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 in shaping plant community changes. 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, 87 in polygons disturbed by thermo-erosion and 48 in mesic environments. Gullying decreased soil moisture by 40 % and thaw front depth by 10 cm in breached polygons, 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 environments. Our results therefore illustrate that wetlands are highly vulnerable to the process of thermo-erosion, which can drive landscape transformation on a relative short period of time for High Arctic perennial plant communities. The succession towards mesic plant communities can have substantial consequences on the food availability for herbivores and methane emissions of Arctic ecosystems.

1 Introduction

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

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

Several forms of ground and massive ice can be found within permafrost (Rowland et al., 2010), especially ice-wedges in regions where winter temperatures enable thermal contraction cracking (Fortier and Allard, 2005; Ewertowski, 2009; Kokelj et al., 2014). 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 m^2 (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).

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 (Ukraintseva et al., 2003; Walker et al., 2009; Cannone et al., 2010). In contrast, little is known about how thermo-erosion gullying affects plant community structure and plant species abundance. Yet, this information is urgently needed as vegetation plays an important role in structuring Arctic ecosystems and regulating permafrost response to climate change (Jorgenson et al., 2010; Gauthier et al., 2011; Legagneux et al., 2012). Wetlands serve as preferred grounds for Arctic herbivores such as snow geese (Gauthier et al., 1996; Massé et al., 2001; Doiron et al., 2014). They are also expected to produce more methane compared to shrub-dominated areas (Olefeldt et al., 2013; Nauta et al. 2015; Treat et al., 2015).

The present study aimed at examining plant community patterns following thermo-

erosion gullying. Bylot Island, where geomorphological and ecological processes in response to climate change have been monitored for over two decades (Allard, 1996; Fortier and Allard, 2004; Gauthier et al., 2013), offered a unique opportunity to specifically assess the response of wetlands to gullying. The following questions were addressed: (1) to what extent thermo-erosion gullying 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 km^2) is characterized by a low-centered polygon landscape that has resulted from ice-wedge development and sediment accumulation during the late Holocene (Ellis and Rochefort, 2004; Fortier and Allard, 2004; Ellis et al., 2008).

Two baseline plant communities can be recognized 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 low-centered polygon rims, sloping terrain and hummocky tundra, support 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 around three gullies that were selected among the 36 identified in the valley (Godin and Fortier, 2012b). These gully networks have originated from snowmelt water infiltration into thermal contraction cracks and the formation of underground tunnels that have ended up collapsing (Fortier et al., 2007). The gullies R08p and R06, respectively 835 and 717 m long, are characterized by ongoing thermo-erosion (Fortier et al., 2007; Godin and Fortier, 2012b) whilst the gully RN08, 180 m long, has not been active in recent years. A total of 197 polygons (i.e. sampling sites) were randomly selected around the three gullies (Table 1; Fig. 1b) and classified into one of four categories (referred hereafter as habitats) that represented the two baseline plant communities (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 system development along the gullies (Fortier et al., 2007; Godin and Fortier, 2012a,b). The habitats were defined as follows: (*i*) intact low-centered wet polygons (n = 62) that were not affected by gullying. Their elevated rims enclose a central depression that retains snow cover during winter and is flooded by snowmelt water during spring (Woo and Young, 2006; Minke et al., 2007). These intact polygons are hydrologically independent, with their water content representing the balance between precipitation inputs (snow and rain) and evapotranspiration outputs (Fortier et al., 2006). ; (*ii*) recently (less than five years) disturbed polygons (n = 44), located along the most recent sections of the gullies, with partially degraded rims, incomplete drainage and heterogeneous water content; (*iii*) more than five-year disturbed polygons (n = 43), with heavily breached rims adjacent to the gullies

and substantial or complete drainage; (*iv*) mesic environments (n = 48), with distinct heterogeneous mesic vegetation. They are found throughout the valley and are thus not necessarily induced by thermo-erosion gullying.

2.3 Environmental condition monitoring

Daily precipitation was recorded with a manual rain gauge throughout summer 2010 at the base camp, located 700 m west of the gully R08p (Gauthier et al., 2010). Soil (top 10 cm) moisture was recorded at the center of each polygon using ECH_2O 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 R08p and R06, and July 30 only in the polygons of the gullyRN08. Thaw front depth was recorded at the polygon centers using a steel rod graduated in centimetre and driven in the active layer. The data collection spanned two years with measurements in July 2009 and 2010 in the polygons of the gullies R08p and R06 and in July 2010 in those situated along the gully RN08. One measure was taken per polygon, except for the mesic 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 site (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 (Daubenmire, 1959) 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 exclosure 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). Exclosures were set up in early July 2012 to avoid any significant grazing by geese. Above-ground biomass was harvested inside the exclosures 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 graminoids present in the exclosures were cut to a standard height, i.e. at an average of 1 cm below the moss surface (Gauthier et al., 1995; Doiron et al., 2014), and live biomass was sorted as follows: *Carex aquatilis*, *Eriophorum angustifolium* and *Eriophorum scheuchzeri* (Cyperaceae); *Luzula arctica* and *Luzula confusa* (Juncaceae); *Anthoxanthum arcticum*, *Arctagrostis latifolia*, *Dupontia fisheri* and *Festuca brachyphylla* (Poaceae). Biomass was then oven-dried at 65°C until constant dry weight and further weighed to ± 0.0001 g using an electronic weighing scale.

2.5 Statistical analyses

Differences in soil moisture, thaw front depth and graminoid above-ground biomass among habitats were tested with a generalized linear mixed model (procedure MIXED, REML

method in SAS, version 9.4, SAS Institute, Cary, NC, USA). Soil moisture, thaw front depth as well as date or year of measurements and the interaction terms were treated as fixed factors and gully as a random factor. Type III sums of squares were used for the calculation of fixed effect *F* statistics while random effects were assessed using a log likelihood ratio test from the full and reduced models (Littell et al., 2006). Post hoc contrasts were performed to ascertain specific differences between habitats at alpha < 0.05 using the LSMEANS statement and Bonferroni adjustment. Canonical Correspondence Analyses (CCA) were conducted to test unimodal relationships between habitats and environmental variables (ter Braak, 1986; Zuur et al., 2007) using the 'vegan' package (Oksanen et al., 2015) in R 3.1.3 (R development core team, 2015). Two matrices were elaborated: one of 197 sites x 65 taxa using their mean cover per site (i.e. polygon), and another of 197 sites x 8 environmental characteristics comprising the following continuous variables: soil moisture, thaw front depth, litter cover, bare ground, grubbing, vascular plant standing dead, standing water and goose feces. Soil moisture measurements obtained on July 30 2010 were used in the analyses.

3 Results

3.1 Environmental conditions

In 2009, above-average spring temperatures led to a rapid snowmelt (June 16) while summer was one of the driest on record (Gauthier et al. 2009). In 2010, despite a relatively warm spring (0.26°C above normal), the high snow pack at the end of the winter (41.6 cm on May 31) delayed the snowmelt in the lowlands to June 28, which was a week later than normal. Summer was characterized by warm and sunny conditions as well as below-average precipitations (cumulative rain of 84 mm vs long-time average of 92 mm; Gauthier et al. 2010). However, the 36 mm received in only five days in mid-July significantly increased soil moisture between the two monitoring dates (significant date effect: df = 1, F = 88.99, *P* <

.001; Fig. 3) and represented an important water input for both intact and disturbed polygons (non-significant habitat x date effect: df = 3, F = 0.51, *P* = 0.68). There was overall a significant difference in soil moisture among habitats (df = 3, F = 79.86, *P* < .001), which was driven both in early and late July by differences between wet polygons and the other habitats (5 July: df = 3, F = 33.41, *P* < .001, 30 July: df = 3, F = 47.36, *P* < .001;Fig. 3, Table A1). Throughout the summer, soil moisture was approximately 40 % higher in wet sites compared to disturbed and mesic environments. We also found a significant difference in thaw front depth between wet polygons and the other habitats (2009: df = 3, F = 21.30, P < .001, 2010: df = 3, F = 33.86, P < .001; Fig. 4, Table A1). Thaw front depth of wet polygons was approximately 10 cm deeper than in disturbed 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). 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 (Table A2). The greatest species richness was found in polygons that were disturbed at least five years ago and where both hydrophilic and mesic species were present (Table 2). The transition from wet polygons to mesic environments was accompanied by significant changes in vascular plant community composition, especially with the decline in Cyperaceae and Poaceae cover and the emergence of Salicaceae species (Table 2). *Carex aquatilis* and *Dupontia fisheri* were respectively present in 100 % and 93 % of the wet polygons sampled where they accounted for 52 % and 26 % of the total vascular plant cover. They were found in only 47 % and 16 % of mesic environments accounting for 9 % and 0.45 % of the total vascular plant cover. In contrast, *Salix arctica* and *Arctagrostis latifolia*, which were found in

approximately half of the wet polygons accounting for 3 % of the total vascular plant cover, were present in 98 % of the mesic environments where they respectively accounted for 50 % and 14 % of the total vascular plant cover. Differences among habitats were also noted in non-vascular taxa. Abundance of lichens such as *Cladonia*, *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 turn-over was observed between habitats with wetland-dominant *Drepanocladus* spp. replaced by *Aulocomnium* spp. in mesic environments.

Moreover, we observed vegetation changes through the decline of graminoid above-ground biomass which varied significantly among habitats (df = 3, F = 11.59, $P < 0.001$;; Fig. 5a; Table A1) and independently of the sampling location (non-significant gully effect: df = 1, LLR = 0.0, $P = 1.0$). Graminoid biomass was nearly five times greater in wet than in mesic environments (29.2 vs 5.9 $g.m^{-2}$; Fig. 2 and 5a). 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. 5b). 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 four studied habitats of the Qarlikturvik valley. Wet polygons were mainly related to high soil moisture and substantial thaw front depth whilst mesic environments were associated with greater litter cover (Fig. 6). A 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. 6).

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 decreasing soil moisture and thaw front depth of low-centered polygons adjacent to gullies. Vegetation is sensitive to this process, and mesic habitat plant species gradually replace hydrophilic species within five to ten years. This vegetation turn-over can have substantial consequences on wildlife biology, permafrost stabilization and ecosystem-level greenhouse gas emissions (Blok et al., 2010; Doiron et al., 2014; McEwing et al., 2015).

4.1 Transition in environmental conditions

Thermo-erosion gullying has led to a significant decrease in soil moisture of disturbed polygons following polygon rim erosion and water runoff through frost cracks. This is consistent with what has been previously observed in gullied areas (Seppälä 1997; Poesen et

al., 2003; Godin and Fortier, 2012a; Godin and Fortier, 2014; Harms et al., 2014) 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). 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).

Decreasing soil moisture 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 warming (Tarnocai et al., 2004; Woo et al., 2007; Akerman and Johansson 2008; Smith et al., 2009; Nauta et al., 2015). 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.

The development of gullies in the Qarlikturvik valley and the subsequent drainage of adjacent low-centered polygons have led to a gradual change in plant communities with vegetation of disturbed polygons leaning towards that of mesic environments. 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 gullying 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 in separating plant community types at high latitudes has indeed been well documented (Hinzman et al., 2005; Daniëls and de Molenaar, 2011; Daniëls et al., 2011; Sandvik and Odland, 2014). Four other variables significantly influenced the distinction among habitats: (*i*) thaw front depth discriminated habitats in the same direction than soil moisture with a 30 % decrease in disturbed polygons and mesic environments compared to intact polygons, which was expected since these two factors are closely related (see section 4.1); (*ii*) litter cover separated mesic environments from the others, which may be explained by increased organic matter related to greater shrub abundance in mesic environments (Zamin et al., 2014); (*iii*) vascular plant standing dead separated wet and recently disturbed polygons from the other habitats, which can be explained by the greater abundance and biomass of Cyperaceae species at these sites (Fig. 5); (*iv*) goose feces were mainly associated with long-time disturbed and mesic environments. While this may suggest a higher use of these habitats by geese, the slower degradation of feces in dryer habitats cannot be ruled out; this has yet to be tested.

The shift in vegetation composition in disturbed polygons was accompanied by significant changes in biomass. Above-ground biomass of graminoids was the greatest in wet polygons, which is concordant with the fact that wetlands are the most productive habitats of forage plants in the Arctic (Sheard and Geale, 1983; Duclos, 2002; Doiron, 2014). It gradually decreased in disturbed polygons as conditions became closer and closer to that of mesic environments and therefore less and less suitable. 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/m^2), 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/m^2). 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) 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).). It remains to quantify the extent to which gullying alters wetland carrying capacity. In addition, the presence of ponds in wetlands provides geese refuges from predators such as arctic fox (Hughes et al., 1994; Lecomte et al., 2009), and their disappearance might also change predator-prey interactions.

Effects of gullying-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 increased carbon release as CO_2 emission through enhanced decomposition. However, no general pattern on ecosystem responses to decreased water table position and subsequent gas emissions has emerged to date (see Grosse et al., 2011 for review). It will thus be crucial to determine in the near future the specific evolution of *Salix* and *Luzula spp* primary production in mesic sites in order to accurately predict the effects of wetland retreat on methane and soil organic carbon cycles.

5 Conclusions

This study illustrates that changes in the hydrological and thermal regimes following the induction of thermo-erosion gullies boost landscape transformation from wet to mesic habitats, providing evidence that permafrost degradation is a critical component of ecosystem modification at high latitudes. Ecological studies should consequently start using an approach that integrates disturbed permafrost monitoring if one wants to more efficiently document climate change effects on arctic terrestrial ecosystems. In addition, while surface warming is expected to alter the ground's thermal regime (Couture and Pollard, 2007), more work should be devoted to the effects of plant communities and vegetation succession on thermal and mechanical stabilization dynamics of disturbed permafrost terrains. This is especially needed since plant community differences between disturbed and intact sites can last several centuries (Cray and Pollard, 2015).

Table A1. Sample sizes and means (± 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.

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

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

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

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

Acknowledgements

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

References

Ackerly, D.: Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance, Ecol. Monogr., 74, 25-44, 2004.

Akerman, H. J. and Johansson, M.: Thawing permafrost and thicker active layer in sub-arctic Sweden, Permafrost Periglac., 19, 279-292, 2008.

Allard, M.: Geomorphological changes and permafrost dynamics: key factors in changing arctic ecosystems. An example from Bylot Island, Nunavut, Canada, Geosci. Can., 23, 205–212, 1996.

Audet, B., Lévesque, E. and Gauthier G.: Seasonal variation in plant nutritive quality for Greater Snow Goose goslings in mesic tundra, Can. J. Bot., 85, 457-462, 2007.

Avis, C. A., Weaver, A. J. and Meissner, K. J.: Reduction in areal extent of high-latitude wetlands in response to permafrost thaw, Nat. Geosci., 4, 444-448, 2011.

Beck, I., Ludwig, R., Bernier, M., Lévesque, E. and Boike, J.: Assessing permafrost degradation and land cover changes (1986-2009) using remote sensing data over Umiujaq, sub-Arctic Québec, Permafrost Periglac., DOI: 10.1002/ppp.1839, 2015.

Beilman, D. W. and Robinson, S. D.: Peatland permafrost thaw and landform type along a climate gradient, in: Proceedings, Eigth International Conference on Permafrost, edited by: Phillips, M., Springman, P. M. and Arenson, S. U., A. A. Balkema, Zurich, Switzerland, 1, 61-65, 2003.

Billings, W. D. and Peterson, K. M: Vegetational change and ice-wedge polygons through the thaw-lake cycle in Arctic Alaska, Arct. Alp. Res., 12, 413–432, 1980.

Blok, D., Heijman, M. M. P. D., Schaepman-Strub, G., Kononov, A. V., Maximov, T. C. and Berendse, F.: Shrub expansion may reduce summer permafrost thaw in Siberia tundra, Glob. Change Biol., 16, 1296-1305, 2010.

Bouchard, F., Laurion, I., Preskienis, V., Fortier, D., Xu, X. and Whiticar, M. J.: Modern to millennium-old greenhouse gases emitted from freshwater ecosystems of the Eastern Canadian Arctic, Biogeosciences Discuss., 12, 11661-11705, doi:10.5194/bgd-12-11661-2015, 2015.

Boulanger-Lapointe, N., Lévesque, E., Boudreau, S., Henry G. H. G. and Schmidt, N. M.: Population stucture and dynamics of Arctic willow (*Salix arctica*) in the High Arctic, J. Biogeogr., 41, 1967-1978, 2014.

Britton, A. J. et al.: Biodiversity gains and losses: evidence for homogenization of Scottish alpine vegetation, Biol. Conserv., 142, 1728-1739, 2009.

Cadieux, M.-C., Gauthier, G., Gagnon, C. A., Lévesque, E., Bêty, J. and Berteaux, D.: Monitoring the environmental and ecological impacts of climate change on Bylot Island, Sirmilik National Park, Université Laval, 113 pp., 2008.

Cannone, N., Lewkowicz, A. G. and Guglielmin, M.: Vegetation colonization of permafrost-related landslides, Ellesmere Island, Canadian High Arctic, J. Geophys. Res., 115, G04020, doi:10.1029/2010JG001384, 2010.

Cray, H. A. and Pollard, W. H.: Vegetation recovery patterns following permafrost disturbance in a Low Arctic setting: case study of Herschel Island, Yukon, Canada, Arct. Antarct Alp. Res., 47, 99-113, 2015.

Chen, Z. H., Chen, W. J. and Leblanc, S. G. and Henry, G. H. R.: Digital photograph analysis for measuring percent plant cover in the Arctic, Arctic, 63, 315–326, 2010.

Christiansen, H. H., Eltzelmuller, B., Isaksen, K., Juliussen, H., Farbrot, H., Humlum, O., Johansson, M., Ingeman-Nielsen, T., Kristensen, L., Hjort, J. et al.: The thermal state of permafrost in the Nordic Area during the International Polar Year 2007-2009, Permafrost Periglac., 21, 156-181, 2010.

Collins, Knutti, R., Arblaster, J., Dufresne, J.-L., Fichefet, T., Friedlingstein, P., Gao, X.,

Gutowski, W. K., Johns, T., Krinner, G. et al.: Long-term climate change: Projections, commitments and irreversibility, in: Climate change 2013: the physical basis, Contribution of working group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, edited by: Stocker, T. F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S. K., Boschung, J., Nauels, A., Xia, Y., Bex, V. and Midgley, P. M., Cambridge University Press, Cambridge, United Kingdom, 2013.

Couture, N. J. and Pollard, W. H.: Modelling geomorphic response to climatic change, Clim. Change, 85, 407–431, 2007.

Dagg, J. and Lafleur, P.: Vegetation community, foliar nitrogen, and temperature effects on tundra CO_2 exchange across a soil moisture gradient, Arct. Antarct. Alp. Res., 43, 189-197, 2011.

Daniëls, F. J. A. and de Molenaar, J. G: Flora and vegetation of Tasiilaq, formerly Angmagssalik, southeast Greenland: a comparison of data between around 1900 and 2007, Ambio, 40, 650-659, 2011.

Daniëls, F. J. A. et al.: Vegetation change in southeast Greenland? Tasiilaq revisited after 40 years, J. Appl. Veg. Sci., 14, 230-241.

Daubenmire, R.: A canopy-coverage method of vegetationnal analysis, Northwest Sci., 33, 43–64, 1959.

Doiron, M.: Impacts des changements climatiques sur les relations plantes-herbivores dans l'Arctique, PhD thesis, Université Laval, 123 pp., 2014.

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.

Ellis, C. J. and Rochefort L.: Long-term sensitivity of a High Arctic wetland to Holocene climate change, 94, 441-454, J. Ecol., 2006.

Ellis, C. J., Rochefort L., Gauthier G. and Pienitz, R.: Paleoecological evidence for transitions between contrasting landforms in a polygon-patterned High Arctic wetland, Arct. Antarct. Alp. Res., 40, 624–637, 2008.

Epstein, H. E., Myers-Smith, I. and Walker, D. A.: Recent dynamics of arctic and sub-arctic vegetation, Environ. Res. Lett., 8, 015040, 6 pp., 2013.

Ewertowski, M.: Ice-wedge pseudomorphs and frost-cracking structures in Weischselian sediments, Central-West Poland, Permafrost Periglac., 20, 316-330, 2009.

Fortier, D. and Allard, M.: Late Holocene syngenetic ice-wedge polygons development, Bylot Island, Canadian Arctic Archipelago, Can. J. Earth Sci., 41, 997–1012, 2004.

Fortier, D. and Allard, M.: Frost-cracking conditions, Bylot Island, Eastern Canadian Arctic 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., Frolking, 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, Biogeochemisty, 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 CO_2 and CH_4 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 CH_4 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., Wilmking, 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 homogeneization 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 CH_4 and CO_2 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.

Ukraintseva, 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., Ukraientseva, 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.

Zamin, T. Z., Brett-Harte, M. S. and Grogan, P.: Evergreen shrubs dominate responses to experimental summer warming and fertilization in Canadian mesic low arctic tundra, J. Ecol., doi: 10.1111/1365-2745.12237, 2014.

Zoltai, S. C., McCormick K. J. and Scotter, G. W.: A natural resource survey of Bylot Island and adjacent Baffin Island, Northwest Territories, Parks Canada, Ottawa, ON, 176 pp., 1983.

Zuur, A. F., Ieno, E. N. and Smith, G. M.: Analysing ecological data, edited by: Gail, M., Krickeberg, K., Samet, J., Tsiatis, A. and Wong, W., Springer, New York, 672 pp., 2007.

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

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

Table 2. Species richness, family total cover and species mean cover of vascular taxa as well as mean cover of non-vascular taxa in each of the four habitats sampled at Bylot Island, Nunavut. Mean species richness is given for sampled areas of 49 dm^2 (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 < 5 years *(n = 44)*	Disturbed polygons > 5 years *(n = 43)*	Mesic environments *(n = 48)*
Vascular taxa				
Total plant species richness	36	37	54	47
Mean plant species richness	8	11	17	15
Plant species cover (%)				
Asteraceae (3)	<<	<	<	<<
Brassicaceae (8)	<	<	0.3	<
Caryophyllaceae (5)	<<	0.1	1.0	0.2
Cyperaceae (4)	17.4	18.5	7.0	1.9
Carex aquatilis	*14.7*	*17.8*	*6.4*	*1.9*
Carex marina	*0*	*<<*	*0*	*0*
Eriophorum angustifolium	*0.5*	*0.4*	*0.5*	*0*
Eriophorum scheuchzeri	*2.1*	*0.4*	*<<*	*<*
Equisetaceae (1)	<	<	<	<
Ericaceae (1)	0	0	<<	<
Fabaceae (2)	<<	<<	0.2	0.1
Juncaceae (3)	<	0.2	3.4	3.0
Luzula arctica	*<<*	*<*	*0.4*	*1.0*
Luzula confusa	*<*	*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
Anthoxanthum arcticum	*0.5*	*<*	*<<*	*<<*
Arctagrostis latifolia	*0.6*	*<*	*0.3*	*3.0*
Dupontia fisheri	*7.4*	*4.8*	*1.8*	*0.1*
Festuca brachyphylla	*<<*	*<*	*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
Salix arctica	*1.2*	*0.9*	*3.1*	*10.8*
Salix herbacea	*0*	*0*	*<*	*0.1*
Salix reticulata	*<<*	*<<*	*0.2*	*1.6*
Salix richardsonii	*<<*	*<<*	*<<*	*<<*
Saxifragaceae (8)	<	0.2	1.5	<
Scrophulariaceae (2)	0.7	0.3	<	<
Non-vascular taxa				
Lichens	<	<	1.9	6.6
Live mosses	53.1	26.6	15.9	44.6
Drepanocladus spp.	*39.9*	*21.4*	*5.1*	*0*
Aulocomnium spp.	*7.5*	*3.2*	*1.4*	*39.3*
Dried mosses	2.9	29.6	18.2	0.9
Fungi	<	0.2	0.1	<
Nostoc sp.	<	<	<<	<<
Cryptogamic crust	<<	<	14.6	5.1

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

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

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

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

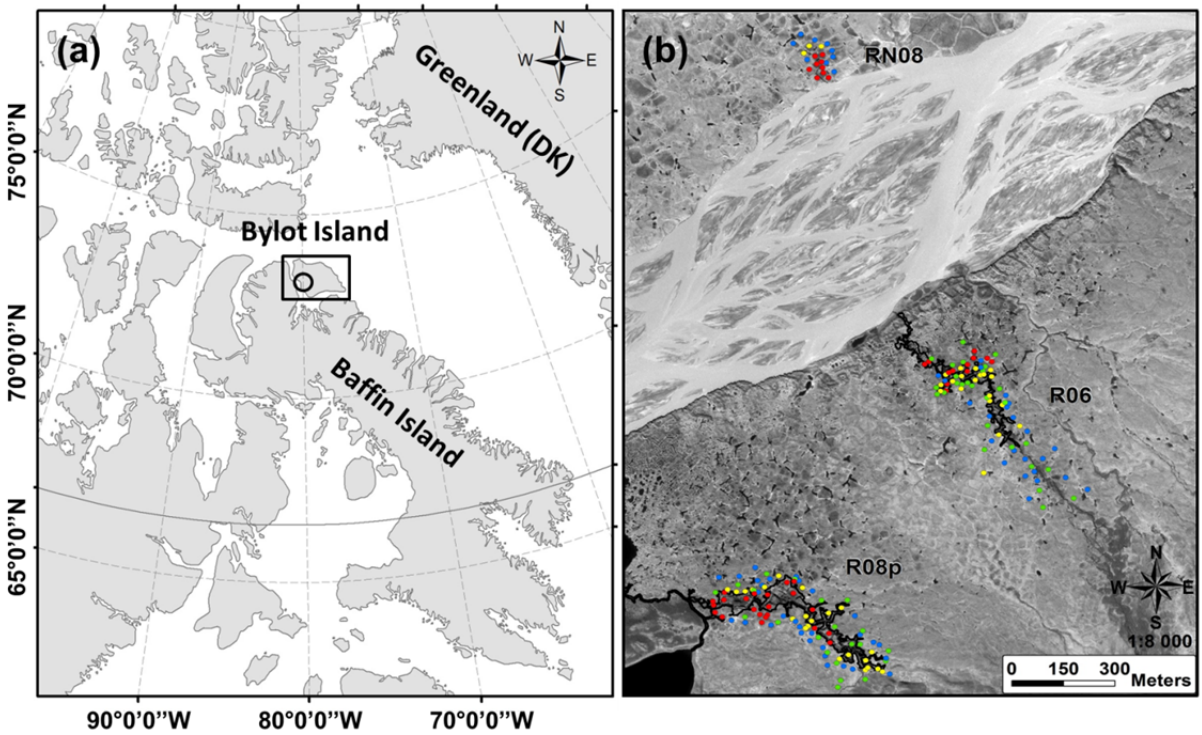

Figure 1. Location of the study area. (a) The Qarlikturvik valley (black circle) of Bylot Island, Nunavut (black rectangle). (b) the 197 sites sampled along three gullies (wet polygons (n = 62): blue circles; < 5-year disturbed polygons (n = 44): yellow circles; > 5-year disturbed polygons (n = 43):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

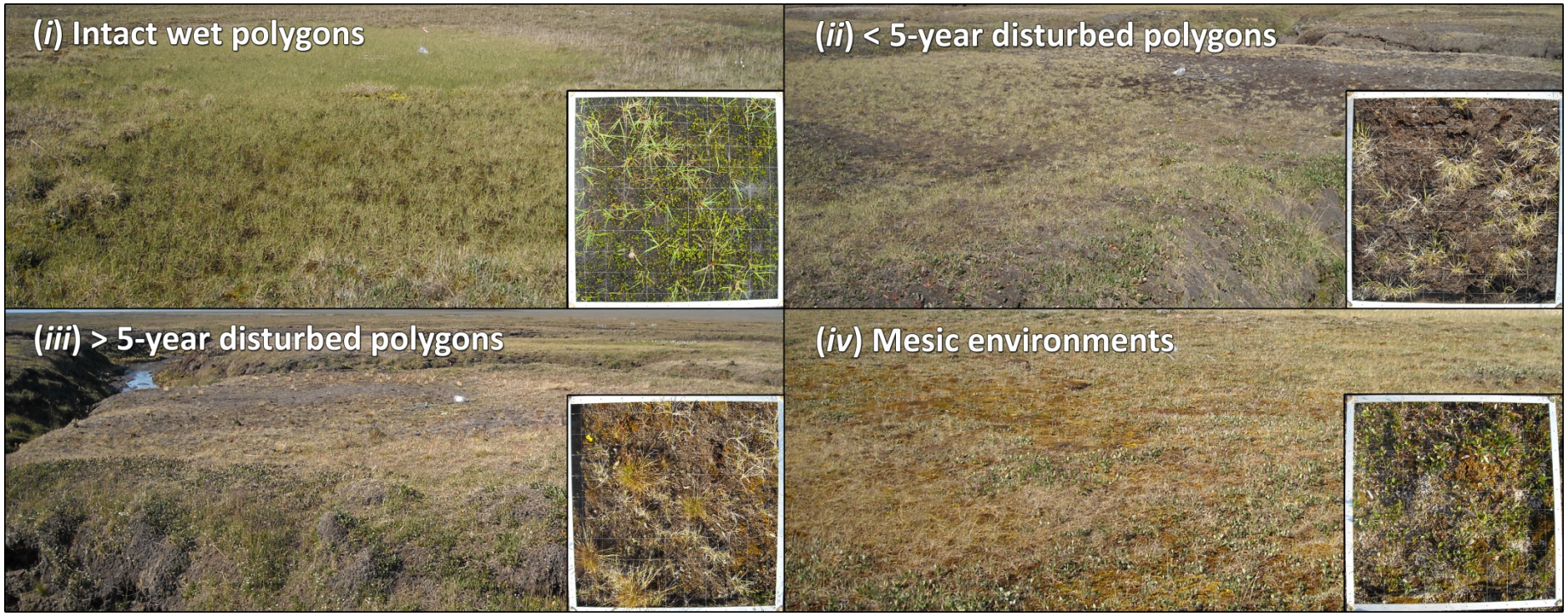

Figure 2. Illustration of the four habitats studied in the Qarlikturvik valley of Bylot Island, Nunavut. The close view at the bottom right of each picture represents the 70 cm x 70 cm quadrats that were used to determine species richness and abundance in each sampling site.

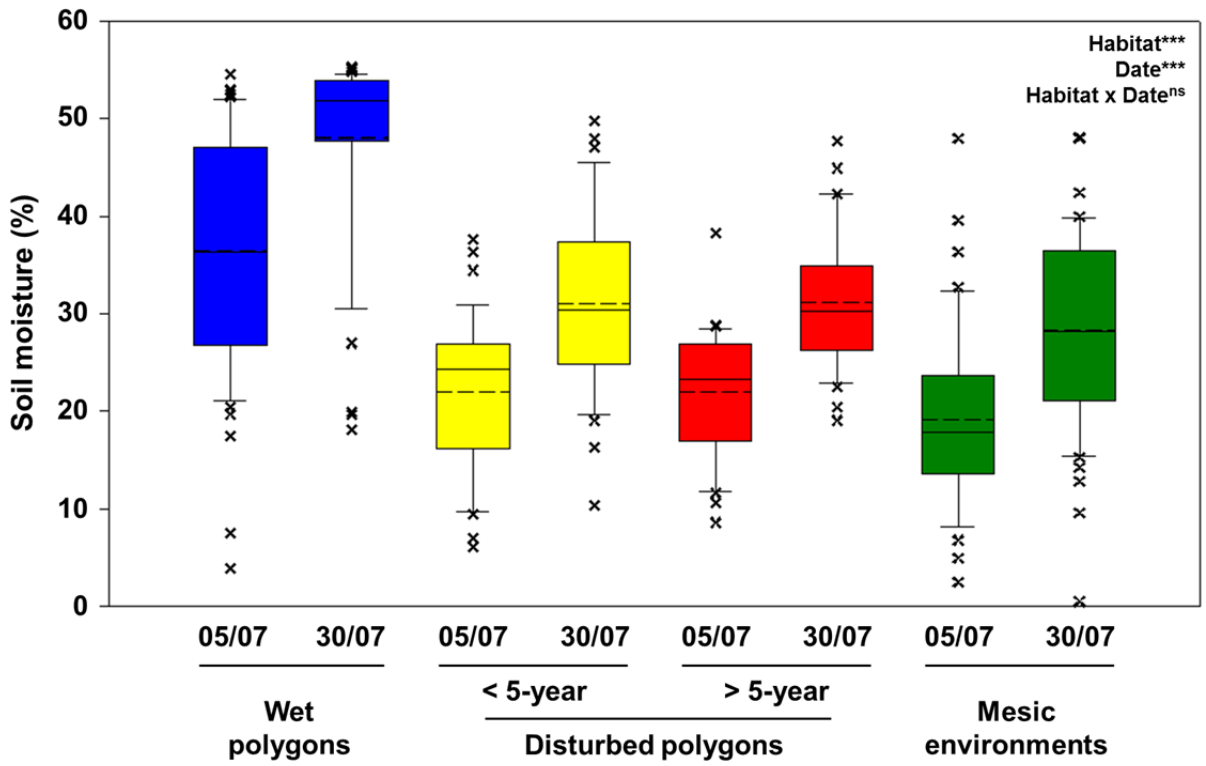

Figure 3. Soil moisture monitored early and late July 2010 in the four habitats studied in the Qarlikturvik valley of Bylot Island, Nunavut. 10th percentiles, lower quartile, median, mean (dash line), upper quartile and 90th percentiles are shown. See Table A1 for sample sizes and post-hoc contrasts.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

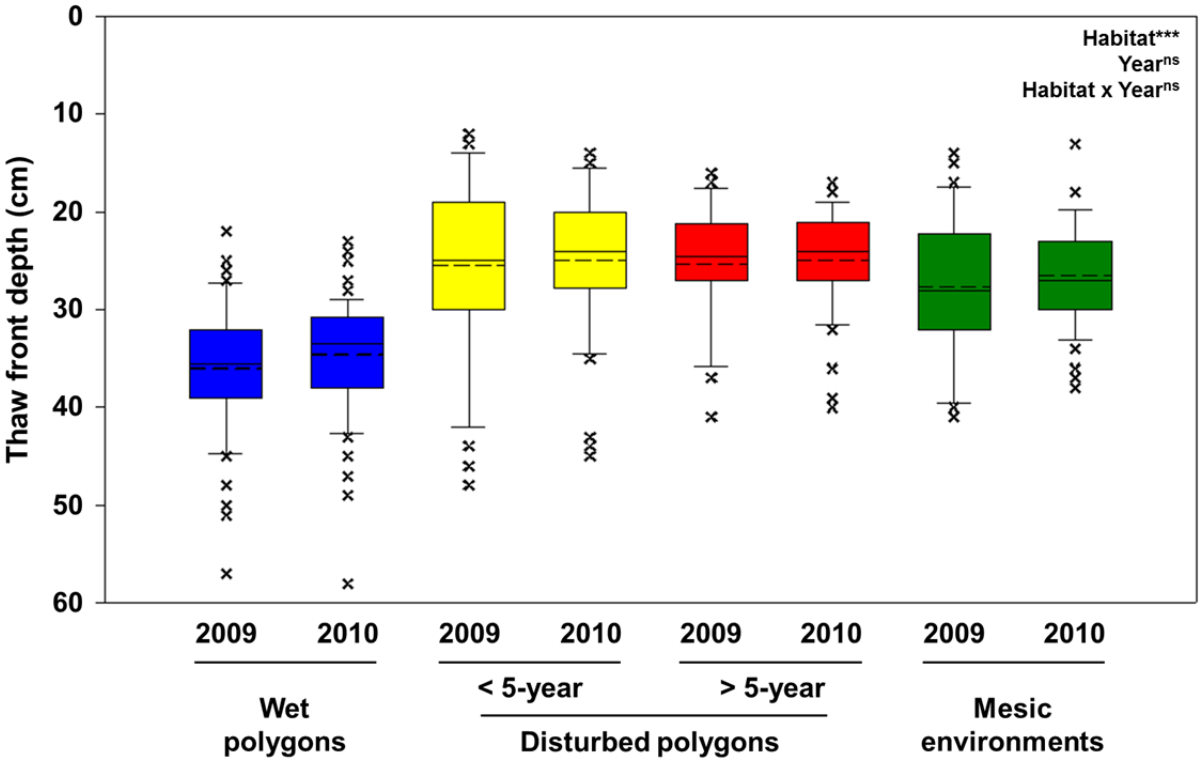

Figure 4. Thaw front depth monitored in July 2009 and 2010 in the four habitats studied in the Qarlikturvik valley of Bylot Island, Nunavut. 10th percentiles, lower quartile, median, mean (dash line), upper quartile and 90th percentiles are shown. See Table A1 for sample sizes and post-hoc contrasts.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

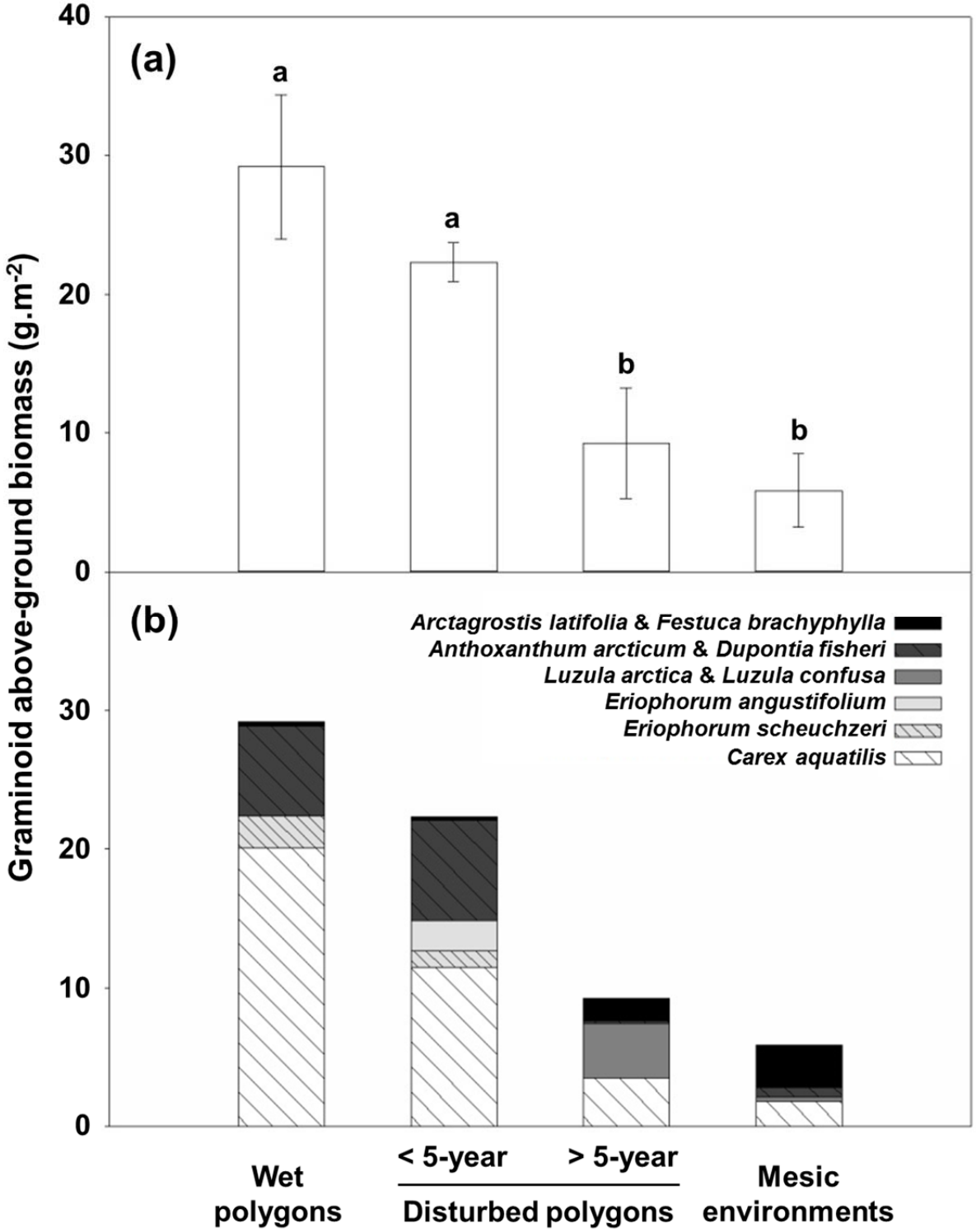

Figure 5. Above-ground biomass of graminoids growing in the four habitats studied in the Qarlikturvik valley of Bylot Island, Nunavut. (a) Mean total biomass (± SE), and (b) mean biomass per species. In panel (b), dashes represent hydrophilic species. n = 5 per habitat. Species aforementioned belong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

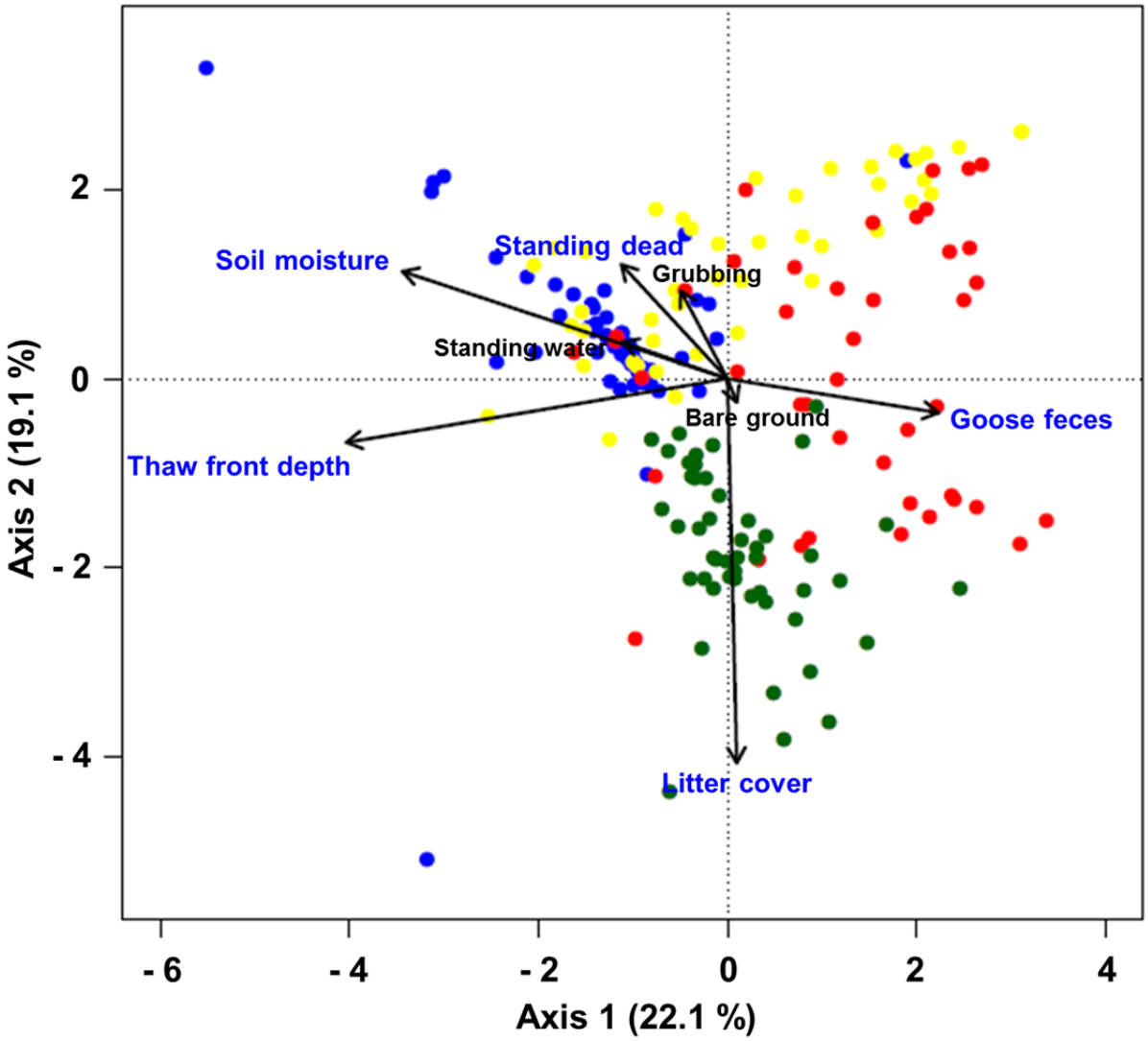

Figure 6. Canonical correspondence analysis (CCA) ordination of the 197 sites sampled in the Qarlikturvik valley of Bylot Island, Nunavut. Wet polygons (n = 62): blue circles; < 5-year disturbed polygons (n = 44): yellow circles; > 5-year disturbed polygons (n = 43): red circles; mesic environments (n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