorgenson et al., 2015b; McEwing et al., 2015).

4.1 ~~Transient~~tion in environmental conditions

The initiation of Tthermo-erosion gullying ~~has~~ led to a significant decrease in soil moisture and thaw-front depth of ~~disturbed~~breached polygons. Both older and recently disturbed polygons had similar soil moisture and thaw-front depth while differing in time since

disturbance, which shows that the change in polygon environmental conditions after
permafrost disturbance was rapid. The decrease in soil moisture following polygon rim
erosion ~~and water runoff through frost cracks. This~~ is consistent with what has been
previously observed in gullied areas (Seppälä 1997; Poesen et al., 2003; Godin and Fortier,
2012a; Godin and Fortier, 2014; Harms et al., 2014; Godin and Fortier, 2015) and concurs
with a modeling analysis showing that the transformation of low-centered to high-centered
polygon landscape following ice wedge ~~melting-degradation~~ is accompanied ~~with-by~~ a
significant alteration in the water balance partitioning (Liljedahl et al., 2012). In our study, all
types of disturbed polygons were recharged by snowfall and~~responded positively to a given~~
~~summer rainfall-event in a similarly way than intact polygons (no significant habitat x date~~
~~interaction).~~ Yet yet disturbed habitats had lower soil moisture than wet polygons, -and a
thorough examination of moisture evolution ~~at the same sites~~ throughout an entire summer
showed that soil moisture of breached polygons was significantly more variable than that of
~~intact-wet~~ polygons at both intra- and inter-polygonal scales (Godin et al., 2015). Given that
soil moisture is an important driver of plant community composition (Muc et al., 1989; Dagg
and Lafleur, 2011), it is no surprise that we observed a shift in vegetation following changes
in moisture regime ~~(see below)~~.

Decreasing soil moisture in the center of disturbed polygons came with decreasing
thaw-front depth. ~~While this result which~~ was expected given that active layer thickness is
closely related to ~~local hydrological processes~~ soil moisture (Nelson et al., 1999; Hinzman et
al., 2005; Minke et al., 2009; Wright et al., 2009; Gangodagamage et al., 2014), ~~it~~ This
result however contrasts with the active layer thickening generally observed in response to
climate warming (Tarnocai et al., 2004; Woo et al., 2007; Akerman and Johansson 2008;
Smith et al., 2009; Nauta et al., 2015), and this is likely due in part to ground surface
subsidence and drainage which follows ice-rich permafrost thawing (Shiklomanov et al.,

2013) and in part to snow accumulation patterns (Godin et al., 2015). Within five years of drainage, thaw-front depth in disturbed polygons decreased by 37 % compared to that in ~~intact~~ wet sites/polygons. This is mainly explained by the greater heat transfer from water and higher thermal conduction rates in wetter polygons that provide substantial melt energy to the frost table (Nelson et al., 1997; Hinzman et al., 2005; Wright et al., 2009; Romanovsky et al., 2010). This effect is also sharpened by the low thermal conductivity of drier moss carpets in disturbed sites-habitats (Wright et al., 2009) and altered local snow conditions within the polygons adjacent to the gullies (Godin et al., 2015).

4.2 Vegetation changes

Overall, the floristic composition of our sampling sites is in line with previous field surveys conducted in the same area (Gauthier et al., 1996; Duclos, 2002; Doiron, 2014). The presence of *Carex aquatilis*, *Eriophorum scheuchzeri* and *Dupontia fisheri* characterizes well the typical vegetation of Arctic wetlands (Jorgenson et al., 2013; Sandvik and Odland, 2014; Lara et al., 2015) whilst that of *Arctagrostis latifolia*, *Luzula* and *Salix spp* are common features of Arctic mesic environments (Audet et al., 2007; Sjogersten et al., 2008). Disturbed polygons were the most diverse sites-habitats given that they offered a middle-range state between wet and mesic conditions where hydrophilic species were still present while mesic environment ones had successfully established.

The development of gullies in the Qarlikturvik valley and the subsequent drainage of adjacent low-centered polygons have led within five to ten years to a gradual change in plant communities with vegetation of disturbed polygons leaning towards a new equilibrium, that of mesic environments. Mesic ~~habitat~~ environment species such as *Luzula* and *Salix spp* have established or increased in cover following the decrease in soil moisture and thaw-front depth and replaced hydrophilic Cyperaceae and Poaceae ~~within ten years after gully initiation.~~

The secondary succession pioneered here by the ~~thermo-erosion~~gullyng process in disturbed polygons follows the directional-species replacement model examined by Svoboda and Henry (1987). ~~It is~~However, by occurring within five to ten years, it has been relatively remarkably more rapid than what is usually documented for the High Arctic where perennial plant communities are highly-largely resistant to disturbance (Hollister et al., 2005; Jonsdottir et al., 2005; Hudson and Henry, 2010) and succession dynamics are slow due to short growing seasons and low summer temperatures (Svoboda and Henry, 1987). For instance, plant cover of northeastern Alaska changed little over a twenty-five year period despite a significant rise in summer temperatures (Jorgenson et al., 2015a). ~~The~~This gradual yet rapid species replacement ~~is~~has been triggered in our system by the hydrological and thermal shift caused by gullyng and favored ~~in our system~~ by the mosaic of wet and mesic habitats allowing for a substantial species pool with both vegetative and sexual reproduction. ~~The vegetation of disturbed polygons can thus lead toward a new equilibrium, that of mesic environments, within a decade.~~

In the canonical ordination analysis, the soil moisture gradient discriminated wet polygons from the other ~~sites~~habitats as well as recently disturbed from ~~long-time~~older disturbed habitats. The 37 % decrease in soil moisture between ~~intaet~~wet and disturbed polygons represents a drastic change of conditions for plant communities and is of similar magnitude than what has been documented in Alaskan drying wetlands as a result of increasing temperatures (Klein et al., 2005). The strong influence of soil moisture in separating plant community types at high latitudes has indeed been well documented (Hinzman et al., 2005; Daniëls and de Molenaar, 2011; Daniëls et al., 2011; Sandvik and Odland, 2014). Four other variables significantly influenced the distinction among habitats: (i) thaw-front depth discriminated habitats in the same direction than soil moisture with a 30 % decrease in disturbed polygons and mesic environments compared to ~~intaet~~wet polygons,

which was expected since these two factors are closely related (see section 4.1); (ii) litter cover separated mesic environments from the others, which may be explained by increased organic matter related to greater shrub abundance in mesic environments (Zamin et al., 2014); (iii) vascular plant standing dead separated wet and recently disturbed polygons from the other habitats, which can be explained by the senescence of Cyperaceae tillers that are highly abundant greater abundance and biomass of Cyperaceae species at these sites-locations (Fig. 5); (iv) goose feces were mainly associated with long-timeolder disturbed and mesic environments. While this may suggest a higher use of these habitats by geese, the slower degradation of feces in dryer habitats cannot be ruled out; this has yet to be tested.

The shift in vegetation composition in disturbed polygons was accompanied by significant changes in biomass. Above-ground biomass of graminoids was the greatest in wet polygons, which is concordant with the fact that wetlands are the most productive habitats of forage plants in the Arctic (Sheard and Geale, 1983; Duclos, 2002; Doiron, 2014). It gradually decreased in disturbed polygons as conditions became closer ~~and closer to that those~~ of mesic environments ~~and therefore less and less suitable~~. Compared to the immediate change in environmental conditions, we nonetheless observed a lag-time in vegetation response to thermo-erosion related disturbance as graminoid biomass differed significantly between recently and older disturbed polygons. In our study, graminoid above-ground biomass of wet polygons was 35 % lower than what Cadieux et al. (2008) found via a long-term plant monitoring on Bylot Island (45.2 g/m²), and 62.7 % lower than what Gauthier et al. (2012) measured in the most productive ~~ungrazed~~ wetlands of the Qarlikturvik Valley (78.4 ± 10.5 g/m²). These contrasts may be explained by varying species composition and to a lesser extent by earlier plant harvesting in our case ~~but more probably by varying species composition~~. Indeed, while we focused on wet polygons dominated by *Carex aquatilis*, Cadieux et al. (2008) and Gauthier et al. (2012) worked on wet sites-polygons dominated by *Dupontia*

fisheri and *Eriophorum scheuchzeri*. Because our study was part of a large scale multisite project on wetland carrying capacity for snow geese (Legagneux et al., 2012; Doiron, 2014), we only focused on forage plant (i.e. graminoids) biomass and did not sample forbs or shrubs. Since above-ground biomass of graminoids account for more than 90 per cent of vascular plant biomass in wetlands (Gauthier et al., 1995), we provide here an accurate estimate of the total above-ground biomass that can be found in these habitats. However, the total above-ground biomass in mesic environments was probably underestimated. For instance, biomass of shrubs and forbs respectively ranged between 22 and 48 g.m⁻² and between 6 and 20 g.m⁻² in ~~the~~ mesic ~~sites-environments~~ adjacent to our study area (E. Lévesque, *unpublished data*). Overall, total above-ground biomass in wetlands and mesic environments is of similar ~~order of magnitude~~ ~~order~~ (50.5 g.m⁻² ± 2.8 SE in wetlands and 44.2 g.m⁻² ± 6.8 SE in mesic tundra for the period 2007-2009; Legagneux et al., 2012).

4.3 Impacts on ecosystems

It is likely that the replacement of hydrophilic plants by mesic vegetation will severely impact wildlife biology. The Qarlikturvik valley of Bylot Island represents an important summer habitat for greater snow geese (Legagneux et al., 2012). It is well documented that this species mostly relies on wetlands for food resources (Gauthier et al., 1995, 2011), especially because graminoids are easily digested ~~thanks-due~~ to their low fiber concentration and rich nutritive elements (Sedinger and Raveling, 1989; Manseau and Gauthier, 1993; Audet et al., 2007). For instance, geese removed respectively 40 % and 31 % of the total annual production of *Dupontia fisheri* and *Eriophorum scheuchzeri* during the period 1990-2007 (Cadieux et al., 2008).✂ It remains to quantify the extent to which gullying alters wetland carrying capacity. In addition, the presence of ponds in wetlands provides geese refuges from predators such as

arctic fox (Hughes et al., 1994; Lecomte et al., 2009), and their disappearance might also change predator-prey interactions.

Effects of gully-induced vegetation changes may finally be visible on variations of greenhouse gas emissions. There is evidence for a strong vegetation control on methane emission from wetlands (Olefeldt et al., 2013; [Lara et al., 2015](#); McEwing et al., 2015; Tveit et al., 2015). In wet polygonal tundra of Northern Siberia, Kutzbach et al. (2004) found for instance that dense *Carex aquatilis* stands emitted more methane than sites with low *Carex* densities. Overall, wetlands and lakes expansion are thought to increase methane emission but also carbon storage (Myers-Smith, 2005; Nauta et al., 2015; Treat et al., 2015; Bouchard et al., 2015). We can therefore expect that the reverse transition from wet to mesic environments observed within our low-centered polygon landscape would lead to reduced methane emission and increased ~~carbon release as~~ CO₂ emission through enhanced decomposition. However, no general pattern on ecosystem responses to decreased water table position and subsequent gas emissions has emerged to date (see Grosse et al., 2011 for review). It will thus be crucial to determine in the near future the specific evolution of *Salix* and *Luzula spp* primary production in mesic ~~sites-environments~~ in order to accurately predict the effects of wetland retreat on methane and soil organic carbon cycles.

5 Conclusions

This study illustrates that changes in the hydrological and thermal regimes following the ~~induction~~inception of thermo-erosion gullies boost landscape transformation from wet to mesic habitats, providing evidence that permafrost ~~degradation~~disturbance is a critical component of ecosystem modification at high latitudes. Ecological studies should consequently start using an approach that integrates disturbed permafrost monitoring if one wants to more efficiently document climate change effects on arctic terrestrial ecosystems. In addition, our latest field observations showed that hydrology and thaw regimes of breached polygons have yet to reach equilibrium with new conditions. Similarly, vegetation remains in transition given that, ten years after disturbance, the cover of dominant shrubs and mesic bryophytes in disturbed polygons is still lower than in adjacent mesic environments. It is currently not possible to predict how long these species would take to out compete declining species and cryptogamic crust and reach a new mesic environment equilibrium. This current state stresses the importance of long-term permafrost-vegetation dynamic monitoring. In addition, while surface warming is expected to alter the ground's thermal regime (Couture and Pollard, 2007), more work should be devoted to the feedback effects of plant communities and vegetation succession on thermal and mechanical stabilization dynamics of disturbed permafrost terrains. This is especially needed since plant community differences between disturbed and intact sites can last several centuries (Cray and Pollard, 2015).

463 **Table A1.** Sample sizes and means (\pm SE) of soil moisture, thaw-front depth and graminoid above-ground biomass in the four habitats studied in
464 the Qarlikturvik valley of Bylot Island, Nunavut. Letters refer to post hoc contrasts that were carried out using the LSMEANS statement and
465 Bonferroni adjustment (procedure MIXED, SAS 9.4). For a given variable, different letters indicate significant differences among habitats.
466

Habitats	Soil moisture 5 Jul 2010 (%)		Soil moisture 30 Jul 2010 (%)		Thaw-front depth Jul 2009 (cm)		Thaw-front depth Jul 2010 (cm)		Above-ground biomass (g/m ²)	
	<i>n</i>	Mean \pm SE	<i>n</i>	Mean \pm SE	<i>n</i>	Mean \pm SE	<i>n</i>	Mean \pm SE	<i>n</i>	Mean \pm SE
Wet polygons	53	36.3 \pm 1.7a	54	48.0 \pm 1.3a	52	36.0 \pm 0.9a	62	34.6 \pm 0.8a	5	29.2 \pm 5.2a
< 5-year disturbed polygons	39	21.9 \pm 1.2b	39	31.0 \pm 1.5b	39	25.5 \pm 1.5b	44	25.0 \pm 1.1b	5	22.3 \pm 1.4a
> 5-year disturbed polygons	33	22.0 \pm 1.1b	33	31.2 \pm 1.2b	32	25.3 \pm 1.1b	43	24.9 \pm 0.8b	5	9.3 \pm 4.0b
Mesic environments	46	19.6 \pm 1.3b	50	28.4 \pm 1.4b	44	27.6 \pm 1.1b	48	26.5 \pm 0.7b	5	5.9 \pm 2.6b

467

468 **Table A2.** List of the vascular plant species inventoried in the Qarlikturvik valley, Bylot Island, Nunavut during the 2009 and 2010 field seasons.
 469 Species names are from the integrated taxonomic information system (ITIS 2011).
 470

Family	Species
Asteraceae	<i>Erigeron uniflorus</i> var. <i>eriocephalus</i> (Vahl) Boivin, <i>Taraxacum hyparcticum</i> Dahlst., <i>Tephroseris palustris</i> (L.) Reichenbach
Brassicaceae	<i>Cardamine bellidifolia</i> L., <i>Cardamine nymanii</i> Gand., <i>Draba cinerea</i> Adams, <i>Draba corymbosa</i> R. Br., <i>Draba glabella</i> Pursh, <i>Draba lactea</i> Adams, <i>Draba nivalis</i> Lilj., <i>Draba</i> sp. ^a , <i>Eutrema edwardsii</i> R. Br.
Caryophyllaceae	<i>Cerastium alpinum</i> L. s. lat., <i>Minuartia rubella</i> (Wahlenb.) Hiern., <i>Silene involucrata</i> (Cham. & Schlecht.) Bocquet subsp. <i>involucrata</i> , <i>Silene uralensis</i> (Rupr.) Bocquet subsp. <i>uralensis</i> , <i>Stellaria longipes</i> Goldie subsp. <i>longipes</i>
Cyperaceae	<i>Carex aquatilis</i> var. <i>minor</i> Boott, <i>Carex marina</i> Dewey, <i>Eriophorum angustifolium</i> Honck subsp. <i>angustifolium</i> , <i>Eriophorum scheuchzeri</i> Hoppe s. lat./ <i>russeolum</i> subsp. <i>leiocarpum</i> Novos.
Equisetaceae	<i>Equisetum arvense</i> L. s. lat.
Ericaceae	<i>Cassiope tetragona</i> var. <i>tetragona</i> (L.) Don
Fabaceae	<i>Astragalus alpinus</i> var. <i>alpinus</i> L. <i>Oxytropis maydelliana</i> ssp. <i>Melanocephala</i> (Hook.) Porsild
Juncaceae	<i>Juncus biglumis</i> L., <i>Luzula arctica</i> Blytt, <i>Luzula confusa</i> Lindebl.
Onagraceae	<i>Epilobium arcticum</i> Sam.
Papaveraceae	<i>Papaver</i> sp (including <i>P. dahlianum</i> , <i>P. cornwalisense</i> , <i>P. lapponicum</i> ssp. <i>occidentale</i>)
Poaceae	<i>Alopecurus borealis</i> Trin., <i>Anthoxanthum arcticum</i> Veldkamp, <i>Arctagrostis latifolia</i> subsp. <i>latifolia</i> (R. Br.) Griseb., <i>Deschampsia brevifolia</i> R. Br., <i>Dupontia fisheri</i> R. Br., <i>Festuca brachyphylla</i> ssp. <i>Brachyphylla</i> Schult. & Schult. f., <i>Phippsia algida</i> (Sol.) R. Br., <i>Pleuropogon sabinei</i> R. Br., <i>Poa arctica</i> R. Br. s. lat.
Polygonaceae	<i>Bistorta vivipara</i> (L.) Delarbre, <i>Oxyria digyna</i> (L.) Hill
Pyrolaceae	<i>Pyrola grandiflora</i> Radius
Ranunculaceae	<i>Ranunculus hyperboreus</i> Rottb., <i>Ranunculus nivalis</i> L.
Rosaceae	<i>Dryas integrifolia</i> Vahl subsp. <i>integrifolia</i> , <i>Potentilla hyparctica</i> Malte subsp. <i>hyparctica</i>
Salicaceae	<i>Salix arctica</i> Pall., <i>Salix herbacea</i> L., <i>Salix reticulata</i> L., <i>Salix richardsonii</i> Hook.
Saxifragaceae	<i>Chrysosplenium tetrandrum</i> (Lund) Th. Fries, <i>Micranthes foliolosa</i> (R. Br.) Gornall, <i>Micranthes hieraciifolia</i> (Waldst. & Kit.) Haworth, <i>Micranthes nivalis</i> (L.) Small, <i>Saxifraga cernua</i> L., <i>Saxifraga cespitosa</i> L., <i>Saxifraga hirculus</i> L., <i>Saxifraga oppositifolia</i> L.
Scrophulariaceae	<i>Pedicularis langsдорffii</i> subsp. <i>arctica</i> (R. Br.) Pennell, <i>Pedicularis sudetica</i> subsp. <i>albolabiata</i> Hult.

471
 472 ^a *Draba* sp. was not counted as a distinct species because it is probably one of the five species already mentioned.

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Table 1. Repartition of the studied polygons per habitat and per gully.

Gullies	Habitats				Total
	Wet polygons	< 5-year disturbed polygons	> 5-year disturbed polygons	Mesic environments	
R08p	30	22	22	21	95
R06	23	19	12	27	81
RN08	9	3	9	0	21
Total	62	44	43	48	197

Table 2. Species richness, family total cover and species mean cover of vascular taxa as well as mean cover of non-vascular taxa in each of the four habitats sampled at Bylot Island, Nunavut. Mean species richness is given for sampled areas of 49 dm² (70 x 70 cm quadrats). Numbers in brackets denote the number of species inventoried in each family. << = cover < 0.01 %; < = cover < 0.1 %.

	Wet polygons (n = 62)	Disturbed polygons		Mesic environments (n = 48)
		< 5 years (n = 44)	> 5 years (n = 43)	
Vascular taxa				
Total plant species richness	36	37	54	47
Mean plant species richness	8	11	17	15
Plant species cover (%)				
Asteraceae (3)	<<	<	<	<<
Brassicaceae (8)	<	<	0.3	<
Caryophyllaceae (5)	<<	0.1	1.0	0.2
Cyperaceae (4)	17.4	18.5	7.0	1.9
<i>Carex aquatilis</i>	14.7	17.8	6.4	1.9
<i>Carex marina</i>	0	<<	0	0
<i>Eriophorum angustifolium</i>	0.5	0.4	0.5	0
<i>Eriophorum scheuchzeri</i>	2.1	0.4	<<	<
Equisetaceae (1)	<	<	<	<
Ericaceae (1)	0	0	<<	<
Fabaceae (2)	<<	<<	0.2	0.1
Juncaceae (3)	<	0.2	3.4	3.0
<i>Luzula arctica</i>	<<	<	0.4	1.0
<i>Luzula confusa</i>	<	0.1	3.0	2.0
Onagraceae (1)	<<	0	0	0
Papaveraceae (1)	0	0	<<	<<
Poaceae (9)	8.7	5.0	2.7	3.4
<i>Anthoxanthum arcticum</i>	0.5	<	<<	<<
<i>Arctagrostis latifolia</i>	0.6	<	0.3	3.0
<i>Dupontia fisheri</i>	7.4	4.8	1.8	0.1
<i>Festuca brachyphylla</i>	<<	<	0.4	<
Polygonaceae (2)	<<	<<	<	<
Pyrolaceae (1)	0	0	<<	0
Ranunculaceae (2)	0	0	<<	<<
Rosaceae (2)	0	0	<	<
Salicaceae (4)	1.2	0.9	3.4	12.6
<i>Salix arctica</i>	1.2	0.9	3.1	10.8
<i>Salix herbacea</i>	0	0	<	0.1
<i>Salix reticulata</i>	<<	<<	0.2	1.6
<i>Salix richardsonii</i>	<<	<<	<<	<<
Saxifragaceae (8)	<	0.2	1.5	<
Scrophulariaceae (2)	0.7	0.3	<	<
Non-vascular taxa				
Lichens	<	<	1.9	6.6
Live mosses	53.1	26.6	15.9	44.6
<i>Drepanocladus</i> spp.	39.9	21.4	5.1	0
<i>Aulacomnium</i> spp.	7.5	3.2	1.4	39.3
Dried mosses	2.9	29.6	18.2	0.9
Fungi	<	0.2	0.1	<
<i>Nostoc</i> spp.	<	<	<<	<<
Cryptogamic crust	<<	<	14.6	5.1

Table 3. Information of the Canonical Correspondence Analysis. CCA-1: first canonical axis; CCA-2: second canonical axis.

	CCA-1	CCA-2
Eigenvalues	0.2208	0.1910
Cumulative % of vegetation data	7.32	13.60
Cumulative % of vegetation-environment relationship	42.8	79.8
Total inertia	3.0172	

Table 4. Canonical correspondence analysis for vegetation in the Qarlikturvik valley of Bylot Island, Nunavut. CCA-1: first canonical axis; CCA-2: second canonical axis. Statistically significant values ($P < 0.05$) after 999 permutations are shown in bold. Standing dead represents the cover of dead attached vascular plants.

Environmental variables	df	χ^2	F	P	CCA-1	CCA-2
Litter cover	1	0.1523	11.4495	0.008	0.0206	-0.8681
Thaw-front depth	1	0.1768	13.2854	0.001	-0.8608	-0.1436
Soil moisture	1	0.0429	3.2206	0.002	-0.7339	0.2424
Standing dead	1	0.0714	5.3688	0.01	-0.2393	0.2588
Bare ground	1	0.0065	0.4889	0.629	0.0207	-0.0522
Standing water	1	0.0090	0.6759	0.534	-0.2365	0.0830
Grubbing	1	0.0240	1.8003	0.097	-0.1051	0.1983
Goose feces	1	0.0329	2.4717	0.028	0.4769	-0.0772
Residual	188	2.5014				

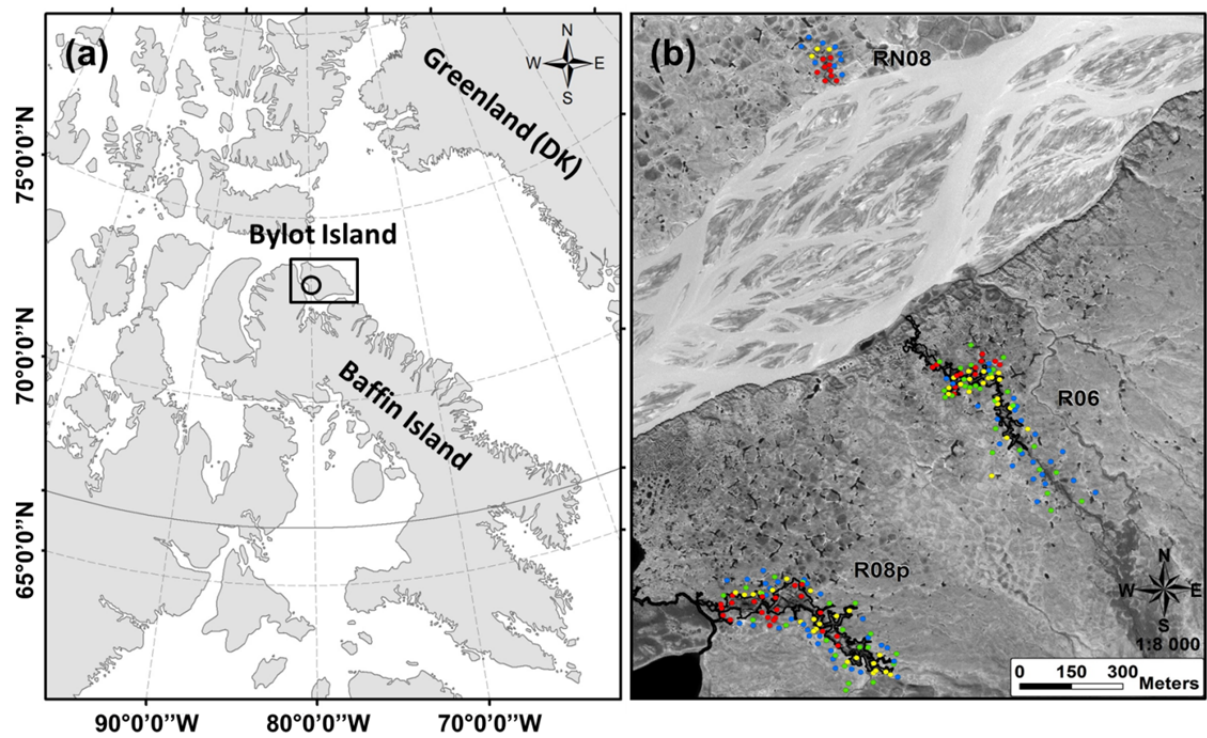


Figure 1. Location of the study area. (a) The Qarlikturvik valley (black circle) of Bylot Island, Nunavut (black rectangle). (b) the 197 sites sampled along three gullies (wet polygons (n = 62): blue circles; < 5-year disturbed polygons (n = 44): yellow circles; > 5-year disturbed polygons (n = 43): red circles; mesic environments (n = 48): green circles).

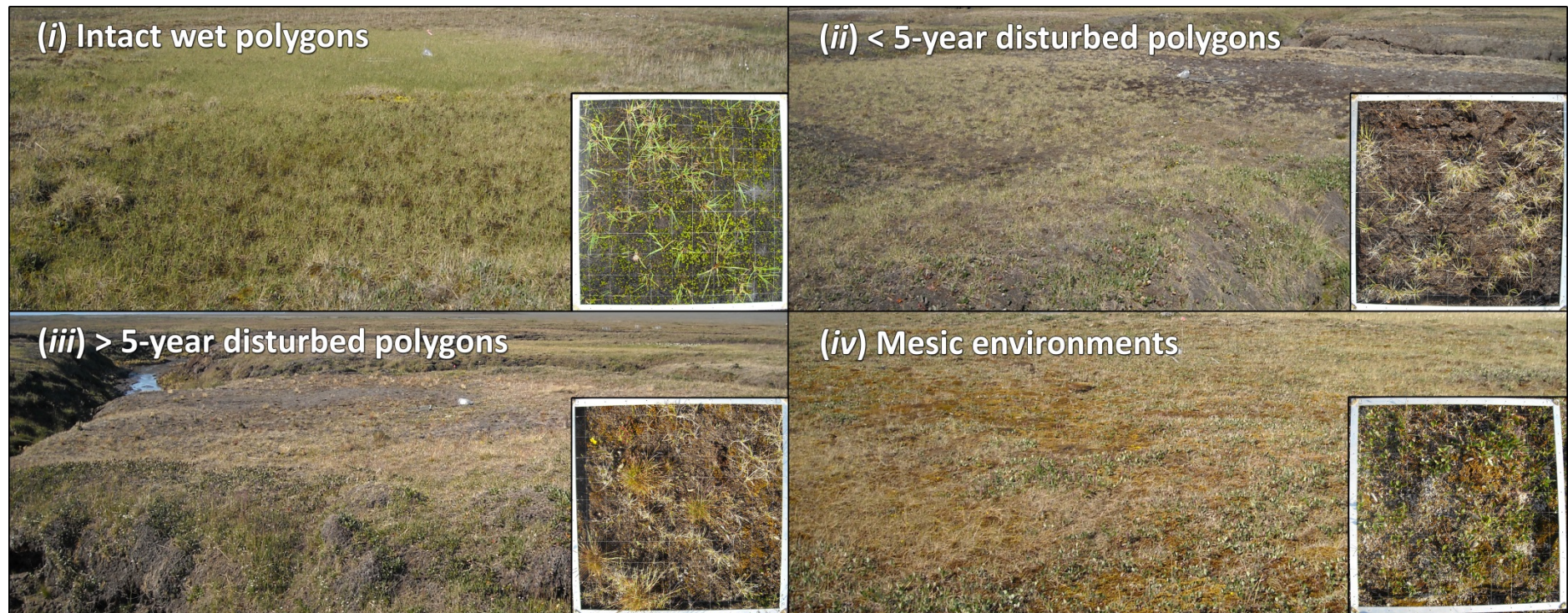


Figure 2. Illustration of the four habitats studied in the Qarlikturvik valley of Bylot Island, Nunavut. The close view at the bottom right of each picture represents the 70 cm x 70 cm quadrats that were used to determine species richness and abundance in each sampling site.

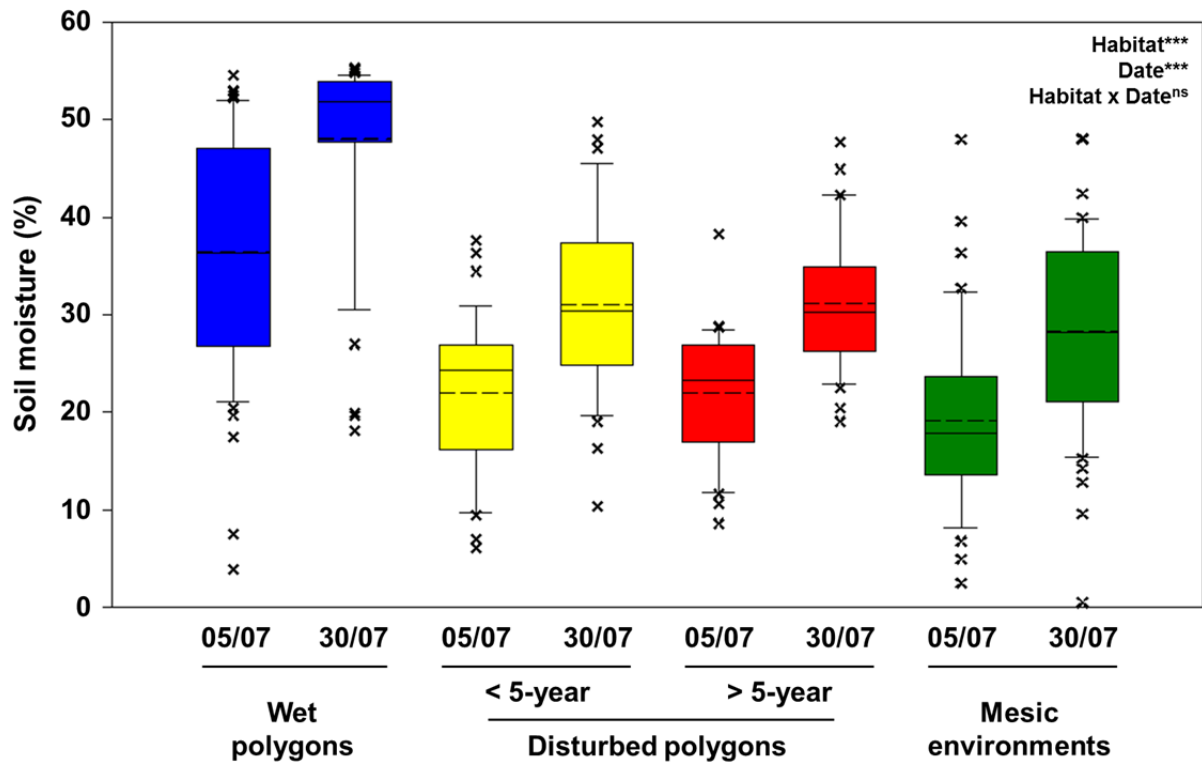


Figure 3. Soil moisture monitored early and late July 2010 in the four habitats studied in the Qarlikturvik valley of Bylot Island, Nunavut. 10th percentiles, lower quartile, median, mean (dash line), upper quartile and 90th percentiles are shown. See Table A1 for sample sizes and post-hoc contrasts. *** $P < .001$, ns: statistically non-significant effect.

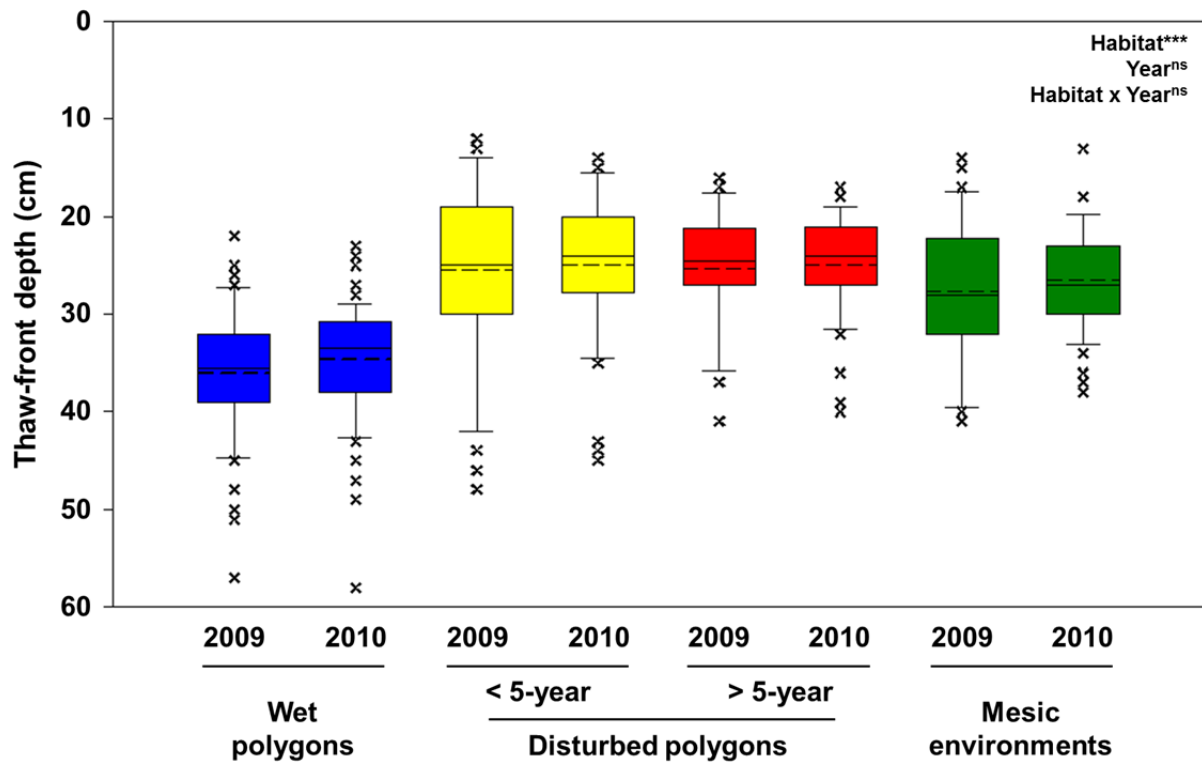


Figure 4. Thaw-front depth monitored in July 2009 and 2010 in the four habitats studied in the Qarlikturvik valley of Bylot Island, Nunavut. 10th percentiles, lower quartile, median, mean (dash line), upper quartile and 90th percentiles are shown. See Table A1 for sample sizes and post-hoc contrasts. *** $P < .001$, ns: statistically non-significant effect.

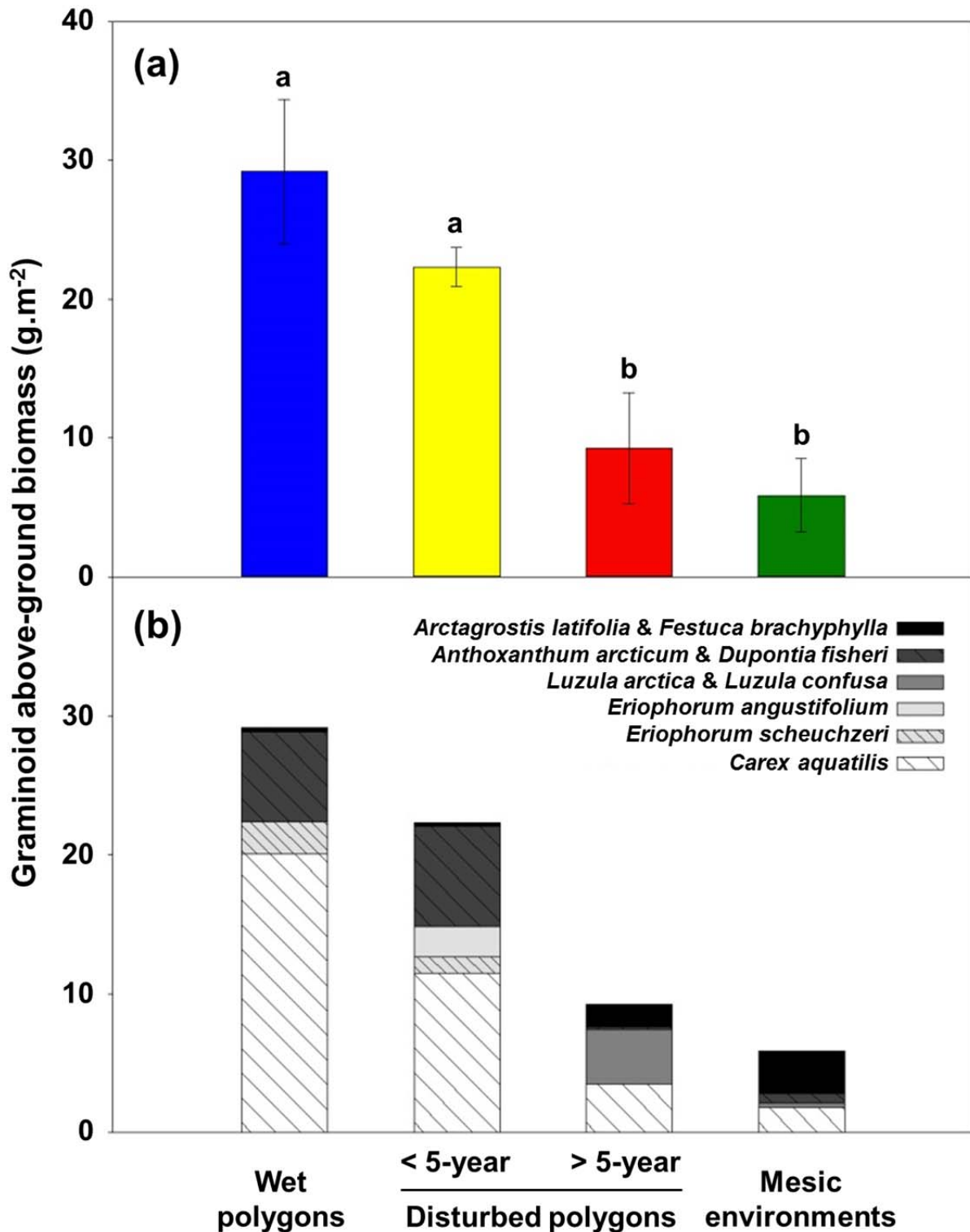


Figure 5. Above-ground biomass of graminoids growing in the four habitats studied in the Qarlikturvik valley of Bylot Island, Nunavut. (a) Mean total biomass (\pm SE), and (b) mean biomass per species. In panel (b), dashes represent hydrophilic species. $n = 5$ per habitat. Species aforementioned belong to the following families: Cyperaceae (*Carex aquatilis*, *Eriophorum angustifolium* and *Eriophorum scheuchzeri*), Juncaceae (*Luzula arctica* and *Luzula confusa*), and Poaceae (*Anthoxanthum arcticum*, *Arctagrostis latifolia*, *Dupontia fisheri* and *Festuca brachyphylla*).

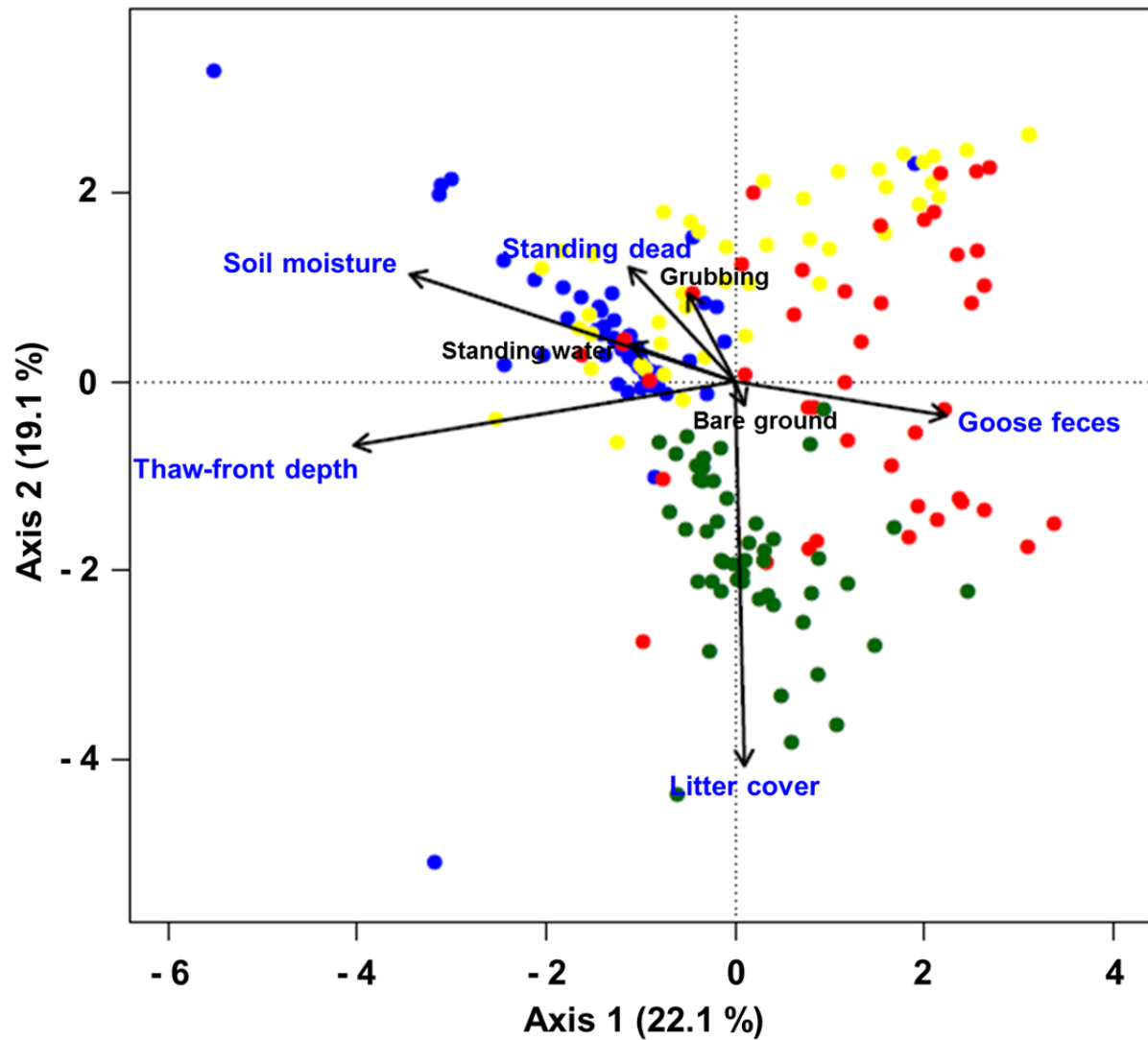


Figure 6. Canonical correspondence analysis (CCA) ordination of the 197 sites sampled in the Qarlikturvik valley of Bylot Island, Nunavut. Wet polygons (n = 62): blue circles; < 5-year disturbed polygons (n = 44): yellow circles; > 5-year disturbed polygons (n = 43): red circles; mesic environments (n = 48): green circles. Blue font indicates statistically significant environmental variables (see Table 4). Standing dead represents the cover of dead attached vascular plants.