

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 reviewers for their thoughtful and thorough comments that were very useful to improve the manuscript. We have carefully revised the manuscript following their suggestions. In particular, we improved the presentation of the methods, revised the statistical models by including ‘gully’ as a random factor (which did not change the results), and restructured the section 4.2 of the Discussion to better emphasize that the vegetation response to changes in soil moisture and thaw front depth is a gradual but relatively rapid change in the context of High Arctic perennial plant communities.

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

Reviewer #1

The study definitely contains the material for a publication that should provide important insights in the understanding of cold ecosystem functioning and in the assessment of potential consequences of current environmental changes at high latitude. However I think that the paper needs important revisions to reach these goals. I am particularly concerned by two points:

- First, the presented results do not support in a clear way the conclusion highlighted in the discussion. P12202 L5-7: the authors claimed that the soil moisture of disturbed sites is more responsive to rainfall while in fig. 1 there is no significant habitat x date interaction and the authors explained the difference in soil moisture date by summer rainfall. I assume that the not shown data give other view but the fig. 1 actually contradicts discussion claim.

Thanks for pointing this out. We wanted to highlight that, although both intact and disturbed polygons responded positively to rainfall events, disturbed polygons showed greater variability of moisture conditions. Our claim was based on the thorough examination of moisture dynamics Godin et al. (2015; companion paper) conducted at the same site along the gully A. We reworked the sentences to make this point clearer.

The authors confront the decrease in graminoid biomass following disturbance to the expected increase in biomass due to warming climate. However, there is no mention about the total above-ground biomass, even limited to vascular plants, meaning: What about the change in biomass when considering graminoids, forbs and more particularly shrubs? Is the decrease in graminoid biomass due to unsuitable conditions (less productive environment) or to the competition with mesic species (similar productivity level but other functional dominance)?

Thanks for pointing this out. Our study was part of a project that was specifically focused on the biomass of forage plants to estimate the effects of disturbance on wetland carrying capacity for snow geese (Legagneux et al., 2012; Doiron, 2014). Therefore, we unfortunately did not sample shrub biomass. There is a low occurrence of Salicaceae species in wet and disturbed polygons (see mean cover % in Table 2), and we are confident that the graminoid above-ground biomass we sampled in these habitats are a good proxy for total above-ground biomass. However, we agree that we underestimated total above-ground biomass in mesic environments where Salicaceae species mean cover averaged > 10 %. We therefore reworked the paragraph in the Discussion, especially by providing shrub and forb biomass estimation

from adjacent mesic polygons (E. Lévesque, unpublished data). We also specified that the decrease in graminoid biomass was related to increasing unsuitable conditions. We finally added 'graminoid' in the y-axis title of Fig. 4 to avoid confusion.

The authors present the results from the multivariate analysis as a clear discrimination of the vegetation of wet polygons from the other habitats (P12203 L1-3) while the fig. 5 rather shows some sort of continuum with the wet polygons and mesic habitats clearly segregated and the intermediated disturbed habitats somewhere between. From my point of view, this gradual change in plant composition should be the core of the message. The authors underlined the rapid changes (in a decadal time, P12201 L18, P12203 L 28) in vegetation but to me this point remains underused.

We agree that the vegetation change from wet to mesic environments is a continuum. We therefore maintained the terms 'gradual change' and 'gradually' throughout the manuscript (P12192 L12, P12201 L8 and L18, P12204 L3). Yet, the transformation of the landscape observed around the gullies within ten years also corresponds to a relatively rapid shift for such High Arctic perennial communities. We rephrased to stress this context.

Moreover, the comparison between the immediate change in soil moisture and thaw front depth (undisturbed vs. disturbed habitats regardless the time since the beginning of the disturbance) and the gradual response of the vegetation represents by itself an interesting but unexploited result that should be linked to biological inertia or succession dynamics responses concepts.

We agree that this comparison has to be better emphasized. While the change in plant community follows a continuum, we do not clearly observe biological inertia (even though some perennial plants maintain themselves after disturbance), but rather a succession dynamic that is relatively rapid (transformation from wet to mesic environment), especially in the context of perennial species and High Arctic short growing seasons. This pattern consequently stresses even more the substantial effect of thermo-erosion on Arctic ecosystems. We reworked the section 4.2 of the Discussion to clarify the message.

- Second, the presentation of the methods, the justification of methodological choices as well as the presentation of the results remain unclear despite a visible effort from the authors to present exhaustive study. A first missing while crucial information is about the identification of the age of the disturbance for the intermediate habitats (<5, >5 years) as well as the mesic habitats. Can we imagine more accurate information about the age (from long-term monitoring?) that could lead to different habitat segregation analyses?

Unfortunately long term monitoring of all the studied polygons is not available and we cannot identify the exact age of disturbed and mesic habitats. However, the detailed monitoring and mapping work of gullies maintained by Daniel Fortier since 1999 (Fortier et al., 2007; Godin and Fortier, 2010, 2012) allows us to differentiate with confidence polygons by classes of increasing time since thermo-erosion disturbance. We reworked the section to better describe the habitat characteristics.

The repartition of the habitats in each gully is also missing.

Thanks for pointing this out, we agree we should have been more precise. We added this information both in the Figure 1 and in the new Table 1.

Concerning this point, I am also surprised to not retrieve the place of the gullies in the statistical models. Actually, the gullies look like true replicates and I assume that the four habitats occurred in each of them. While the presented analyses (the linear models) are based

on unreplicated design (meaning poor statistical value), perform the analyses on average values per gully would improve the representativeness of the study.

Thanks for pointing this out. We agree and reanalyzed the dataset using gully as a random factor in a generalized mixed model (procedure MIXED, REML method in SAS). We obtained the same results, i.e. the differences in soil moisture, thaw front depth and graminoid above-ground biomass among habitats were independent from the gully location.

The results section often repeats between brackets statistical results presented in the tables and the figures. Moreover the tables and figures also provide redundant information (the values in the table 1 are graphically presented in the fig 2 and 3). Such redundancy is at least unnecessary and can lead eventually to hide the message.

We agree and put Table 1 in the Supplement.

Specific comments

P12194 L5-9: It seems illogical to state that the vegetation response is unknown along with this response contrasts with literature. Rephrase

We reworked the sentence emphasizing disturbances such as landslides that are related to permafrost degradation.

P12196 L7-19: The first habitat category is marked by (i) and the 3 other not. (ii), (iii) and (iv) are missing.

We added (ii), (iii) and (iv) to mark the other habitat categories.

P12196 L23: Was the thaw front depth measured in each site in 2009 and 2010 or did the data collection start in 2009 and was completed in 2010? Clarify.

Thaw front depth measurements started in 2009 and were completed in 2010. We added this information in the Methods.

P12196 L25: Why the determination of thaw front depth necessitated 3 measures in the mesic sites and not in the other? Justify.

We conducted three measurements of thaw front depth in mesic environments because of their heterogeneity.

P12197 L17-18: Why two different grid size for above-ground biomass harvesting? Justify

Two grid sizes were used because of the difference in vegetation structure and biomass of forage plants related to habitat heterogeneity. A smaller sampling area was necessary in homogeneous wet polygons than in heterogeneous mesic habitats. We added this information in the Methods.

P12198 L5: The choice of statistical models is unclear: Why log transform the soil moisture and thaw front depth data to analyse them with GLM eventually (L3) while GLM are actually designed to analyse non-normal data set using link functions?

Thanks for pointing this out. We made a typing error, and actually used a General Linear Model and not a Generalized one. Because General Linear Models represent a standard approach that requires the assumption of normality to be valid, we log-transformed soil moisture and thaw front depth data prior to analyses. Following your suggestion above, we reanalyzed the data including the gully factor and used a mixed model approach. We therefore did not log-transformed the data this time. We reworked the sentences in the Statistical analyses section.

P12198 L16: What is “eco-terrain”?

“Eco-terrain” referred to habitat category. We replaced “eco-terrain sites” by “habitats”.

P12198 L20: I know soil moisture and soil water content but “soil moisture content” sounds wrong.

We replaced “soil moisture content” by “soil moisture” throughout the manuscript.

P12198 L17: For “vegan” package, cite Oksanen et al. (2012) and for R, cite R development core team (2013).

We added this information in the text and the references section.

P12200 L1: Concerning this paragraph: I think the analyses of habitat effects for each plant group (shrubs, mosses) can be useful and provide new lightening.

We already mention in this section of the Results the decline of graminoid cover and the increase of shrub cover between wet and mesic habitats (see also Table 2) while providing statistical analyses on changes in graminoid above-ground biomass (Fig. 4). We agree moss and shrub biomass would provide additional information. However, as we pointed out above, we unfortunately did not sample biomass for these groups and thus cannot provide additional analyses.

P12200 L2: What about the 7 missing species, cryptogam species I presume, but why considered them for the CCA and not in the characterization of the plant community?

Thanks for pointing this out. Aside from the 59 vascular plant species, we sampled 6 non-vascular taxa: lichens, green and dried mosses, Nostoc, fungi and cryptogamic crust (total number of taxa sampled = 65). We erroneously included a taxa referring to unidentified vascular plants, which was marginal and present in only two polygons. After double-checking, we removed it from the canonical correspondence analysis. The mean cover of the 6 non-vascular taxa was included in a new version of Table 2 and we rephrased the plant community characterization by presenting how their abundance (especially that of lichens and mosses) differed among habitats.

P12200 L17: What is B1 the authors refer to?

Fig. B1 is the figure that can be found in the Supplement.

P12201 L15-18: Check for sequence of tense.

We checked, and only the present tense is now used throughout the sequence.

P12202 L16-18: I don’t see the interest of this sentence.

We agree and removed the sentence.

Technical comments

P12195 L7: “landscape” instead of “ladnscape”.

We made the change.

P12198 L2: There is a weird redundant typing error with the double “f” throughout the manuscript.

Sorry but we do not see this typing error in the pdf version we have.

P12203 L25: “to” instead of “and”.

We made the change.

P12204 L3: space between “decrease” and “in”.

We made the change.

P12205 L9: missing closing brackets after Massé et al., 2001.

We made the change.

Reviewer #2

The authors present 2 years of soil moisture, thaw depth, and vegetation characteristic measurements from undisturbed low centered and degraded ice wedge polygons in the high Canadian Arctic. Large difference is found in biomass, species and abundance between all the groups, while it is only the undisturbed low centered polygon that is distinctly different in thaw and soil moisture. The manuscript is mostly clearly written, with clarification only needed at a few places. I was however disappointed at the discussion section as it is mostly read as a literature review and did not address the finding above (large vegetation characteristic differences not mimicked in the hydrology and thaw). I think there is a danger in simplifying (averaging) the hydrological characteristics like the authors have done (due to the large seasonal variability) and then performing fancy statistics and make conclusions when the results come out as statistically significant. I would like the authors to address the question (which is based upon observing Figure 2-4) why is there such a large site-to-site variability in vegetation characteristics while soil moisture and thaw is nearly identical in most of the groups?

P12196 L8-9: Unclear what the authors mean with “...i.e. with intact rims and non-apparent ice wedges.” If there are rims there should be ice wedges (??)

We agree. As stated above, we reworked the section to present more clearly the habitat characteristics.

P12196 L7-14: The naming of the sites can be made clearer. I am specifically thinking about 1) the name choice of the “mesic” sites, which if I understand it correctly, has also experienced ground subsidence that occurred much earlier than the “more than five year disturbed polygons”; and consistency in naming of sites between text and figures. I think it would help the readability if the names referred to age or degree or absence of recent ice wedge degradation. I also recommend to expand the description of respective polygon group in general and include the photo of the sites in the manuscript (not the supplemental).

We reworked the habitat characteristics, especially to better highlight that the mesic environments represent one common habitat of the valley and are not necessarily induced by thermo-erosion gullyng (Hughes et al., 1994). We kept the site naming as it was since it refers to the common semantics used to describe the main plant communities of the study area (Gauthier et al., 1995; Duclos, 2002; Ellis and Rochefort, 2004; Gauthier et al., 2012). We finally checked for the consistency in the naming of sites between text and figures, and included the pictures of habitats in the manuscript (Fig. 2).

P12199 L17: What does “habitat x date” mean?

This term refers to the response of habitats to rainfall events that occurred between the two monitoring dates (July 5 vs. July 30). Both intact and disturbed polygons responded positively to precipitations, i.e. soil moisture increased in all polygons between the two monitoring

dates, and consequently the habitat x date interaction was non-significant.

P12199 L21: I suggest removal of the second portion of the sentence, from “Which was also driven by significant differences between wet polygons and the other habitats...”. It is unclear, while the next sentence provides the message much more effectively.

We rephrased.

P12199 L23-25: This sentence is unclear. Please clarify.

We rephrased.

It is rather intriguing that the difference in vegetation characteristics is so large between all polygon groups, while the differences in soil moisture and thaw (as presented) are relatively small. I would like to see the authors expanding on that observation (which is not currently addressed) in their discussion.

Thanks for pointing this out. We believe that the 37 % decrease in soil moisture and 30 % decrease in thaw front depth observed between intact and disturbed polygons rather correspond to a marked than a small difference. We reworked the Discussion including comments on this observation.

P12201: The observations of decreased soil moisture concur with an earlier model experiment on the role of ice wedge degradation or polygon type on water balance components (see Liljedahl et al. 2012), which is a quite relevant reference for this manuscript.

Thanks for pointing this out. We referred to this article in the Discussion.

P12202 L5-7: If you are not presenting this data, then do not add this new information to the discussion! Is there a reference for it? Same goes for P12204 L4-5.

We agree and referred to Godin et al. (2015) for the information concerning soil moisture variability. We added information on mean cover of non-vascular plant taxa in Table 2.

P12204 L10: Please be clear. What do you mean with “our results provide a new perspective”?

We deleted this sentence.

The discussion is rather long and become a literature review at places. My recommendation would be to build the discussion on references that are already provided (intro/background) and focus the discussion on integrating those with your results. For example, there is a long description about geese in the discussion, but were they even mentioned in the intro?

We lightened the Discussion by deleting redundant comments. We had already mentioned in the Introduction that wetlands are critical habitats for Arctic herbivores, and therefore added “such as snow geese” to clarify the message.

P12206 L5-7: What do the authors mean with this sentence? Please clarify.

We deleted this sentence.

References

- Doiron, M., Gauthier, G. and Lévesque, E.: Effects of experimental warming on nitrogen concentration and biomass of forage plants for an arctic herbivore, *J. Ecol.* 102, 508-517, 2014.
- Duclos, I.: Milieux mésiques et secs de l’Île Bylot, Nunavut (Canada): caractérisation et

- utilisation par la Grande Oie des Neiges. MSc thesis, Université du Québec à Trois-Rivières, Trois-Rivières, 113 pp., 2002.
- Ellis, C. J. and Rochefort L.: Century-scale development of polygon-patterned tundra wetland, Bylot Island (73° N, 80° W), *Ecology*, 4, 963-978, 2004.
- Fortier, D., Allard, M. and Shur, Y.: Observation of rapid drainage system development by thermal erosion of ice wedges on Bylot Island, Canadian Arctic Archipelago, *Permafrost Periglac.*, 18, 229–243, 2007.
- Gauthier, G., Hughes, R. J., Reed, R., Beaulieu, J. and Rochefort, L.: Effect of grazing by greater snow geese on the production of graminoids at an arctic site (Bylot Island, NWT, Canada). *J. Ecol.*, 83, 653–664, 1995.
- Godin, E. and Fortier, D.: Geomorphology of thermo-erosion gullies – case study from Bylot Island, Nunavut, Canada, in: *Proceedings, 6th Canadian Permafrost Conference and 63rd Canadian Geotechnical Conference*, Calgary, 2010.
- Godin, E. and Fortier, D.: Fine scale spatio-temporal monitoring of multiple thermo-erosion gullies development on Bylot Island, eastern canadian archipelago, in: *Proceedings, Tenth International Conference on Permafrost (TICOP)*, Salekhard, Russia, 7 pp., 2012.
- Godin, E. Fortier, D. and Lévesque, E.: Nonlinear thermal and moisture dynamics of high Arctic wetland polygons following permafrost disturbance, *Biogeosciences Discuss.*, 12, 11797-11831, doi:10.5194/bgd-12-11797-11831, 2015
- Hughes, R. J., Gauthier, G. and Reed, A.: Summer habitat use and behaviour of Greater Snow Geese *Anser caerulescens*, *Wildfowl*, 45, 49-64, 1994.
- Legagneux, P., Gauthier, G., Berteaux, D., Bêty, J., Cadieux, M.-C., Bilodeau, F., Bolduc, E., McKinnon, L., Tarroux, A., Therrien, J.-F., Morissette, L. and Krebs, C. J.: Disentangling trophic relationships in a High Arctic tundra ecosystem through food web modeling, *Ecology*, 93, 1707-1716, 2012.

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

N. Perreault^{1,2}, E. Lévesque^{1,2}, D. Fortier^{2,3}, L. J. Lamarque^{1,2}

¹Département des Sciences de l'environnement, Université du Québec à Trois-Rivières,
Trois-Rivières, QC, G9A 5H7, Canada

²Centre d'études nordiques, Université Laval, Québec, QC, G1V 0A6, Canada

³Département de géographie, Université de Montréal, Montréal, QC, H2V 2B8, Canada

Correspondence to: E. Lévesque (Esther.Levesque@uqtr.ca)

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 of thermo-erosion ~~processes~~ in shaping plant community changes. ~~Over two years, we~~ We explored over two years the influence of environmental factors on plant species richness, abundance and biomass studying 197 sites including 62 in intact low-centered polygons that covered the whole transition from intact wet, to disturbed 87 in polygons disturbed by thermo-erosion and 48 in mesic habitats environments. ~~While~~ Gullying decreased soil moisture by 40 % and thaw front depth by 10 cm in breached polygons, ~~we observed~~ which has entailed a gradual yet marked vegetation shift 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 ~~sites environments~~. Our results therefore illustrate that wetlands are highly vulnerable to the process of thermo-erosion ~~processes, which can drive landscape transformation on a relative short period of time for High Arctic perennial plant communities.~~ ~~that~~ The succession towards mesic plant communities may can rapidly have substantial consequences on ~~promote the decrease of the~~ food availability for herbivores and ~~reduce~~ 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). ~~For instance, permafrost~~Permafrost impedes water to drain to deeper soil layers ~~and maintaining maintains~~ a perched water table and saturated soils which favors the existence of wetlands~~across the Arctic~~ (Woo, 2012; Natali et al., 2015). ~~These wet habitats are dominated by highly productive graminoid species which offer abundant high quality food for arctic herbivores (Manseau and Gauthier, 2003; Doiron, 2014) while significantly contributing to methane emission (Brummel et al., 2012; Bouchard et al., 2014).~~ 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). ~~This~~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).

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 tunneling and the development of gully networks in both aeolian and organic depositional environments which cover about 20 000 m² (Fortier et al., 2007; Godin and Fortier, 2010, 2012a). A fine-scale spatio-temporal monitoring study of the six largest gullies showed that their development rate ranges 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 eroded area throughout the valley (Godin and Fortier, 2014).

~~The extent to which vegetation is affected by thermo-erosion gullying is currently unknown, and contrasts with the extensive literature that has documented increased plant abundance, growth and biomass as well as shrub expansion northward in response to climate warming.~~ 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; Boulanger-Lapointe et al., 2014; Naito and Cairns, 2015). Substantial work has also been devoted to the vegetation response to disturbances such as landslides associated with permafrost degradation (Ukrantseva 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~~ ~~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, which 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), ~~which on the other hand may reduce active layer thickness and permafrost thaw rate (Blok et al., 2010).~~

The present study aimed at examining plant community patterns following thermo-erosion ~~processes~~ gullyng. Bylot Island, where geomorphological and ecological processes in response to climate change have been monitored for over two decades (~~Gauthier et al., 1995;~~ 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 valley (*ca* 50 km²) is characterized by a low-centered polygon ~~patterned landscape~~ landscape that ~~has results resulted~~ from ice-wedge development and sediment accumulation during the late Holocene (Ellis and Rochefort, 2004; Fortier and Allard, 2004; Ellis et al.,

2008). ~~It is defined by elevated ridges that enclose a central depression usually flooded by snowmelt water (Woo and Young, 2006; Minke et al., 2007).~~

Two ~~main-baseline~~ plant communities can be recognized ~~at the study site in the valley~~. 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 Lowlow-centered polygon rims, sloping terrain and hummocky tundra, support ~~mesic species such as individuals of~~ *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 snow geese, brown and collared lemmings (Gauthier et al., 1995; Gruyer et al., 2008), and thus represent a critical environment for tundra food web (Gauthier et al., 2011; Legagneux et al., 2012).

2.2 Field sites

Our work was specifically conducted ~~along-around~~ three gullies that were selected among the 36 identified in the valley (~~Fig. 1b~~; Godin and Fortier, 2012b). These gully networks have originated from snowmelt water infiltration into thermal contraction cracks and the formation of underground tunnels that have ended up collapsing (Fortier et al., 2007). All three were located in the low-centered polygon complex of the Qarlikturvik valley. The Gullies gullies AR08p and BR06, respectively 835 and 717 m long, are characterized by substantial-ongoing thermo-erosion processes (Fortier et al., 2007; Godin and Fortier, 2012b) whilst the gully-C RN08, 180 m long, has not been active in recent years. A total of 197 polygons (i.e. sampling sites) (i.e. polygons) were randomly selected along-around the three gullies (Table 1; Fig. 1b

~~n = 95, 79 and 21 for gully A, B and C, respectively).~~) and ~~They were~~ classified into one of four ~~polygon~~ categories (referred hereafter as habitats) that ~~were defined by the following characteristics:~~ represented the two baseline plant communities (wet and mesic) as well as increasing levels of thermo-erosion related disturbance. The disturbed habitats were sorted via a visual assessment of the polygon rim integrity coupled with a recent close monitoring of drainage ~~observation system development along the gullies and polygon location along the gully~~ (Fortier et al., 2007; Godin and Fortier, 2012^{a,b}). The habitats were ~~sorted~~ defined as follows: (i) ~~undisturbed intact low-centered~~ wet polygons (n = 62); ~~encompassing sites~~ 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). ~~i.e. with intact rims and non-apparent ice wedges;~~ (ii) recently (less than five years) disturbed polygons (n = 44), ~~characterizing sites~~ located along the ~~gully~~ most recent sections of the gullies, and that have been recently perturbed, i.e. with partially degraded rims, ongoing incomplete drainage and apparent ice wedges heterogeneous water content; (iii) more than five-year disturbed polygons (n = 43), ~~representing sites where rims are with~~ heavily breached rims adjacent to the gullies degraded and substantial or complete drainage ~~is almost complete~~; (iv) mesic environments (n = 48), ~~characterizing sites located along the oldest gully sections and where rims have entirely collapsed with distinct heterogeneous mesic vegetation. They are found throughout the valley and are thus not necessarily induced by thermo-erosion gullyng.~~

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 AR08p (Gauthier et al., 2010). Soil (top 10 cm) moisture ~~content~~ was recorded at the center of each polygon using ECH₂O EC-5 moisture sensors 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 AR08p and BR06, and July 30 only in the polygons of the gully CRN08-polygons. Thaw front depth was recorded at the polygon centers ~~of each polygon~~ using a steel rod graduated in centimetre and driven in the active layer. ~~This was done late July 2009 and 2010 in polygons located along gullies A and B, and mid-July 2010 in those situated along gully C~~ 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, except for the mesic ~~sites-environments~~ where three measurements were randomly conducted because of the heterogeneity of this type of habitat. In this case, means per site were calculated prior to analyses.

2.4 Plant community characterization

Species richness and abundance were determined in each polygon in July 2009 or 2010 using randomly placed 70 cm x 70 cm quadrats within areas that were representative of the ~~habitatssite~~ (Fig. 2). Abundances of vascular plants, lichens, mosses, *Nostoc* sp., 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 method~~ (Daubenmire, 1959) ~~was then applied~~ were used on each quadrat picture overlain a 7 cm grid to evaluate species cover as the projection on the

ground of all species above-ground parts.

Five polygons 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 grids of 25 cm x 25 cm for wet and recently disturbed polygons and of 50 cm x 20 cm for long-time 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 ~~vegetation-graminoids~~ present in the enclosures ~~was-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-live vascular species biomass were-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~~-content and-~~, thaw front depth and graminoid above-ground biomass between-among habitats were tested with a generalized linear mixed model (procedure GLM-MIXED, REML method in SAS, version 9.4, SAS Institute, Cary, NC, USA). Soil moisture~~-content~~, thaw front depth as well as date or year of measurements and the interaction terms were ~~the-treated as fixed~~ factors included in the model 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). ~~SNK-post-Post~~ hoc contrasts were performed to ascertain specific differences between habitats at $\alpha < 0.05$ using the LSMEANS statement and Bonferroni adjustment. ~~Differences in graminoid above-ground biomass between habitats were tested using a one-way analysis of variance (procedure ANOVA). Distributions of variables were tested for normality prior to analyses using Shapiro-Wilk test (procedure UNIVARIATE). Contrary to graminoid above-ground biomass ($W = 0.95$, $P = 0.42$), soil moisture content ($W = 0.96$, $P < .001$) and thaw front depth ($W = 0.98$, $P = 0.002$) did not meet normal distribution assumptions, therefore analyses were performed on log-transformed data for these two variables (Tabachnik and Fidell, 1996; Quinn and Keough, 2002).~~ Canonical Correspondence Analyses (CCA) were conducted to test unimodal relationships between ~~eco-terrain sites~~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 ~~66-species~~65 taxa using ~~species-their~~ mean cover per site (i.e. polygon), and another of 197 sites x 8 environmental characteristics comprising the following continuous variables: soil moisture~~-content~~, 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 ~~ones~~ 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

~~(June 28)~~. 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 significantly increased
soil moisture ~~were an important water input for the polygons and explain the significant~~
~~difference observed in soil moisture~~ between the two monitoring dates (significant date effect:
 $df = 1$, $F = 55.5088.99$, $P < .001$; Fig. 23) 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 ~~also overall~~ a significant difference in soil moisture ~~content~~ among habitats
 ($df = 3$, $F = 38.0279.86$, $P < .001$; Fig. 2), which was driven both in early and late July by
 differences between wet polygons and the other habitats (early 5 July: $df = 3$, $F = 18.7233.41$,
 $P < .001$, late 30 July: $df = 3$, $F = 19.3447.36$, $P < .001$; Fig. 3, Table 4A1). Throughout the
 summer, soil moisture was approximately 40 % higher in wet sites compared to disturbed and
 mesic ~~ones environments~~. ~~There was no significant habitat x date interaction ($df = 3$, $F = 0.06$,
 ~~$P = 0.98$).~~ We also found a significant difference in thaw front depth ~~among habitats ($df = 3$,
 ~~$F = 51.51$, $P < 0.001$; Fig. 3), which was also driven by significant differences~~ between wet
 polygons and the other habitats (2009: $df = 3$, $F = 20.5421.30$, $P < .001$, 2010: $df = 3$, $F =$
 $33.0933.86$, $P < .001$; Fig. 4, Table A1). Thaw front depth of wet polygons was approximately
 10 cm deeper than in disturbed and mesic sites (35-36 vs 25-27 cm) for both years of
monitoring (non-significant year effect: $df = 1$, $F = 1.52$, $P = 0.22$, non-significant habitat x
year effect: $df = 3$, $F = 0.12$, $P = 0.95$). ~~There was no significant difference between years of~~
~~thaw front depth monitoring ($df = 1$, $F = 0.46$, $P = 0.50$; Fig. 3) and no significant habitat x~~
~~year interaction ($df = 3$, $F = 0.14$, $P = 0.94$).~~ We did not find any 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 (~~Appendix A~~ [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 ~~sites-environments~~ and ~~accounted~~ [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 ~~sites-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*, *Stereoacaulon* and *Peltigera* sp. increased in polygons disturbed for at least five years and mesic environments \(Table 2\). Mosses were mostly found live in wet polygons and mesic environments and dried in disturbed sites \(Table 2\), while a significant species turnover was observed between habitats with wetland-dominant *Drepanocladus* spp. replaced by *Aulacomnium* spp. in mesic environments.](#)

[Moreover, we observed](#) ~~Vegetation changes were also observed~~ through the decline of graminoid above-ground biomass which varied significantly among habitats ($df = 3$, $F = 11.59$, $P < 0.001$; ~~Table 1~~; Fig. [4a5a](#); [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 ~~sites-environments~~ (29.2 vs 5.9 g.m⁻²; Fig. [2](#) and [4a5a](#); ~~Appendix B~~). 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 sites, respectively; Fig. 4b5b). Above-ground biomass of *Luzula spp*, *Arctagrostis latifolia* and *Festuca brachyphylla* was contrastingly fifteen times greater in mesic than in wet habitats (4.45 vs 0.29 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 ~~eco-terrain units~~ four studied habitats defined in the polygon-patterned landscape of the Qarlikturvik valley. Wet polygons were mainly related to high soil moisture ~~content~~ and substantial thaw front depth (~~i.e. active layer thickness~~) whilst mesic environments were associated with greater litter cover (Fig. 56). A gradual vegetation transition was also observed along the soil moisture gradient from the polygons disturbed less than five years ago to the ones that have been disturbed for a longer period of time (Fig. 56).

4 Discussion

Sustainability of wetlands at high latitudes 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-erosion and the development of gullies (Fortier et al., 2007; Godin and Fortier, 2014). We show here that thermo-erosion significantly alters wetlands by ~~rapidly~~ decreasing soil moisture ~~content~~ and thaw front depth of low-centered polygons adjacent to gullies. ~~More importantly,~~ ~~v~~Vegetation ~~was~~ is sensitive to this process, and mesic habitat plant species ~~replaced~~ gradually replace hydrophilic ~~ones-species~~ within ~~a~~ five to ten years span. This vegetation turn-over ~~can has have~~ substantial consequences on wildlife biology, permafrost stabilization and ecosystem-level greenhouse gas emissions (Blok et al., 2010; Doiron et al., 2014; McEwing et al., 2015).

4.1 Transition in environmental conditions

Thermo-erosion gullying has led to a significant decrease ~~of in~~ soil moisture ~~content~~ of disturbed polygons following polygon rim erosion and water runoff through frost cracks, ~~which~~ 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). and concurs with a modeling analysis showing that the transformation of low-centered to high-centered polygon landscape following ice-wedge melting is accompanied with a significant alteration in the water balance partitioning (Liljedahl et al., 2012). ~~While intact wet sites store important quantities of water during spring snowmelt and summer rainfalls, gully formation rapidly reduces water conservation capacity of breached polygons due to polygon ridge erosion and water runoff through frost cracks leading to increased hydrological connectivity (Fortier et al., 2007; Godin and Fortier, 2014).~~ In our study, disturbed polygons responded positively to a given summer rainfall event in a similarly way than intact polygons (no significant habitat x date interaction). Yet, 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 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).

However, disturbed polygons still responded positively to summer rainfalls, and their summer volumetric water content was much more dependent of these rainfalls than in wet sites (data not shown). This is in line with the work of Godin et al. (submitted to special issue) at the polygon scale, who found that soil moisture content variability in disturbed sites is significantly greater than in undisturbed polygons.

Decreasing soil moisture ~~content~~ in disturbed polygons came with decreasing thaw front depth. While this result was expected given that active layer thickness is closely related to local hydrological processes (Nelson et al., 1999; Hinzman et al., 2005; Minke et al., 2009; Wright et al., 2009; Gangodagamage et al., 2014), it contrasts with the active layer thickening generally observed in response to climate ~~change~~ warming (Tarnocai et al., 2004; Woo et al., 2007; Akerman and Johansson 2008; Smith et al., 2009; Nauta et al., 2015). ~~In addition, the values of thaw front depth obtained at our sampled sites are of similar order of magnitude than those measured by Godin et al. (submitted to special issue) in their intact and disturbed polygons.~~ Within five years of drainage, thaw front depth in disturbed polygons decreased by 37 % compared to that in intact wet sites. 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 (Wright et al., 2009).

4.2 Vegetation changes

Overall, the floristic composition of our sampled 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 as they offered a middle-range state between wet and mesic conditions.

~~Gully~~ The development of gullies in the Qarlikturvik valley and the subsequent drainage of adjacent low-centered polygons ~~has~~ have led to a ~~radical~~ gradual change in plant communities with vegetation of disturbed polygons leaning towards that of mesic environments, thus illustrating the standard plant succession following climatic and/or geomorphic variations (Billings and Peterson, 1980; Ellis and Rochefort, 2006; Woo & Young, 2006). Mesic habitat 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 process in disturbed polygons follows the directional-species replacement model examined by Svoboda and Henry (1987). It is however relatively more rapid than what is usually documented for the High Arctic where perennial plant communities are highly 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). The gradual yet rapid species replacement is 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 as well as recently disturbed from long-time disturbed habitats.

The 37 % decrease in soil moisture between intact 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 ~~content~~ in separating plant community types at high latitudes has indeed been ~~previously~~ well documented (Hinzman et al., 2005; Daniëls and de Molenaar, 2011; Daniëls et al., 2011; Sandvik and Odland, 2014). ~~This is particularly the case of Ducloux (2002), who surveyed mesic and dried habitats of Bylot Island, and Mann et al. (2002), who reported that vegetation community changes in Alaska over the past 8-13,000 years mostly relied on soil moisture changes.~~ 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 intact polygons, which was expected since these two factors are closely related ~~to each other~~ (see section 4.1); (ii) litter cover separated mesic ~~polygons~~ environments from the others, which ~~can~~ 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 greater abundance and biomass of Cyperaceae species at these sites (Fig. 45); (iv) goose feces were mainly associated with long-time disturbed and mesic ~~sites~~ 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.

Overall, the floristic composition of our sampled 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* also characterizes well the typical vegetation of Arctic wetlands (Jorgenson et al., 2013; Sandvik and Odland, 2014; Lara et al., 2015). While the highest in disturbed polygons, species richness increased from wet and mesic environments, which is concordant with previous work showing changes in species richness in response to climate change (Britton et al., 2009; Pauli et al., 2012; Ross et al., 2012; Sandvik and Odland, 2014). More interestingly, we highlight here the rapidity of vegetation transition in response to gully development, which can be surprising given that Arctic plant communities can be highly resistant to disturbance (Hollister et al., 2005; Jonsdottir et al., 2005; Hudson and Henry, 2010). Mesic habitat species such as *Luzula* and *Salix spp* have gradually established following the decrease in soil moisture and thaw front depth, and completely replaced hydrophilic Cyperaceae and Poaceae within ten years after gully initiation. Plant species turn-over was also observed in moss species (data not shown), with mesic habitat *Aulacomnium* sp. replacing wetland dominant *Drepanochladus* sp. (Ellis and Rochefort, 2004; Pouliot et al., 2009). Given that previous work has mainly characterized long term sensitivity of wetlands to climate and geomorphologic changes (Woo & Young, 2006; Myers-Smith et al., 2008), our results offer a new perspective on vegetation response to ongoing global change.

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 of mesic environments and therefore less and less suitable. Effects of thermo-erosion gullyng were

~~however opposite to that of climate warming, which tends to increase plant biomass across continents and latitudes (Baldwin et al., 2014).~~ 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 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) ~~used~~ worked on wet sites 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 mesic sites adjacent to our study area (E. Lévesque, unpublished data). Overall, total above-ground biomass in wetlands and mesic environments is of similar 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 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). ~~Thus, the degradation of wetland habitat following thermo-erosion gullyng will probably limit the availability of high-quality food to geese since mesic habitats have a lower carrying capacity than wetlands (Massé et al., 2001). It remains to quantify the extent to which gullyng alters wetland carrying capacity. Moreover, climate warming can speed up the seasonal decline in nutritive quality of forage plants, eventually impacting goose gosling size and conditions (Doiron, 2014).~~ 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 gullyng-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; 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 ~~greater 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

469 to determine in the near future the specific evolution of *Salix* and *Luzula spp* primary
470 production in mesic sites in order to accurately predict the effects of wetland retreat on
471 methane and soil organic carbon cycles.

5 Conclusions

This study illustrates that changes ~~the shift~~ in the hydrological and thermal regimes following the induction of thermo-erosion gullies boost ~~the transition~~landscape transformation of from wet to mesic ~~plant communities~~habitats within low-centered polygon landscapes, providing evidence that permafrost degradation is a critical component of ~~vegetation~~ecosystem modification at high latitudes. ~~More importantly, gully effects such as increasing drainage and wetland degradation go in the opposite direction to what is generally observed in response to climate warming.~~ 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, while surface warming is expected to alter the ground's thermal regime (Couture and Pollard, 2007), more work should be devoted to the ~~understanding of the feedback effects of~~ plant communities and vegetation succession ~~may have on the~~ thermal and mechanical stabilization dynamics of disturbed permafrost terrains ~~disturbed by thermo-erosion gully~~. This is especially needed since plant community differences between disturbed and ~~undisturbed~~intact sites can last several centuries (Cray and Pollard, 2015).

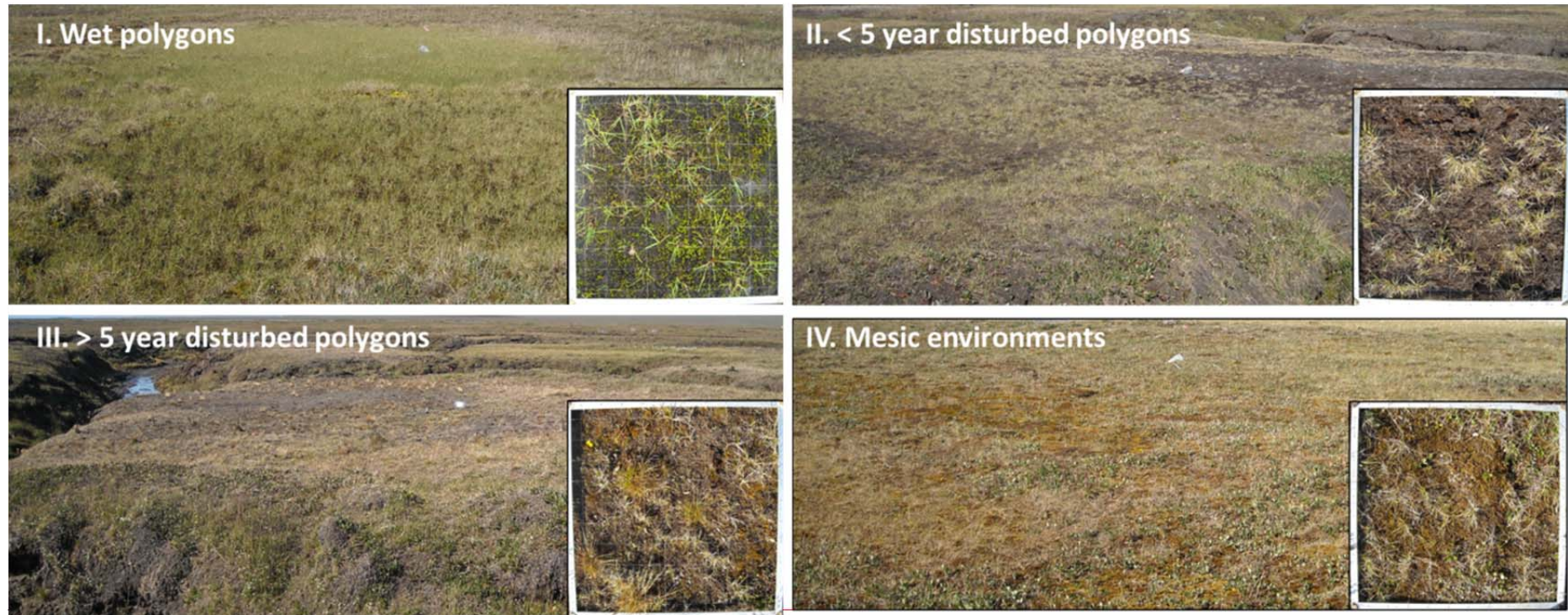
Table A1. Sample sizes and means (\pm SE) of soil moisture, thaw front depth and graminoid above-ground biomass in the four habitats studied in the Qarlikturvik valley of Bylot Island, Nunavut. Letters refer to post hoc contrasts that were carried out using the LSMEANS statement and Bonferroni adjustment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

<u>Habitats</u>	<u>Soil moisture</u> <u>5 Jul 2010 (%)</u>		<u>Soil moisture</u> <u>30 Jul 2010 (%)</u>		<u>Thaw front depth</u> <u>Jul 2009 (cm)</u>		<u>Thaw front depth</u> <u>Jul 2010 (cm)</u>		<u>Above-ground</u> <u>biomass (g/m²)</u>	
	<u>n</u>	<u>Mean \pm SE</u>	<u>n</u>	<u>Mean \pm SE</u>	<u>n</u>	<u>Mean \pm SE</u>	<u>n</u>	<u>Mean \pm SE</u>	<u>n</u>	<u>Mean \pm SE</u>
<u>Wet polygons</u>	<u>53</u>	<u>36.3 \pm 1.7a</u>	<u>54</u>	<u>48.0 \pm 1.3a</u>	<u>52</u>	<u>36.0 \pm 0.9a</u>	<u>62</u>	<u>34.6 \pm 0.8a</u>	<u>5</u>	<u>29.2 \pm 5.2a</u>
<u>< 5-year disturbed polygons</u>	<u>39</u>	<u>21.9 \pm 1.2b</u>	<u>39</u>	<u>31.0 \pm 1.5b</u>	<u>39</u>	<u>25.5 \pm 1.5b</u>	<u>44</u>	<u>25.0 \pm 1.1b</u>	<u>5</u>	<u>22.3 \pm 1.4a</u>
<u>> 5-year disturbed polygons</u>	<u>33</u>	<u>22.0 \pm 1.1b</u>	<u>33</u>	<u>31.2 \pm 1.2b</u>	<u>32</u>	<u>25.3 \pm 1.1b</u>	<u>43</u>	<u>24.9 \pm 0.8b</u>	<u>5</u>	<u>9.3 \pm 4.0b</u>
<u>Mesic environments</u>	<u>46</u>	<u>19.6 \pm 1.3b</u>	<u>50</u>	<u>28.4 \pm 1.4b</u>	<u>44</u>	<u>27.6 \pm 1.1b</u>	<u>48</u>	<u>26.5 \pm 0.7b</u>	<u>5</u>	<u>5.9 \pm 2.6b</u>

493 | **Appendix-Table A2.** List of the vascular plant species inventoried in the Qarlikturvik valley, Bylot Island, Nunavut during the 2009 and 2010
 494 field seasons. Species names are from the integrated taxonomic information system (ITIS 2011).
 495

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.

496
 497 ^a *Draba* sp. was not counted as a distinct species because it is probably one of the five species already mentioned.



498
499
500

Appendix B. Illustration of the four low-centered polygon habitats studied in the Qarlikturvik valley of Bylot Island, Nunavut.

501 **Acknowledgements**

502 The authors are grateful to the Inuit community of Pond Inlet and to Parks Canada-Sirmilik
503 National Park, Centre d'études nordiques (CEN) and Dr Gilles Gauthier (Université Laval)
504 for the access to the field camp during summers 2009, 2010 and 2012. We also thank
505 Alexandre Guertin-Pasquier, Etienne Godin, Jonathan Lasnier, Stephanie Coulombe and
506 Coralie Henry-Brouillette for their fieldwork support as well as Alexandre Moreau, Stephan
507 Ouellet, Noémie Boulanger-Lapointe for their help with statistical analyses. This project was
508 funded by the International Polar Year program of the Government of Canada, Fonds
509 Québécois de la Recherche sur la Nature et les Technologies (FQRNT), Natural Sciences and
510 Engineering Research Council of Canada (NSERC), Network of Centers of Excellence of
511 Canada ArcticNet, Northern Scientific Training Program (NSTP), NSERC CREATE Training
512 Program in Northern Environmental Sciences (EnviroNorth) and Groupe de Recherche en
513 Biologie Végétale (GRBV) of Université du Québec à Trois-Rivières. Essential logistic
514 support was provided by Polar Continental Shelf Program (Natural Resources Canada).

515 References

- 516 [Ackerly, D.: Functional strategies of chaparral shrubs in relation to seasonal water deficit and](#)
 517 [disturbance, Ecol. Monogr., 74, 25-44, 2004.](#)
- 518 Akerman, H. J. and Johansson, M.: Thawing permafrost and thicker active layer in sub-arctic
 519 Sweden, Permafrost Periglac., 19, 279-292, 2008.
- 520 Allard, M.: Geomorphological changes and permafrost dynamics: key factors in changing
 521 arctic ecosystems. An example from Bylot Island, Nunavut, Canada, Geosci. Can., 23,
 522 205–212, 1996.
- 523 Audet, B., Lévesque, E. and Gauthier G.: Seasonal variation in plant nutritive quality for
 524 Greater Snow Goose goslings in mesic tundra, Can. J. Bot., 85, 457-462, 2007.
- 525 Avis, C. A., Weaver, A. J. and Meissner, K. J.: Reduction in areal extent of high-latitude
 526 wetlands in response to permafrost thaw, Nat. Geosci., 4, 444-448, 2011.
- 527 [Baldwin, A. H., Jensen, K. and Schönfeldt, M.: Warming increases plant biomass and reduces](#)
 528 [diversity across continents, latitudes, and species migration scenarios in experimental](#)
 529 [wetland communities, Glob. Change Biol., 20, 835-850, 2014.](#)
- 530 Beck, I., Ludwig, R., Bernier, M., Lévesque, E. and Boike, J.: Assessing permafrost
 531 degradation and land cover changes (1986-2009) using remote sensing data over Umiujaq,
 532 sub-Arctic Québec, Permafrost Periglac., DOI: 10.1002/ppp.1839, 2015.
- 533 Beilman, D. W. and Robinson, S. D.: Peatland permafrost thaw and landform type along a
 534 climate gradient, in: Proceedings, Eighth International Conference on Permafrost, edited by:
 535 Phillips, M., Springman, P. M. and Arenson, S. U., A. A. Balkema, Zurich, Switzerland, 1,
 536 61-65, 2003.
- 537 Billings, W. D. and Peterson, K. M.: Vegetational change and ice-wedge polygons through the
 538 thaw-lake cycle in Arctic Alaska, Arct. Alp. Res., 12, 413–432, 1980.
- 539 Blok, D., Heijman, M. M. P. D., Schaepman-Strub, G., Kononov, A. V., Maximov, T. C. and
 540 Berendse, F.: Shrub expansion may reduce summer permafrost thaw in Siberia tundra,
 541 Glob. Change Biol., 16, 1296-1305, 2010.
- 542 [Bouchard, F., Francus, P., Pienitz, R., Laurion, I. and Feyte, S.: Subarctic thermokarst ponds:](#)
 543 [Investigating recent landscape evolution and sediment dynamics in thawed permafrost of](#)
 544 [Northern Québec \(Canada\), Arct. Antarct. Alp. Res., 46, 251-271, 2014.](#)
- 545 Bouchard, F., Laurion, I., Preskienis, V., Fortier, D., Xu, X. and Whitticar, M. J.: Modern to
 546 millennium-old greenhouse gases emitted from freshwater ecosystems of the Eastern
 547 Canadian Arctic, Biogeosciences Discuss., 12, 11661-11705, doi:10.5194/bgd-12-11661-
 548 2015, 2015.
- 549 Boulanger-Lapointe, N., Lévesque, E., Boudreau, S., Henry G. H. G. and Schmidt, N. M.:
 550 Population structure and dynamics of Arctic willow (*Salix arctica*) in the High Arctic, J.
 551 Biogeogr., 41, 1967-1978, 2014.
- 552 Britton, A. J. et al.: Biodiversity gains and losses: evidence for homogenization of Scottish
 553 alpine vegetation, Biol. Conserv., 142, 1728-1739, 2009.
- 554 [Brummel, M. E., Farrell, R. E. and Siciliano, S. D.: Greenhouse gas soil production and](#)
 555 [surface fluxes at a high arctic polar oasis, Soil Biol. Biochemistry, 52, 1-12, 2012.](#)
- 556 Cadieux, M.-C., Gauthier, G., Gagnon, C. A., Lévesque, E., Bêty, J. and Berteaux, D.:
 557 Monitoring the environmental and ecological impacts of climate change on Bylot Island,
 558 Sirmilik National Park, Université Laval, 113 pp., 2008.
- 559 [Cannone, N., Lewkowicz, A. G. and Guglielmin, M.: Vegetation colonization of permafrost-](#)
 560 [related landslides, Ellesmere Island, Canadian High Arctic, J. Geophys. Res., 115, G04020,](#)
 561 [doi:10.1029/2010JG001384, 2010.](#)
- 562 Cray, H. A. and Pollard, W. H.: Vegetation recovery patterns following permafrost
 563 disturbance in a Low Arctic setting: case study of Herschel Island, Yukon, Canada, Arct.

564 Antarct Alp. Res., 47, 99-113, 2015.
 565 Chen, Z. H., Chen, W. J. and Leblanc, S. G. and Henry, G. H. R.: Digital photograph analysis
 566 for measuring percent plant cover in the Arctic, Arctic, 63, 315–326, 2010.
 567 Christiansen, H. H., Eltzelmüller, B., Isaksen, K., Juliussen, H., Farbrot, H., Humlum, O.,
 568 Johansson, M., Ingeman-Nielsen, T., Kristensen, L., Hjort, J. et al.: The thermal state of
 569 permafrost in the Nordic Area during the International Polar Year 2007-2009, Permafrost
 570 Periglac., 21, 156-181, 2010.
 571 Collins, Knutti, R., Arblaster, J., Dufresne, J.-L., Fichet, T., Friedlingstein, P., Gao, X.,
 572 Gutowski, W. K., Johns, T., Krinner, G. et al.: Long-term climate change: Projections,
 573 commitments and irreversibility, in: Climate change 2013: the physical basis, Contribution
 574 of working group I to the Fifth Assessment Report of the Intergovernmental Panel on
 575 Climate Change, edited by: Stocker, T. F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.
 576 K., Boschung, J., Nauels, A., Xia, Y., Bex, V. and Midgley, P. M., Cambridge University
 577 Press, Cambridge, United Kingdom, 2013.
 578 Couture, N. J. and Pollard, W. H.: Modelling geomorphic response to climatic change, Clim.
 579 Change, 85, 407–431, 2007.
 580 Dagg, J. and Lafleur, P.: Vegetation community, foliar nitrogen, and temperature effects on
 581 tundra CO₂ exchange across a soil moisture gradient, Arct. Antarct. Alp. Res., 43, 189-197,
 582 2011.
 583 Daniëls, F. J. A. and de Molenaar, J. G.: Flora and vegetation of Tasiilaq, formerly
 584 Angmagssalik, southeast Greenland: a comparison of data between around 1900 and 2007,
 585 Ambio, 40, 650-659, 2011.
 586 Daniëls, F. J. A. et al.: Vegetation change in southeast Greenland? Tasiilaq revisited after 40
 587 years, J. Appl. Veg. Sci., 14, 230-241.
 588 Daubenmire, R.: A canopy-coverage method of vegetation analysis, Northwest Sci., 33,
 589 43–64, 1959.
 590 Doiron, M.: Impacts des changements climatiques sur les relations plantes-herbivores dans
 591 l'Arctique, PhD thesis, Université Laval, 123 pp., 2014.
 592 Doiron, M., Gauthier, G. and Lévesque, E.: Effects of experimental warming on nitrogen
 593 concentration and biomass of forage plants for an arctic herbivore, J. Ecol. 102, 508-517,
 594 2014.
 595 Duclos, I.: Milieux mésiques et secs de l'Île Bylot, Nunavut (Canada): caractérisation et
 596 utilisation par la Grande Oie des Neiges. MSc thesis, Université du Québec à Trois-
 597 Rivières, Trois-Rivières, 113 pp., 2002.
 598 Ellis, C. J. and Rochefort L.: Century-scale development of polygon-patterned tundra
 599 wetland, Bylot Island (73° N, 80° W), Ecology, 4, 963-978, 2004.
 600 Ellis, C. J. and Rochefort L.: Long-term sensitivity of a High Arctic wetland to Holocene
 601 climate change, 94, 441-454, J. Ecol., 2006.
 602 Ellis, C. J., Rochefort L., Gauthier G. and Pienitz, R.: Paleoecological evidence for transitions
 603 between contrasting landforms in a polygon-patterned High Arctic wetland, Arct. Antarct.
 604 Alp. Res., 40, 624–637, 2008.
 605 Epstein, H. E., Myers-Smith, I. and Walker, D. A.: Recent dynamics of arctic and sub-arctic
 606 vegetation, Environ. Res. Lett., 8, 015040, 6 pp., 2013.
 607 Ewertowski, M.: Ice-wedge pseudomorphs and frost-cracking structures in Weichselian
 608 sediments, Central-West Poland, Permafrost Periglac., 20, 316-330, 2009.
 609 Fortier, D. and Allard, M.: Late Holocene syngenetic ice-wedge polygons development, Bylot
 610 Island, Canadian Arctic Archipelago, Can. J. Earth Sci., 41, 997–1012, 2004.
 611 Fortier, D. and Allard, M.: Frost-cracking conditions, Bylot Island, Eastern Canadian Arctic
 612 archipelago, Permafrost Periglac., 16, 145-161, 2005.

- Fortier, D., Allard, M. and Pivot, F.: [A late-Holocene record of loess deposition in ice-wedge polygons reflecting wind activity and ground moisture conditions, Bylot Island, eastern Canadian Arctic, Holocene, 16, 635-646, 2006.](#)
- Fortier, D., Allard, M. and Shur, Y.: Observation of rapid drainage system development by thermal erosion of ice wedges on Bylot Island, Canadian Arctic Archipelago, *Permafrost Periglac.*, 18, 229–243, 2007.
- Gangodagamage, C., Rowland, J. C., Hubbard, S. S., Brumby, S. P., Liljedahl, A. K., Wainwright, H., Wilson, C. J., Altmann, G. L., Dafflon, B., Peterson, J. et al.: Extrapolating active layer thickness measurements across Arctic polygonal terrain using LiDAR and NDVI data sets, *Water Resour. Res.*, 50, doi:10.1002/2013WR014283, 2014.
- Gauthier, G., Bêty, J., Cadieux, M.-C., Legagneux, P., Doiron, M., Chevallier, C., Lai, S., Tarroux, A. and Berteaux D.: [Long-term monitoring at multiple trophic levels suggests heterogeneity in responses to climate change in the Canadian Arctic tundra, Phil. Trans. R Soc. B, 368: 20120482, 12 pp., 2013.](#)
- Gauthier, G., Cadieux, M.-C., Lefebvre, J., Bêty, J. and Berteaux D.: Population study of Greater Snow Geese and its nesting habitat on Bylot Island, Nunavut, in 2009: A progress report, 31 pp., 2009.
- Gauthier, G., Cadieux, M.-C., Lefebvre, J., Bêty, J. and Berteaux D. Population study of Greater Snow Geese and its nesting habitat on Bylot Island, Nunavut, in 2010: A progress report, 32 pp., 2010.
- Gauthier, G., Cadieux, M.-C., Lefebvre, J., Bêty, J. and Berteaux D. Population study of Greater Snow Geese and its nesting habitat on Bylot Island, Nunavut, in 2012: A progress report, 36 pp., 2012.
- Gauthier, G., Berteaux D., Bêty, J., Tarroux, A., Therrien, J.-F., McKinnon, L., Legagneux, P. and Cadieux, M.-C.: The tundra food web of Bylot Island in a changing climate and the role of exchanges between ecosystems, *Ecoscience*, 18, 223-235, 2011.
- Gauthier, G., Hughes, R. J., Reed, R., Beaulieu, J. and Rochefort, L.: Effect of grazing by greater snow geese on the production of graminoids at an arctic site (Bylot Island, NWT, Canada). *J. Ecol.*, 83, 653–664, 1995.
- Gauthier, G., Rocheford, L. and Reed, A.: The exploitation of wetland ecosystems by herbivores on Bylot Island, *Geosci. Can.*, 23, 253–259, 1996.
- Godin, E. and Fortier, D.: Geomorphology of thermo-erosion gullies – case study from Bylot Island, Nunavut, Canada, in: *Proceedings, 6th Canadian Permafrost Conference and 63rd Canadian Geotechnical Conference, Calgary, 2010.*
- Godin, E. and Fortier, D.: Fine scale spatio-temporal monitoring of multiple thermo-erosion gullies development on Bylot Island, eastern canadian archipelago, in: *Proceedings, Tenth International Conference on Permafrost (TICOP), Salekhard, Russia, 7 pp., 2012a.*
- Godin, E. and Fortier, D.: Geomorphology of a thermo-erosion gully, Bylot Island, Nunavut, Canada, *Can. J. Earth Sci.*, 49, 979-986, 2012b.
- Godin, E., Fortier, D. and Coulombe, S.: Effects of thermo-erosion gullying on hydrologic flow networks, discharge and soil loss, *Environ. Res. Lett.*, 9, 10 pp., doi:10.1088/1748-9326/9/10/105010, 2014.
- Godin, E. Fortier, D. and Lévesque, E.: Nonlinear thermal and moisture dynamics of high Arctic wetland polygons following permafrost disturbance, *Biogeosciences Discuss.*, 12, 11797-11831, doi:10.5194/bgd-12-11797-2015, 2015.
- Grosse, G., Harden, J., Turetsky, M., McGuire A. D., Camill, P., Tarnocai, C., Frohking, S., Schuur, E. A. G., Jorgenson, T., Marchenko, S. et al.: Vulnerability of high-latitude soil organic carbon in North America to disturbance, *J. Geophys. Res.*, 116, G00K06, doi:10.1029/2010JG001507, 2011.

- Gruyer, N. G., Gauthier, G. and Berteaux, D.: Cyclic dynamics of sympatric lemming populations on Bylot Island, Nunavut, Canada, *Can. J. Zool.*, 86, 910-917, 2008.
- Günther, F., Overduin, P. P., Sandakov, A. V., Grosse, G. and Grigoriev, M. N.: Short- and long-term thermo-erosion of ice-rich permafrost coasts in the Laptev Sea region, *Biogeosciences*, 10, 4297-4318, 2013.
- Harms, T. K., Abbott, B. W. and Jones, J. B.: Thermo-erosion gullies increase nitrogen available for hydrologic export, *Biogeochemistry*, 117, 299-311, 2014.
- Hinzman, L. D., Bettez, N. D., Bolton, W. R., Chapin III, F. S., Dyurgerov, M. B., Fastie, C. L., Griffith, B., Hollister, R. D., Hope, A., Huntington, H. P. et al.: Evidence and implications of recent climate change in northern Alaska and other arctic regions, *Clim. Change*, 72, 251-298, 2005.
- Hollister, R. D., Webber, P. J. and Tweedie, C. E.: The response of Alaskan arctic tundra to experimental warming: differences between short- and long-term responses, *Glob. Change Biol.*, 11, 525-536, 2005.
- Hudson, J. M. G. and Henry, G. H. R.: High Arctic plant community resists 15 years of experimental warming, *J. Ecol.*, 98, 1035-1041, 2010.
- Hughes, R. J., Reed, A. and Gauthier, G. Space and habitat use by greater snow goose broods on Bylot Island, Northwest Territories. *J. Wildlife Manage.*, 58, 536-545. 1994.
- IPY, International Polar Year: Climate Change Impact on Canadian Arctic Tundra, Protocols for taking vertical photographs and field measurements of plant height for biomass and LAI estimation in Arctic tundra (for vegetation height < 0.5 m), <http://ipytundra.ca/protocols>, 2012.
- Jonsdottir, I. S., Magnusson, B., Gudmunsson, J., Elmarsdottir, A. and Hjartarson, H.: Variable sensitivity of plant communities in Iceland to experimental warming, *Glob. Change Biol.*, 11, 553-563, 2005.
- Jorgenson, M. T., Harden, S., Kanevskiy, M., O'Donnell, J., Wickland, K., Ewing, S., Manies, K., Zhuang, Q., Shur, Y., Striegl, R. and Koch, J.: Reorganization of vegetation, hydrology and soil carbon after permafrost degradation across heterogeneous boreal landscapes, *Environ. Res. Lett.*, 8, 13 pp., doi:10.1088/1748-9326/9/10/105010, 2013.
- Jorgenson, M. T., Romanosky, V., Harden, S., Shur, Y., O'Donnell, J., Schuur E. A. G., Kanevskiy, M. and Marchenko, S.: Resilience and vulnerability of permafrost to climate change, *Can. J. For. Res.*, 40, 1219-1236, 2010.
- Jorgenson, M. T., Shur, Y. T. and Pullman, E. R.: Abrupt increase in permafrost degradation in Arctic Alaska, *Geophys. Res. Lett.*, 33, L02503, doi:10.1029/2005GRL024960, 2006.
- Kokelj, S. V., Lantz, T. C., Wolfe, S. A., Kanigan, J. C., Morse, P. D., Coutts, R., Molina-Giraldo, N. and Burn, C. R.: Distribution and activity of ice wedges across the forest-tundra transition, western Arctic Canada, *J. Geophys. Res. Earth Surf.*, 119, doi:10.1002/2014JF003085, 2014.
- Kutzbach, H. J., Wagner, D. and Pfeiffer, E. M.: Effect of microrelief and vegetation on methane emission wet polygonal tundra, Lena Delta, Northern Siberia. *Biogeochemistry*, 69, 341-362, 2004.
- Lara, M. J., McGuire, A. D., Euskirchen, E. S., Tweedie, C. E., Hinkel, K. M., Skurikhin, A. N., Romanovsky, V. E., Grosse, G., Bolton, W. R. and Genet, H.: Polygonal tundra geomorphological change in response to warming alters future CO₂ and CH₄ flux on the Barrow Peninsula, *Glob. Change Biol.*, 21, 1634-1651, 2015.
- Lecomte, N., Gauthier, G. and Giroux, J.-F.: A link between water availability and nesting success mediated by predator-prey interactions in the Arctic, *Ecology*, 90, 465-475, 2009.
- Legagneux, P., Gauthier, G., Berteaux, D., Bêty, J., Cadieux, M.-C., Bilodeau, F., Bolduc, E., McKinnon, L., Tarroux, A., Therrien, J.-F., Morissette, L. and Krebs, C. J.: Disentangling

- trophic relationships in a High Arctic tundra ecosystem through food web modeling, *Ecology*, 93, 1707-1716, 2012.
- Levy, J. S., Head, J. W. and Marchant, D. R.: The role of thermal contraction crack polygons in cold-desert fluvial systems, *Antarct. Sci.*, 20, 565-579, 2008.
- Liljedahl, A. K., Hinzman, L. D. and Schulla, J.: Ice-wedge polygon type controls low-gradient watershed-scale hydrology, in: Proceedings, Tenth International Conference on Permafrost (TICOP), Salekhard, Russia, 6 pp., 2012.
- Littell, R. C., Milliken, G. A., Stroup, W. W., Wolfinger, R. D. and Schabenberger, O.: SAS® for Mixed Models, 2nd edn, SAS Institute Inc, Cary, NC, 2006.
- Manseau, M. and Gauthier, G.: Interactions between greater snow geese and their rearing habitat, *Ecology*, 74, 2045–2055, 1993.
- Massé, H., Rochefort, L. and Gauthier, G.: Carrying capacity of wetland habitats used by breeding greater snow geese, *J. Wildlife Manage.*, 65, 271–281, 2001.
- McEwing, K. R., Fisher, J. P. and Zona, D.: Environmental and vegetation controls on the spatial variability of CH₄ emission from wet-sedges and tussock tundra ecosystems in the Arctic, *Plant Soil*, 338, 37-52, 2015.
- Minke, M., Donner, D., Karpov, N. S., de Klerk, P. and Joosten, H.: Distribution, diversity, development and dynamics of polygon mires: examples from Northeast Yakutia (Siberia), *Peatlands Int.*, 1, 36–40, 2007.
- Minke, M., Donner, D., Karpov, N. S., de Klerk, P. and Joosten, H.: Patterns in vegetation composition, surface height and thaw depth in polygon mires in the Yakutian Arctic (NE Siberia): a microtopographical characterisation of the active layer, *Permafrost Periglac.*, 20, 357–368, 2009.
- Muc, M., Freedman, B. and Svoboda, J.: Vascular plant communities of a polar oasis at Alexandra Fiord (79°N), Ellesmere Island, Can. J. Bot., 67, 1126-1136, 1989.
- Myers-Smith, I. H.: Carbon exchange and permafrost collapse: implications for a changing climate, MSc thesis, University of Alaska Fairbanks, Fairbanks, 66 pp., 2005.
- Myers-Smith, I. H., Warden, J. W., Wilkening, M., Fuller, C. C., McGuire, A. D. and Chapin III, F. S.: Wetland succession in a permafrost collapse: interactions between fire and thermokarst, *Biogeosciences*, 5, 1273-1286, 2008.
- Naito, A. T. and Cairns, D. M.: Patterns of shrub expansion in Alaskan arctic river corridors suggest phase transition, *Ecol. Evol.*, 5, 87-101, 2015.
- Natali, S. M., Schuur, E. A. G., Mauritz, M., Schade, J. D., Celis, G., Crummer, K. G., Johnston, C., Krapek, J., Pegoraro, E., Salmon, V. G. and Webb, E. E.: Permafrost thaw and soil moisture driving CO₂ and CH₄ release from upland tundra, *J. Geophys. Res. Biogeosci.*, 120, doi:10.1002/2014JG002872, 2015.
- Nauta, A. L., Heijmans, M. M. P. D., Blok, D., Limpens, J., Elberling, B., Gallagher, A., Li, B., Petrov, R. E., Maximov, T. C., van Huissteden, J. and Berendse, F.: Permafrost collapse after shrub removal shifts tundra ecosystem to a methane source, *Nature Clim. Change*, 5, 67-70, 2015.
- Nelson, F. E., Shiklomanov, N. I. and Mueller, G. R.: Variability of active-layer thickness at multiple spatial scales, North-central Alaska, U.S.A, *Arct. Antarct. Alp. Res.*, 31, 179-186, 1999.
- Nelson, F. E., Shiklomanov, N. I., Hinkel, K. M. and Brown J.: Decadal results from the Circumpolar Active Layer Monitoring (CALM) program, *Proceedings, Ninth International Conference on Permafrost*, edited by: Hinkel, K. M. and Kane, D. L., 1273-1280, University of Alaska Press, Fairbanks, Alaska, 2008.
- New, M., Liverman, D., Schroder, H. and Anderson, K.: Four degrees and beyond: the potential for a global temperature increase of four degrees and its implications, *Phil. Trans. R. Soc. A*, 369, 6-19, 2011.

NOAA (National Oceanic and Atmospheric Administration), Arctic Research Program: Arctic Report Card, edited by: Jeffries, M. O., Richter-Menge, J. and Overland, J. E., <http://www.arctic.noaa.gov/reportcard>, 2014.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., O'Hara, B., Simpson, G. L., Solymos, P., Stevens, M. H. M. and Wagner, H.: *vegan: Community ecology package, R package version 2.2-1*, 2015.

Olefeldt, D., Turetsky, M. R., Crill, P. M. and McGuire, A. D.: Environmental and physical controls on northern terrestrial methane emissions across permafrost zones, *Glob. Change Biol.*, 19, 589-603, 2013.

Payette, S., Delwaide, A., Caccianiga, M. and Beauchemin, M.: Accelerated thawing of subarctic peatland permafrost over the last 50 years, *Geophys. Res. Lett.*, 31, L18208, 2004.

Pauli, K. et al.: High Arctic vegetation after 70 years: a repeated analysis from Svalbard, *Pol. Biol.*, 33, 635-639, 2012.

Perreault, N.: *Impact de la formation de ravins de thermo-erosion sur les milieux humides, Ile Bylot, Nunavut, Canada, MSc thesis, Université du Québec à Trois-Rivières, 104 pp., 2012.*

Poesen, J., Nachtergaele, J., Verstraeten, G. and Valentin, C.: Gully erosion and environmental change: importance and research needs, *Catena*, 50, 91-133, 2003.

Pouliot, R., Rochefort, L. and Gauthier, G.: Moss carpets constrain the fertilizing effects of herbivores on graminoid plants in arctic polygon fens, *Botany*, 87, 1209-1222, 2009.

R Development Core Team: *R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0, URL http://www.R-project.org*, 2015.

Ross, L. C. et al.: Biotic homogenization of upland vegetation: patterns and drivers at multiple spatial scales over five decades, *J. Veg. Sci.*, 23, 755-770, 2012.

Rowland, J. C., Jones, C. E., Altmann, G., Bryan, B., Crosby, B. T., Geernaert, G. L., Hinzman, L. D., Kane, D. L., Lawrence, D. M., Mancino, A., Marsh, P., McNamara, J. P., Romanosky, V. E., Toniolo, H., Travis, B. J., Trochim, E. and Wilson C. J.: Arctic landscapes in transition: responses to thawing permafrost, *Eos Trans. Am. Geophys. Union*, 91, 229-236, 2010.

Romanovsky, V. E., Smith, S. L., and Christiansen, H. H.: Permafrost thermal state in the polar Northern Hemisphere during the international polar year 2007–2009: a synthesis, *Permafrost Periglac.*, 21, 106-116, doi:10.1002/ppp.689, 2010.

Sandvik, S. M. and Odland, A.: Changes in alpine snowbed-wetland vegetation over three decades in norther Norway, *Nordic J. Bot.*, 32, 377-384, 2014.

Sedinger, J. S., White, R. G., Mann, F. E., Burris, F. A. and Kedrowski, R. A.: Apparent metabolizability of alfalfa components by yearling Pacific Black Brant, *J. Wildl. Manage.*, 53, 726-734, 1989.

Seppälä, M.: Piping causing thermokarst in permafrost, Ungava Peninsula, Quebec, Canada, *Geomorphology*, 20, 313–319, 1997.

Sheard, J. W. and Geale, D. W.: Vegetation studies at Polar Bear Bass, Bathurst Island, N.W.T., I. Classification of plant communities, *Can. J. Bot.*, 61, 1618-1636, 1983.

Shiklomanov, N. I., Streletskiy, D. A., Nelson, F. E., Hollister, R. D., Romanovsky, V. E., Tweedie, C. E., Bockheim, J. G. and Brown, J.: Decadal variations of active-layer thickness in moisture-controlled landscapes, Barrow, Alaska, *J. Geophys. Res.*, 115, G00I04, 2010.

Sjöberg, Y.: Linking water and permafrost dynamics, PhD thesis, Stockholm University, 27 pp., 2015.

- Smith, S.: Trends in permafrost conditions and ecology in northern Canada: Ecosystem Status and Trends 2010, Technical Thematic Report No. 9, Canadian Councils of Resource Ministers, Ottawa, ON, iii + 22 p, 2011.
- Smith, S. L., Burgess, M. M., Riseborough, D. and Nixon, F. M.: Recent trends from Canadian Permafrost Thermal Monitoring network sites, *Permafrost Periglac.*, 16, 19-30, 2005.
- Smith, S. L., Wolfe, S. A., Riseborough, D. W. and Nixon, F. M.: Active-layer characteristics and summer climatic indices, Mackenzie Valley, Northwest Territories, Canada, *Permafrost Periglac.*, 20, 201-220, 2009.
- Tarnocai, C., Nixon, F. M. and Kutny, L.: Circumpolar-Active-Layer-Monitoring (CALM) sites in the Mackenzie Valley, Northwestern Canada, *Permafrost Periglac.*, 15, 141-153, 2004.
- Treat, C. C., Natali, S. M., Ernakovitch, J., Iversen, C. M., Lupascu, M., McGuire, A. D., Norby, R. J., Chowdhury, T. R., Richter, A., Santruckova, H. et al.: A pan-Arctic synthesis of CH₄ and CO₂ production from anoxic soil incubations, *Glob. Change. Biol.*, doi:10.1111/gcb.12875, 2015
- Tveit, A. T., Urich, T., Frenzel, P. and Svenning, M. M.: Metabolic and trophic interactions modulate methane production by Arctic peat microbiota in response to warming, *Proc. Nat. Ac. Sci.*, doi:10.1073/pnas.1420797112, 2015.
- Ukraitseva, N. G., Streletskaya, I. D., Ermokhina, K. A. and Yermakov, S. Yu.: Geochemical properties of plant-soil-permafrost systems on landslide slopes, Yamal, Russia, in: Proceedings, Tenth International Conference on Permafrost, Zurich, Switzerland, 1149-1154, 2003.
- USGCRP: Global Climate Change Impacts in the United States, edited by: Karl, T. R., Melillo, J. M. and Peterson, T. C., United States Global Change Research Program, Cambridge University Press, New York, NY, 2009.
- ter Braak, C. J. F.: Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis, *Ecology*, 67, 1167–1179, 1986.
- Vonk, J. E., Mann, P. J., Dowdy, K. L., Davydova, A., Davydov, S. P., Zimov, N., Spencer, R. G. M., Bulygina, E. B., Eglinton, T. I. and Holmes, R. M.: Dissolved organic carbon loss from Yedonna permafrost amplified by ice wedge thaw, *Environ. Res. Lett.*, 8, 9 pp., doi:10.1088/1748-9326/8/3/035023, 2013.
- Walker, D. A., Leibman, M. O., Epstein, H. E., Forbes, B. C., Bhatt, U. S., Raynolds, M. K., Comiso, J. C., Gubarkov, A. A., Khomutov, A. V., Jia, G. J., Kaarlejärvi, E., Kaplan, J. O., Kumpula, T., Kuss, P., Matyshak, G., Moskalenko, N. G., Orekhov, P., Romanovsky, V. E., Ukraitseva, N. G. and Yu, Q.: Spatial and temporal patterns of greenness on the Yamal Peninsula, Russia: interactions of ecological and social factors affecting the Arctic normalized difference vegetation index, *Environ. Res. Lett.*, 4, 16 pp., doi:10.1088/1748-9326/4/4/045004, 2009.
- Woo, M.-K.: Permafrost hydrology, Springer, New York, NY, 564 pp., 2012.
- Woo, M.-K. and Young, K. L.: High Arctic wetlands: their occurrence, hydrological characteristics and sustainability, *Journal of Hydrology*, 320, 432–450, 2006.
- Woo, M.-K., Kane, D. L., Carey, S. K. and Yang, D.: Progress in permafrost hydrology in the new millennium, *Permafrost Periglac.*, 19, 237–254, 2008.
- Woo, M.-K., Mollinga, M. and Smith, S. L.: Climate warming and active layer thaw in the boreal and tundra environments of the Mackenzie Valley, *Can. J. Earth Sci.*, 44, 733-743, 2007.
- Wright, N., Hayashi, M. and Quinton, W. L.: Spatial and temporal variations in active layer thickness and their implication on runoff generation in peat-covered permafrost terrain, *Water Resources Res.*, 45, W05414, 2009.

860 Zamin, T. Z., Brett-Harte, M. S. and Grogan, P.: Evergreen shrubs dominate responses to
 861 experimental summer warming and fertilization in Canadian mesic low arctic tundra, *J.*
 862 *Ecol.*, doi: 10.1111/1365-2745.12237, 2014.
 863 Zoltai, S. C., McCormick K. J. and Scotter, G. W.: A natural resource survey of Bylot Island
 864 | and adjacent Baffin Island, Northwest Territories, Parks Canada, Ottawa, ON, 176 pp.,
 865 1983.
 866 Zuur, A. F., Ieno, E. N. and Smith, G. M.: Analysing ecological data, edited by: Gail, M.,
 867 | Krickeberg, K., Samet, J., Tsiatis, A. and Wong, W., Springer, New York, 672 pp., 2007.

Table 1. Sample sizes and means (\pm SE) of soil moisture content, thaw front depth and graminoid above-ground biomass in the four low-centered polygon habitats studied in the Qarlikturvik valley of Bylot Island, Nunavut. Letters refer to SNK post hoc contrasts. For a given variable, different letters indicate significant differences among habitats.

Habitat	Soil moisture July 5 2010 (%)		Soil moisture July 30 2010 (%)		Thaw front depth July 2009 (cm)		Thaw front depth July 2010 (cm)		Above-ground biomass (g/m ²)	
	n	Mean \pm SE	n	Mean \pm SE	n	Mean \pm SE	n	Mean \pm SE	n	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 polygons	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

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

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

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 polygons (n = 48)
		< 5 years (n = 44)	> 5 years (n = 43)	
Total species richness	36	37	54	47
Mean species richness	8	11	17	15
Plant 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	<	<

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

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	0.1911 <u>0.1910</u>
Cumulative % of vegetation data	7.29 <u>7.32</u>	13.60
Cumulative % of vegetation-environment relationship	42.8	79.8
Total inertia	3.0295 <u>3.0172</u>	

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. 1524 <u>1523</u>	11. 4008 <u>4495</u>	0.004008	0. 0212 <u>0206</u>	0. 8682 <u>8681</u>
Thaw front depth	1	0.1768		0.001	-	-
Soil moisture	1	0. 0430 <u>0429</u>	13. 2230 <u>2854</u>	0.006002	0. 8607 <u>8608</u>	0. 1439 <u>1436</u>
Standing dead	1	0. 0715 <u>0714</u>	3. 2157 <u>2206</u>	0.00701	-	0. 2425 <u>2424</u>
Bare ground	1	0. 0067 <u>0065</u>	5. 3467 <u>3688</u>	0.640629	-0.2393	0. 2580 <u>2588</u>
Standing water	1	0.0090	0. 4983 <u>4889</u>	0. 5495 <u>534</u>	0. 0209 <u>0207</u>	-
Grubbing	1	0.0240	3. 2157 <u>2206</u>	0. 0880 <u>97</u>	0. 7341 <u>7339</u>	0. 0529 <u>0522</u>
Goose feces	1	0. 0330 <u>0329</u>	0. 6728 <u>6759</u>	0.025028	-0.2365	0. 0829 <u>0830</u>
Residual	188	2. 5133 <u>5014</u>	1. 7932 <u>8003</u>		0. 1052 <u>1051</u>	0. 1982 <u>1983</u>
					0.4769	-
						0. 0768 <u>0772</u>

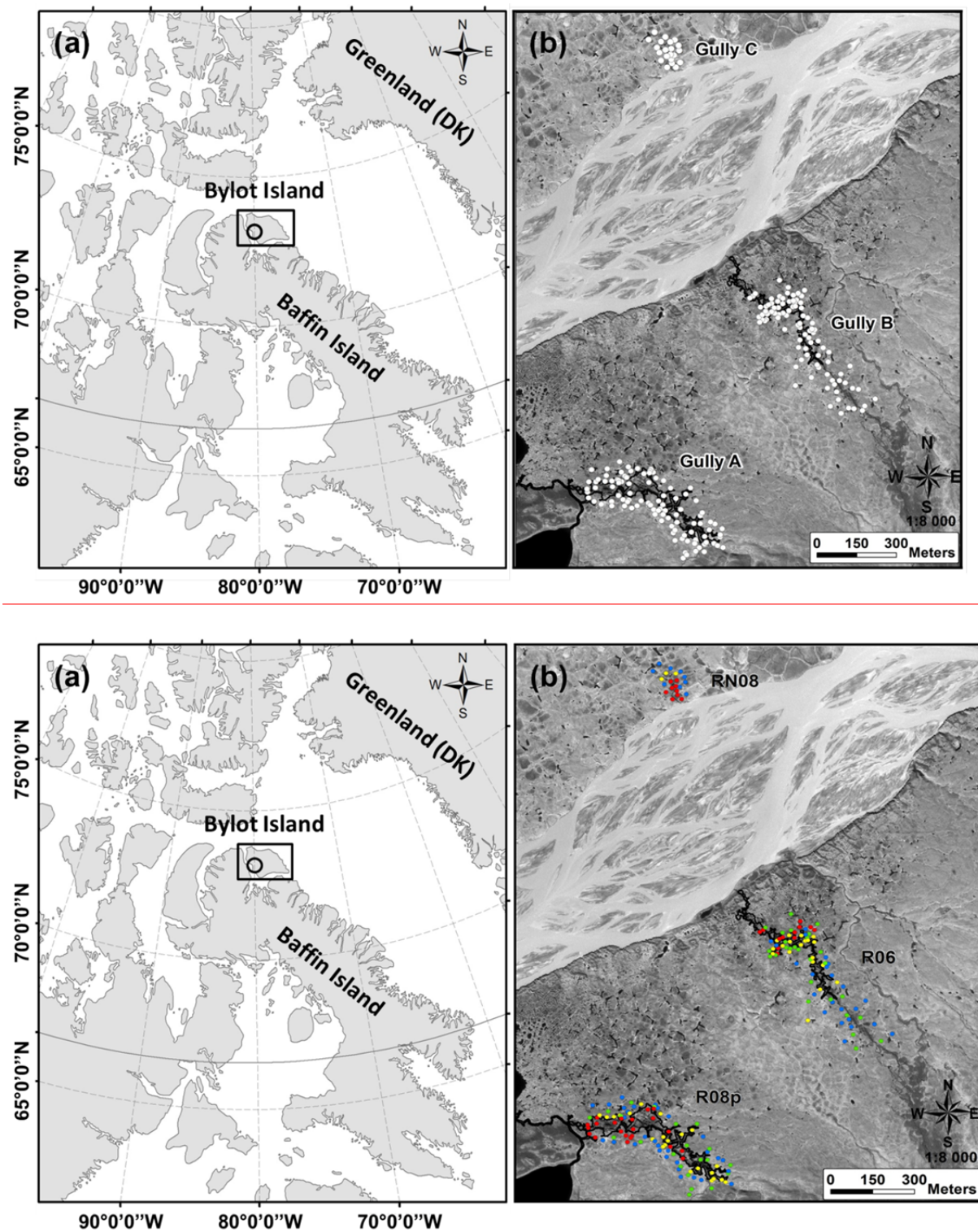


Figure 1. Location of the study area. (a) The Qarlikturvik valley (black circle) of Bylot Island, Nunavut (black rectangle). (b) the three gullies and the 197 sampling polygons (white dots) located in the Qarlikturvik valley sites sampled along three gullies (wet polygons (n = 62): blue circles; < 5-year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

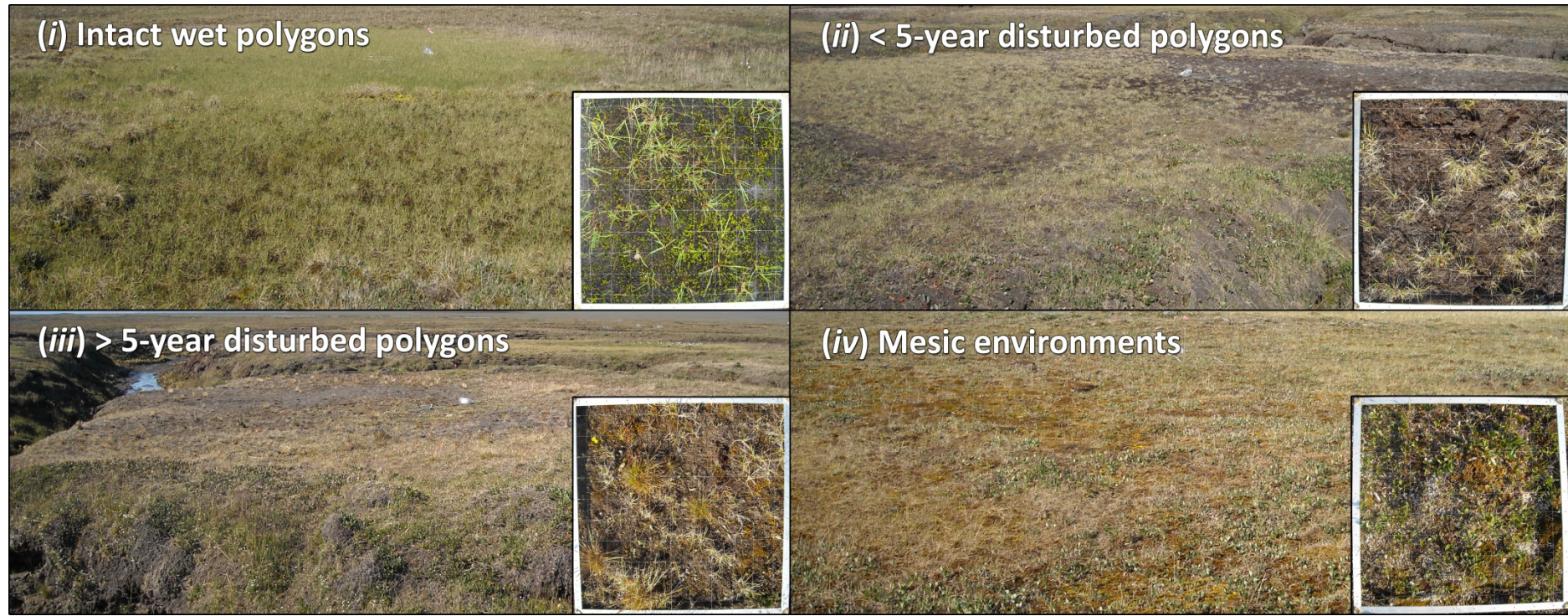


Figure 2. Illustration of the four habitats studied in the Qarlikturvik valley of Bylot Island, Nunavut. The close view at the bottom right of each picture represents the 70 cm x 70 cm quadrats that were used to determine species richness and abundance in each sampling site.

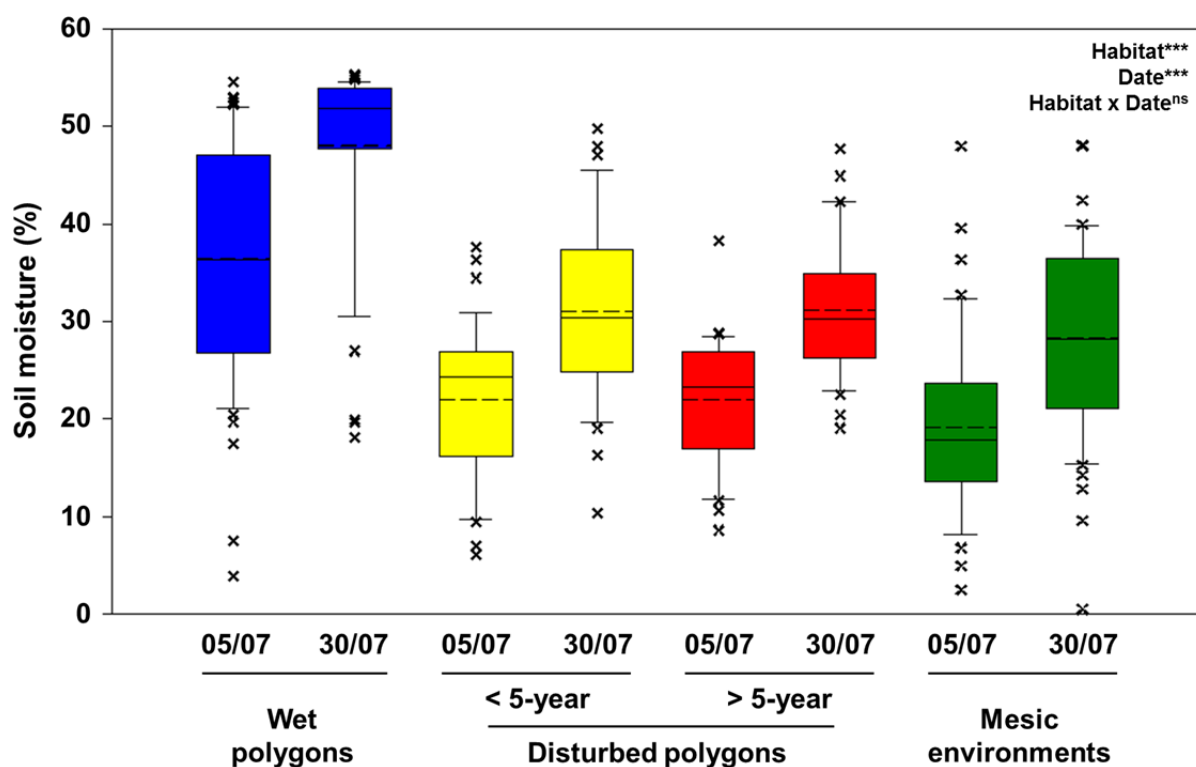
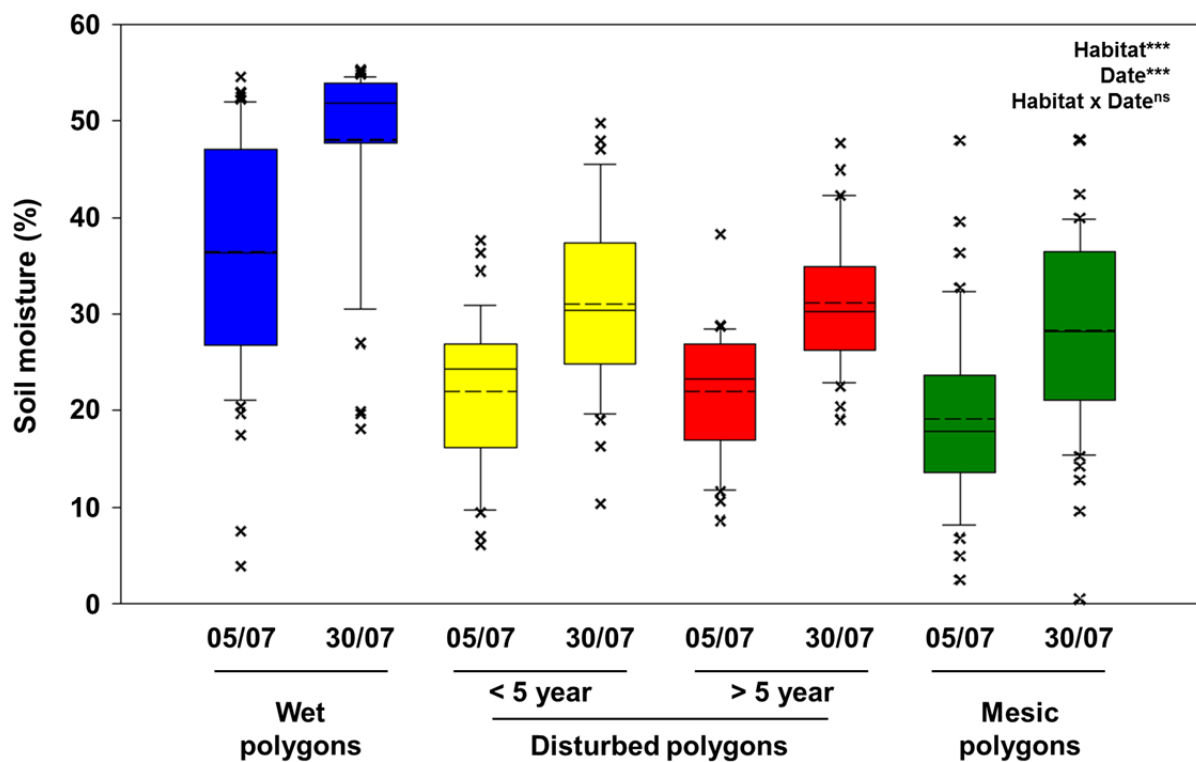


Figure 23. Soil moisture content-monitored early and late July 2010 in the four low-centered polygon-habitats studied in the Qarlikturvik valley of Bylot Island, Nunavut. 10th percentiles, lower quartile, median, mean (dash line), upper quartile and 90th percentiles are shown. See Table A1 for sample sizes and post-hoc contrasts. *** $P < .001$, ns: statistically non-significant effect.

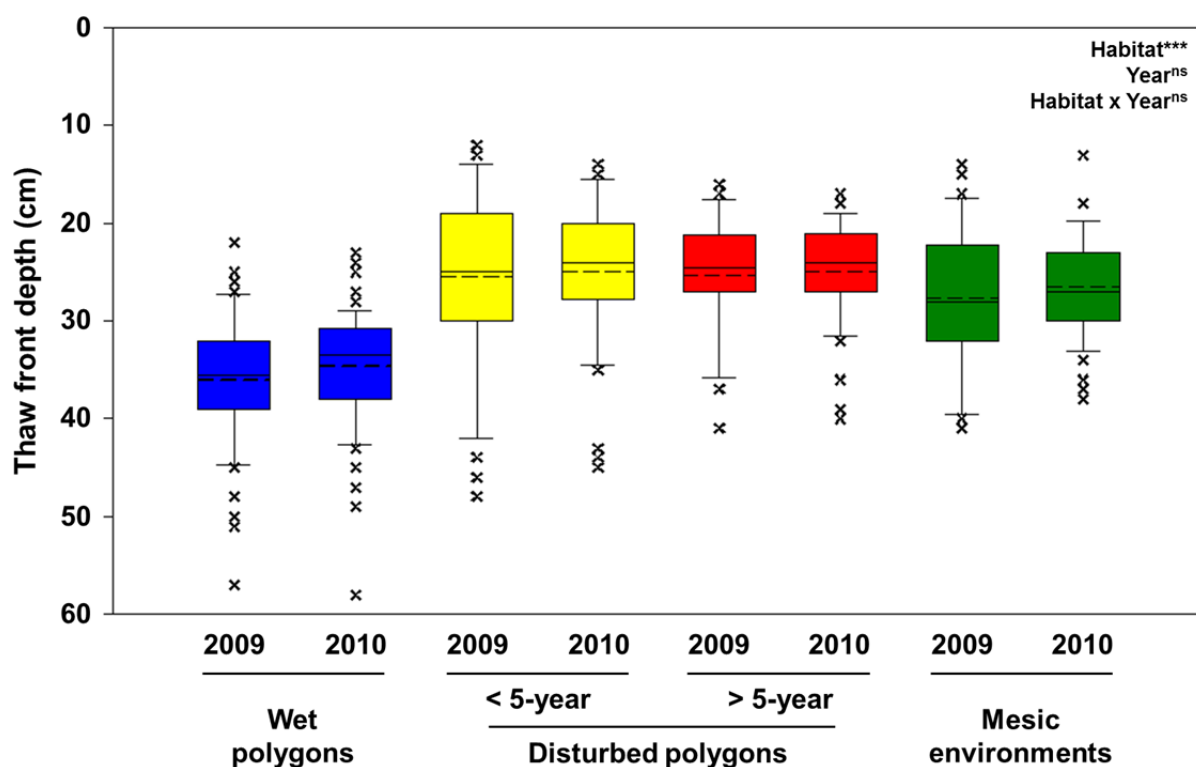
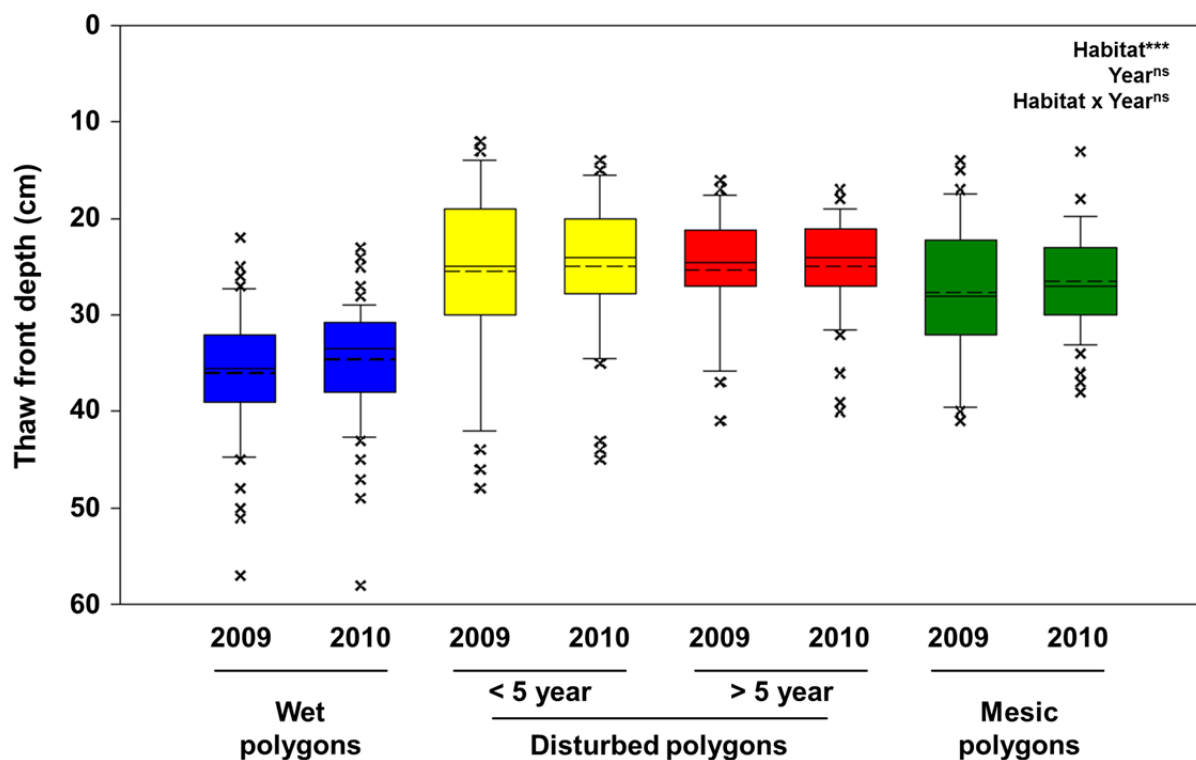
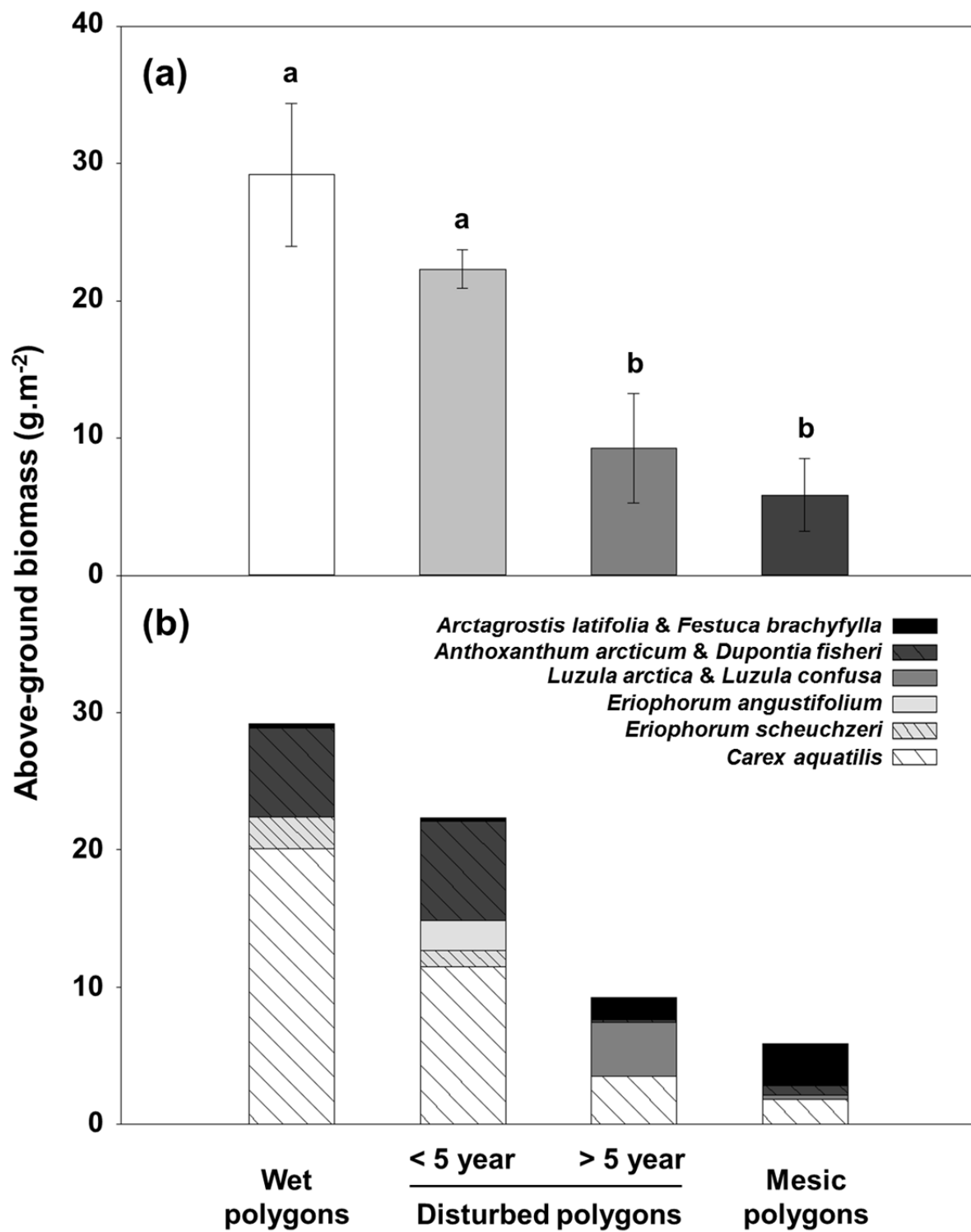


Figure 34. Thaw front depth monitored in July 2009 and 2010 in the four **low-centered polygon**-habitats studied in the Qarlikturvik valley of Bylot Island, Nunavut. 10th percentiles, lower quartile, median, mean (dash line), upper quartile and 90th percentiles are shown. See Table A1 for sample sizes and post-hoc contrasts. *** $P < .001$, ns: statistically non-significant effect.



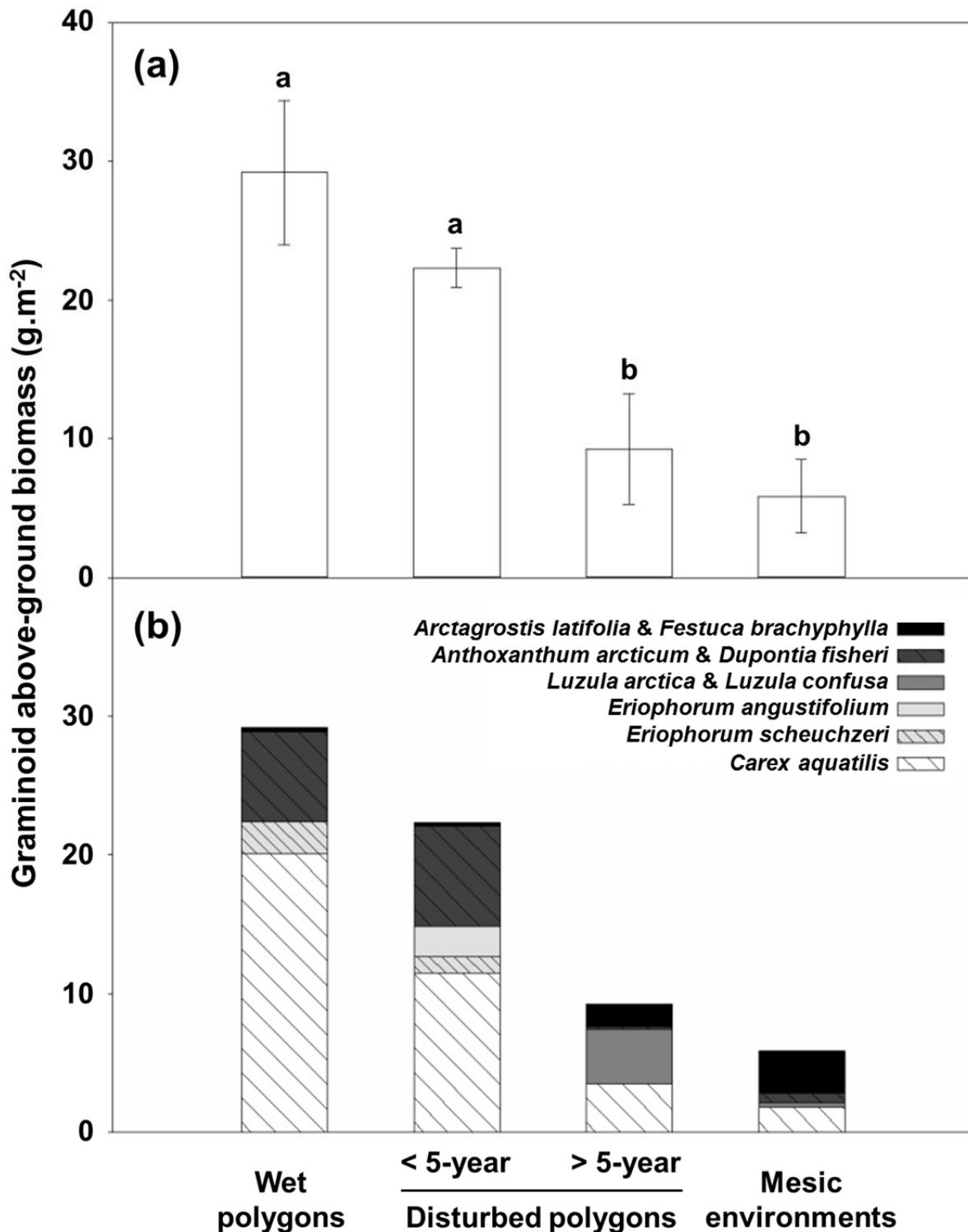


Figure 45. Above-ground biomass of graminoids growing in the four low-centered-polygon habitats studied in the Qarlikturvik valley of Bylot Island, Nunavut. (a) Mean total biomass (\pm SE), and (b) mean biomass per species. In panel (b), dashes represent hydrophilic species. $n = 5$ per habitat. Species 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*).

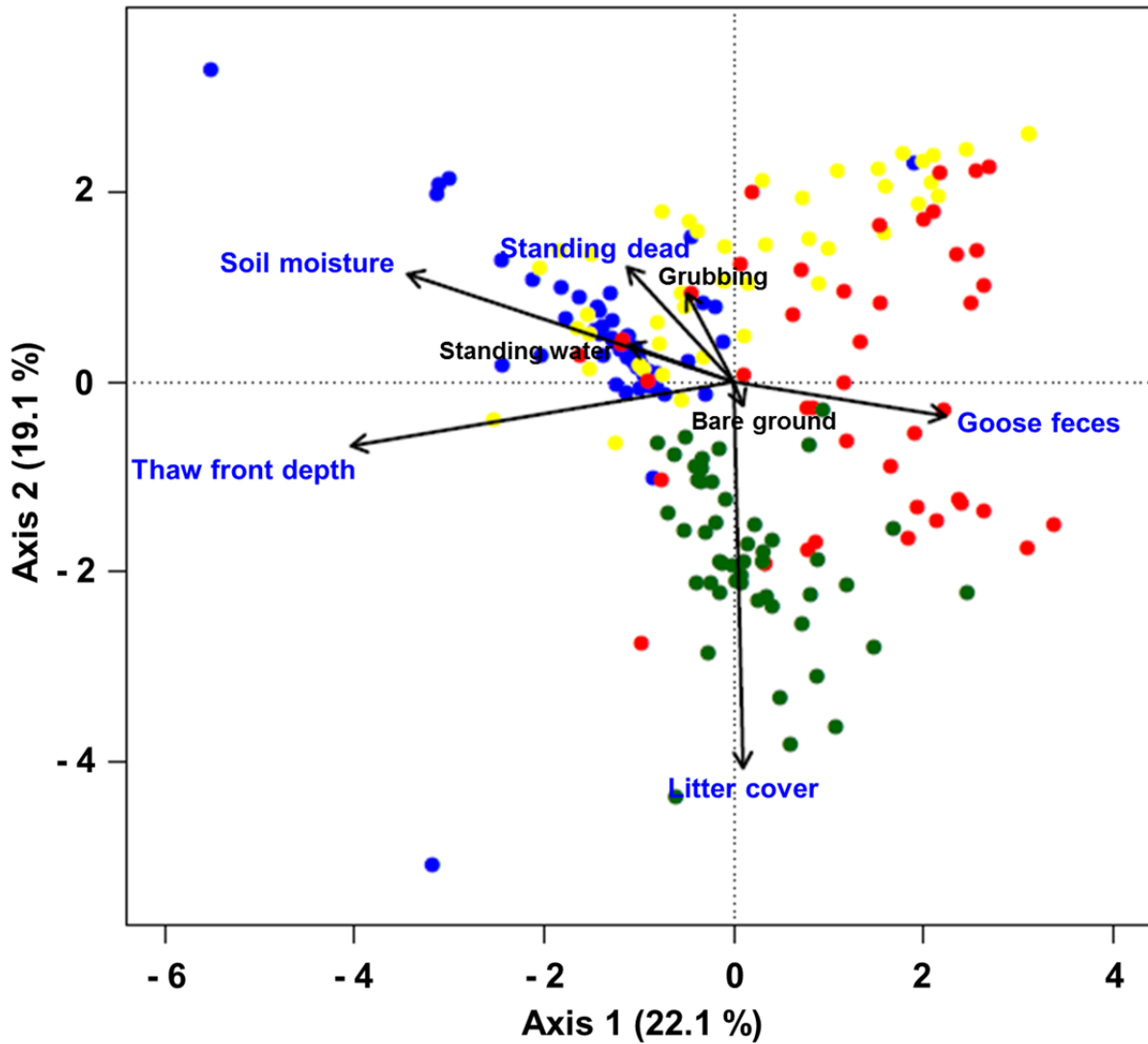


Figure 56. Canonical correspondence analysis (CCA) ordination of the 197 sites sampled in the Qarlikturvik valley of Bylot Island, Nunavut. Wet polygons (n = 62): blue circles; < 5-5-year disturbed polygons (n = 44): yellow circles; > 5-5-year disturbed polygons (n = 43): red circles; mesic environments (n = 48): green circles. Blue font indicates statistically significant environmental variables (see Table 4). Standing dead represents the cover of dead attached vascular plants.