1 Abstract

2 Continuous permafrost zones with well-developed polygonal ice-wedge networks are 3 particularly vulnerable to climate change. Thermo-mechanical erosion can initiate the 4 development of gullies that lead to substantial drainage of adjacent wet habitats. How 5 vegetation responds to this particular disturbance is currently unknown but has the potential to 6 strongly disrupt function and structure of Arctic ecosystems. Focusing on three major gullies 7 of Bylot Island, Nunavut, we aimed at estimating the impacts of thermo-erosion on plant 8 community changes. We explored over two years the influence of environmental factors on 9 plant species richness, abundance and biomass in 62 low-centered wet polygons, 87 low-10 centered disturbed polygons and 48 mesic environment sites. Gullying decreased soil 11 moisture by 40 % and thaw-front depth by 10 cm in the center of breached polygons within 12 less than five years after the inception of ice wedge degradation, entailing a gradual yet 13 marked vegetation shift from wet to mesic plant communities within five to ten years. This 14 transition was accompanied by a five times decrease in graminoid above-ground biomass. 15 Soil moisture and thaw-front depth changed almost immediately following gullying initiation 16 as they were of similar magnitude between older (> 5 years) and recently (< 5 years) disturbed 17 polygons. In contrast, there was a lag-time in vegetation response to the altered physical 18 environment with plant species richness and biomass differing between the two types of 19 disturbed polygons. To date (ten years after disturbance), the stable mesic environment cover 20 has still to be reached. Our results illustrate that wetlands are highly vulnerable to the process 21 of thermo-erosion, which can drive landscape transformation on a relative short period of time 22 for High Arctic perennial plant communities (five to ten years). Such succession towards 23 mesic plant communities can have substantial consequences on the food availability for 24 herbivores and methane emissions of Arctic ecosystems.

25 **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).

32 Permafrost is tightly associated with biophysical components such as air temperatures, 33 soil conditions, surface water, groundwater, snow cover and vegetation (Jorgenson et al., 34 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; 35 Natali et al., 2015). Permafrost degradation that would increase subsurface drainage and 36 37 reduce the extent of lakes and wetlands at high latitudes (Avis et al., 2011; Jorgenson et al., 38 2013; Beck et al., 2015) would thus have major consequences on ecosystem structure and 39 function (Collins et al., 2013; Jorgenson et al., 2013). It would also strongly influence 40 variations of active layer depths (Wright et al., 2009; Shiklomanov et al., 2010; 41 Gangodagamage et al., 2014), as illustrated by long-term monitoring sites throughout the 42 circumpolar North (Tarnocai et al., 2004; Nelson et al., 2008; Smith et al., 2009; Shiklomanov 43 et al., 2010).

44 Several forms of ground and massive ice can be found within permafrost (Rowland et 45 al., 2010), especially ice wedges in regions where winter temperatures enable thermal 46 contraction cracking (Fortier and Allard, 2005; Ewertowski, 2009; Kokelj et al., 2014; 47 Jorgenson et al., 2015b; Sarrazin and Allard, 2015). Continuous permafrost zones with well-48 developed polygonal ice-wedge networks are particularly vulnerable to climate change 49 because ice wedges are usually found near the top of permafrost (Smith et al., 2005;

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Jorgenson et al., 2006; Woo et al., 2008; Vonk et al., 2013). In these regions, thawing 50 51 permafrost can result in ground ice erosion and displacement of sediments, carbon and 52 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., 53 54 2011), in Siberia (Günther et al., 2013) and in the Antarctic Dry Valleys (Levy et al., 2008). 55 On Bylot Island, Nunavut, thermo-mechanical erosion by water has initiated permafrost tunneling and the development of gully networks in aeolian, organic and colluvial 56 depositional environments of nearly 158 000 m² (Fortier et al., 2007; Godin and Fortier, 57 58 2012a; Godin et al., 2014; Veillette et al., 2015). A fine-scale spatio-temporal monitoring of the six largest gullies showed that their development rate ranged from 14 to 25 m.yr⁻¹ going 59 up to 80 m.yr⁻¹ during their inception (Godin and Fortier, 2012b), leading to substantial 60 61 changes in the drainage network and increasing eroded area throughout the valley (Godin et 62 al., 2014). To date, the contribution of thermal-erosion and lateral erosion processes in 63 permafrost feedbacks to climate has yet to be documented.

64 Many observational and experimental studies have documented shifts in tundra plant 65 community structure and plant species productivity in response to warming temperatures 66 (Jonsdottir et al., 2005; Hudson and Henry, 2010; Epstein et al., 2013; Naito and Cairns, 67 2015). Substantial work has also been devoted to the vegetation response to disturbances such 68 as landslides associated with permafrost degradation (Ukraintseva et al., 2003; Walker et al., 69 2009; Cannone et al., 2010). In contrast, little is known about how thermo-erosion gullying 70 affects plant community structure and plant species abundance. Yet, this information is 71 urgently needed as vegetation plays an important role in structuring Arctic ecosystems and 72 regulating permafrost response to climate change (Jorgenson et al., 2010; Gauthier et al., 73 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 74

also expected to produce more methane compared to shrub-dominated areas (Olefeldt et al.,
2013; Nauta et al. 2015; Treat et al., 2015).

77 The present study aimed at examining plant community patterns following thermo-78 erosion gullying. Bylot Island, where geomorphological and ecological processes in response 79 to climate change have been monitored for over two decades (Allard, 1996; Fortier and 80 Allard, 2004; Gauthier et al., 2013), offered a unique opportunity to specifically assess the 81 response of wetlands to gullying. The following questions were addressed: (1) to what extent 82 thermo-erosion gullying modifies environmental conditions of low-centered wetland 83 polygons? (2) how do plant communities cope with these geomorphological changes, i.e. do we observe shifts in plant diversity, abundance and productivity? 84

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86 2 Methods

87 2.1 Study area

88 This study took place in the Qarlikturvik valley of Bylot Island, Nunavut, Canada (73°09'N, 89 79°57'W; Fig. 1a). Bound to the North and South by plateaus < 500 m asl, it connects C-79 90 and C-93 glaciers to the Navy Board Inlet sea via a proglacial river. The sampling sites were specifically located in the valley floor ($ca 65 \text{ km}^2$), which is characterized by a low-centered 91 92 polygon landscape that has resulted from ice wedge development and sediment accumulation 93 during the late Holocene (Ellis and Rochefort, 2004; Fortier and Allard, 2004; Ellis et al., 94 2008). Two baseline vegetation types can be recognized. Wetlands, often associated with 95 intact low-centered polygons, represent ca 23 % of the valley area (Hughes et al., 1994) and 96 are dominated by sedges (Carex aquatilis, Eriophorum angustifolium, Eriophorum 97 scheuchzeri,), grasses (Dupontia fisheri, Pleuropogon sabinei; Gauthier et al., 1995) and fen 98 mosses (Drepanocladus spp.; Ellis et al., 2008; Pouliot et al., 2009). Mesic environments, 99 such as low-centered polygon rims, gently sloping terrain and hummocky tundra, support a more diverse group of species including *Salix* spp., *Vaccinium uliginosum*, *Arctagrostis latifolia*, *Poa arctica* and *Luzula confusa* with *Aulocomnium* spp. as dominant moss species
(Zoltai et al., 1983). As a result, the valley houses many herbivores such as snow geese (in
summer) and brown and collared lemmings (Gauthier et al., 1995; Gruyer et al., 2008), thus
representing a critical environment for tundra food web (Gauthier et al., 2011; Legagneux et
al., 2012).

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107 **2.2 Field sites**

108 Our work was specifically conducted around three gullies that were selected among the 36 109 identified in the valley (Godin and Fortier, 2012b). These gully networks have originated 110 from snowmelt water infiltration into cavities of the frozen active layer and the subsequent 111 formation of underground tunnels that have ended up collapsing (Fortier et al., 2007; Godin 112 and Fortier, 2010). The gullies R08p and R06, respectively 835 and 717 m long, are 113 characterized by ongoing thermo-erosion (Fortier et al., 2007; Godin and Fortier, 2012b) 114 whilst the gully RN08, 180 m long, has not been active in recent years. A total of 197 115 sampling sites were randomly selected around the three gullies (Table 1; Fig. 1b) and 116 classified into one of four categories (referred hereafter as habitats) that represented the two 117 baseline vegetation types (wet and mesic) as well as increasing levels of disturbance related to 118 thermo-erosion. The disturbed habitats were sorted via a visual assessment of the low-119 centered polygon rim integrity coupled with a recent close monitoring of drainage system 120 development along the gullies (Fortier et al., 2007; Godin and Fortier, 2012a,b). The habitats 121 were defined as follows: (i) intact low-centered wet polygons (n = 62) that were not affected 122 by gullying. Their elevated rims enclose a central depression that retains snow cover during 123 winter and is flooded by snowmelt water during spring (Woo and Young, 2006; Minke et al., 124 2007). These polygons are hydrologically independent, with their water content representing

125 the balance between precipitation inputs (snow and rain) and evapotranspiration outputs 126 (Fortier et al., 2006); (ii) less than five-year (recently) disturbed polygons (n = 44), located 127 along the most recent sections of the gullies, with partially degraded rims, incomplete 128 drainage and heterogeneous water content; (iii) more than five-year (older) disturbed 129 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 130 131 vegetation. They are found on the rim of polygons and in adjacent areas and are generally not 132 induced by thermo-erosion gullying but rather dependent on local sedimentary and 133 hydrological dynamics.

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135 **2.3 Environmental condition monitoring**

136 Daily precipitation was recorded with a manual rain gauge throughout summer 2010 at the 137 base camp, located 700 m west of the gully R08p (Gauthier et al., 2010). Soil (top 10 cm) 138 moisture was recorded at the center of each sampling site using ECH₂O EC-5 moisture 139 sensors (accuracy of \pm 3 % VWC, resolution of \pm 0.1 % VWC) connected to Em5b 140 dataloggers (Decagon Devices, WA, USA). Measurements were carried out in 2010, both July 141 5 (early season) and July 30 (late season) along the gullies R08p and R06, and July 30 only 142 along the gully RN08. Thaw-front depth was recorded at the center of each sampling site 143 using a graduated steel rod driven into the thawed active layer. The data collection spanned 144 two years with measurements in July 2009 and 2010 in the polygons of the gullies R08p and 145 R06 and in July 2010 in those situated along the gully RN08. One measure was taken in each 146 of the wet and disturbed sampled polygons whereas three random measurements were 147 conducted in each mesic environment site because of the heterogeneity of this type of habitat. 148 In this case, a mean per site was calculated prior to analyses.

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150 **2.4 Plant community characterization**

151 Species richness and abundance were determined at each site in July 2009 or 2010 using three 152 randomly placed 70 cm x 70 cm quadrats that were vertically photographed at ca 1.3 m from 153 the ground (see detailed protocols in Chen et al., 2010 and the IPY CiCAT, 2012; Fig. 2). 154 Abundances of vascular plants, lichens, mosses, Nostoc spp., fungi, cryptogamic crust, bare 155 ground, litter, vascular plant standing dead, standing water, signs of grubbing and goose feces 156 were evaluated as cover percentages using photography analyses (Perreault, 2012). 157 Daubenmire cover abundance classes (Daubenmire, 1959) were used on each quadrat picture 158 overlain by a 7-cm grid to evaluate species cover as the projection on the ground of all species 159 above-ground parts.

Five sampling sites per habitat were also randomly selected along the gullies R08p and 160 161 R06 to measure above-ground biomass of graminoid species. At each site, an exclosure of 1 162 m x 1 m was made of chicken wire 30 cm high and supported by wooden stakes at each 163 corner (see Gauthier et al., 1995). Exclosures were set up in early July 2012 to avoid any 164 significant grazing by geese. Above-ground biomass was harvested inside the exclosures near 165 peak production in early August 2012 using random grids of 25 cm x 25 cm for wet and 166 recently disturbed polygons and of 50 cm x 20 cm for older disturbed polygons and mesic 167 environments. Two different grid sizes were used because of the difference in structure of the 168 vegetation (herbaceous vs. shrubs) associated with the habitat heterogeneity (Legagneux et al., 169 2012). All graminoids present in the random grids were cut to a standard height, i.e. at an 170 average of 1 cm below the moss surface (Gauthier et al., 1995; Doiron et al., 2014), and live 171 biomass was sorted as follows: Carex aquatilis, Eriophorum angustifolium and Eriophorum 172 scheuchzeri (Cyperaceae); Luzula arctica and Luzula confusa (Juncaceae); Anthoxanthum 173 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 174

 175 ± 0.0001 g using an electronic weighing scale.

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177 **2.5 Statistical analyses**

178 Differences in soil moisture, thaw-front depth and graminoid above-ground biomass among 179 habitats were tested with a generalized linear mixed model (procedure MIXED, REML 180 method in SAS, version 9.4, SAS Institute, Carv, NC, USA). Soil moisture, thaw-front depth 181 as well as date or year of measurements and the interaction terms were treated as fixed factors 182 and gully as a random factor. Type III sums of squares were used for the calculation of fixed 183 effect F statistics while random effects were assessed using a log likelihood ratio test from the 184 full and reduced models (Littell et al., 2006). Post hoc contrasts were performed to ascertain 185 specific differences between habitats at alpha < 0.05 using the LSMEANS statement and 186 Bonferroni adjustment. Canonical Correspondence Analyses (CCA) were conducted to test 187 unimodal relationships between habitats and environmental variables (ter Braak, 1986; Zuur 188 et al., 2007) using the 'vegan' package (Oksanen et al., 2015) in R 3.1.3 (R development core 189 team, 2015). Two matrices were elaborated: one of 197 sites x 65 taxa using their mean cover 190 per site, and another of 197 sites x 8 environmental characteristics comprising the following 191 continuous variables: soil moisture, thaw-front depth, litter cover, bare ground, grubbing, 192 vascular plant standing dead, standing water and goose feces. Soil moisture measurements 193 obtained on July 30 2010 were used in the analyses.

194

195 **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. 200 201 Summer was characterized by warm and sunny conditions as well as below-average 202 precipitations (cumulative rain of 84 mm vs long-time average of 92 mm; Gauthier et al. 203 2010). However, the 36 mm received in only five days in mid-July 2010 significantly 204 increased soil moisture between the two monitoring dates in all habitats (significant date effect: df = 1, F = 88.99, P < .001; Fig. 3). There was overall a significant difference in soil 205 206 moisture among habitats (df = 3, F = 79.86, P < .001), which was associated with differences 207 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 208 209 approximately 40 % higher in wet polygons compared to disturbed polygons and mesic 210 environments. We also found a significant difference in thaw-front depth between wet 211 polygons and the other habitats (2009: df = 3, F = 21.30, P < .001, 2010: df = 3, F = 33.86, P 212 <.001; Fig. 4, Table A1). Thaw-front depth of wet polygons was approximately 10 cm deeper 213 than in disturbed polygons and mesic environments for both years of monitoring (35-36 vs 214 25-27 cm). The two types of disturbed polygons thus showed similar soil moisture and thaw-215 front depth despite their differing time since disturbance inception. There was no significant 216 effect of gully location (df = 2, LLR = 1.6, P = 0.21 for soil moisture, df = 2, LLR = 0.0, P217 =1.0 for thaw-front depth).

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219 **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 225 Poaceae cover and the emergence of Salicaceae species (Table 2). Carex aquatilis and 226 Dupontia fisheri were respectively present in 100 % and 93 % of the wet polygons sampled 227 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 228 229 vascular plant cover. In contrast, Salix arctica and Arctagrostis latifolia, which were found in 230 approximately half of the wet polygons accounting for 3 % of the total vascular plant cover, 231 were present in 98 % of the mesic environments where they respectively accounted for 50 % 232 and 14 % of the total vascular plant cover. Differences among habitats were also noted in 233 non-vascular taxa. Abundance of lichens such as Cladonia spp., Stereoacaulon spp. and 234 Peltigera spp. increased in polygons disturbed for at least five years and mesic environments 235 (Table 2). Mosses were mostly found living in wet polygons and mesic environments and 236 dried (i.e. dead) in disturbed polygons (Table 2), while a significant species turn-over was 237 observed between habitats with wetland-dominant Drepanocladus species replaced by 238 Aulocomnium species in mesic environments.

239 Moreover, we observed vegetation changes through the decline of graminoid aboveground biomass which varied significantly among habitats (df = 3, F = 11.59, P < 0.001; Fig. 240 241 5a; Table A1). Graminoid biomass was nearly five times greater in wet than in mesic environments (29.2 vs 5.9 g.m⁻²) and decreased twofold between < 5-year disturbed and > 5-242 243 year disturbed polygons (22.3 vs 9.3 g.m⁻²; Figs 2 and 5a). Differences were mainly driven by 244 the decline of hydrophilic species, i.e. Carex aquatilis, Eriophorum scheuchzeri, 245 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 polygons, respectively; 246 247 Fig. 5b). Above-ground biomass of Luzula spp., Arctagrostis latifolia and Festuca 248 brachyphylla was contrastingly nine times greater in mesic than in wet habitats (3.30 vs 0.35 g.m⁻²) and twenty-four times greater in > 5-year disturbed than in < 5-year disturbed polygons 249

250 (5.61 vs 0.23 g.m⁻²).

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252 **3.3 Relationships between plant communities and environmental variables**

The first two axes of the Canonical Correspondence Analysis retained 14 % of the vegetation 253 254 data variance and 80 % of the vegetation-environment relationship variance (Table 3). Five of 255 the eight environmental variables tested were significant within the canonical model (P < .05, 256 999 permutations), but only three - litter cover, thaw-front depth and soil moisture - showed 257 high correlations with the canonical axes (Table 4). Thaw-front depth and soil moisture were 258 strongly related to the first axis, while litter cover was mainly associated with the second axis 259 (Table 4). Altogether, these variables discriminated well the four studied habitats of the 260 Qarlikturvik valley. Wet polygons were mainly related to high soil moisture and substantial 261 thaw-front depth whilst mesic environments were associated with greater litter cover (Fig. 6). 262 The gradual vegetation transition was also observed from < 5-year to > 5-year disturbed 263 polygons following the soil moisture shift in these habitats (Fig. 6).

264

265 4 Discussion

266 Sustainability of wetlands at high latitudes essentially relies on perennial frozen ground that 267 prevents drainage and allows wet soil conditions (Woo and Young, 2006; Ellis et al., 2008). 268 However, snowmelt water run-off through ice-wedge polygon landscapes can initiate thermal 269 erosion of the permafrost and the development of gullies (Fortier et al., 2007; Godin and 270 Fortier, 2014). We showed here that permafrost gullying significantly altered wetlands by 271 changing the original polygon microtopography, and decreasing soil moisture and thaw-front 272 depth of disturbed polygons along the gullies. Vegetation was sensitive to this process, and 273 mesic environment plant species gradually replaced hydrophilic species within five to ten 274 years, although the full transition has yet to be reached. This vegetation turn-over can have

substantial consequences on wildlife biology, permafrost stabilization and ecosystem-level
greenhouse gas emissions (Blok et al., 2010; Doiron et al., 2014; Jorgenson et al., 2015b;
McEwing et al., 2015).

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279 4.1 Transient environmental conditions

280 The initiation of thermo-erosion gullving led to a significant decrease in soil moisture and 281 thaw-front depth of breached polygons. Both older and recently disturbed polygons had 282 similar soil moisture and thaw-front depth while differing in time since disturbance, which 283 shows that the change in polygon environmental conditions after permafrost disturbance was 284 rapid. The decrease in soil moisture following polygon rim erosion is consistent with what 285 has been previously observed in gullied areas (Seppälä 1997; Poesen et al., 2003; Godin and 286 Fortier, 2012a; Godin and Fortier, 2014; Harms et al., 2014; Godin and Fortier, 2015) and 287 concurs with a modeling analysis showing that the transformation of low-centered to high-288 centered polygon landscape following ice wedge degradation is accompanied by a significant 289 alteration in the water balance partitioning (Liljedahl et al., 2012). In our study, all types of 290 polygons were recharged by snowfall and summer rainfall, yet disturbed habitats had lower 291 soil moisture than wet polygons and a thorough examination of moisture evolution throughout 292 an entire summer showed that soil moisture of breached polygons was significantly more 293 variable than that of wet polygons at both intra- and inter-polygonal scales (Godin et al., 294 2015). Given that soil moisture is an important driver of plant community composition (Muc 295 et al., 1989; Dagg and Lafleur, 2011), it is no surprise that we observed a shift in vegetation 296 following changes in moisture regime.

Decreasing soil moisture in the center of disturbed polygons came with decreasing thaw-front depth, which was expected given that active layer thickness is closely related to soil moisture (Nelson et al., 1999; Hinzman et al., 2005; Minke et al., 2009; Wright et al., 300 2009; Gangodagamage et al., 2014). This result, however, contrasts with the active layer 301 thickening generally observed in response to climate warming (Tarnocai et al., 2004; Woo et 302 al., 2007; Akerman and Johansson 2008; Smith et al., 2009; Nauta et al., 2015), and this is 303 likely due in part to ground surface subsidence and drainage which follows ice-rich 304 permafrost thawing (Shiklomanov et al., 2013) and in part to snow accumulation patterns 305 (Godin et al., 2015). Within five years of drainage, thaw-front depth in disturbed polygons 306 decreased by 37 % compared to that in wet polygons. This is mainly explained by the greater 307 heat transfer from water and higher thermal conduction rates in wetter polygons that provide 308 substantial melt energy to the frost table (Nelson et al., 1997; Hinzman et al., 2005; Wright et 309 al., 2009; Romanovsky et al., 2010). This effect is also sharpened by the low thermal 310 conductivity of drier moss carpets in disturbed habitats (Wright et al., 2009) and altered local 311 snow conditions within the polygons adjacent to the gullies (Godin et al., 2015).

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313 4.2 Vegetation changes

314 Overall, the floristic composition of our sampling sites is in line with previous field surveys 315 conducted in the same area (Gauthier et al., 1996; Duclos, 2002; Doiron, 2014). The presence 316 of Carex aquatilis, Eriophorum scheuchzeri and Dupontia fisheri characterizes well the 317 typical vegetation of Arctic wetlands (Jorgenson et al., 2013; Sandvik and Odland, 2014; Lara 318 et al., 2015) whilst that of Arctagrostis latifolia, Luzula and Salix spp are common features of 319 Arctic mesic environments (Audet et al., 2007; Sjogersten et al., 2008). Disturbed polygons 320 were the most diverse habitats given that they offered a middle-range state between wet and 321 mesic conditions where hydrophilic species were still present while mesic environment ones 322 had successfully established.

The development of gullies in the Qarlikturvik valley and the subsequent drainage of adjacent low-centered polygons have led within five to ten years to a gradual change in plant 325 communities with vegetation of disturbed polygons leaning toward a new equilibrium, that of 326 mesic environments. Mesic environment species such as Luzula and Salix spp have 327 established or increased in cover following the decrease in soil moisture and thaw-front depth 328 and replaced hydrophilic Cyperaceae and Poaceae. The secondary succession pioneered here 329 by the gullying process in disturbed polygons follows the directional-species replacement 330 model examined by Svoboda and Henry (1987). However, by occurring within five to ten 331 years, it has been remarkably more rapid than what is usually documented for the High Arctic 332 where perennial plant communities are largely resistant to disturbance (Hollister et al., 2005; 333 Jonsdottir et al., 2005; Hudson and Henry, 2010) and succession dynamics are slow due to 334 short growing seasons and low summer temperatures (Svoboda and Henry, 1987). For 335 instance, plant cover of northeastern Alaska changed little over a twenty-five year period 336 despite a significant rise in summer temperatures (Jorgenson et al., 2015a). This gradual yet 337 rapid species replacement has been triggered in our system by the hydrological and thermal 338 shift caused by gullying and favored by the mosaic of wet and mesic habitats allowing for a 339 substantial species pool with both vegetative and sexual reproduction.

340 In the canonical ordination analysis, the soil moisture gradient discriminated wet 341 polygons from the other habitats as well as recently disturbed from older disturbed habitats. 342 The 37 % decrease in soil moisture between wet and disturbed polygons represents a drastic 343 change of conditions for plant communities and is of similar magnitude than what has been 344 documented in Alaskan drying wetlands as a result of increasing temperatures (Klein et al., 345 2005). The strong influence of soil moisture in separating plant community types at high 346 latitudes has indeed been well documented (Hinzman et al., 2005; Daniëls and de Molenaar, 347 2011; Daniëls et al., 2011; Sandvik and Odland, 2014). Four other variables significantly 348 influenced the distinction among habitats: (i) thaw-front depth discriminated habitats in the 349 same direction than soil moisture with a 30 % decrease in disturbed polygons and mesic

350 environments compared to wet polygons, which was expected since these two factors are 351 closely related (see section 4.1); (ii) litter cover separated mesic environments from the 352 others, which may be explained by increased organic matter related to greater shrub 353 abundance in mesic environments (Zamin et al., 2014); (iii) vascular plant standing dead 354 separated wet and recently disturbed polygons from the other habitats, which can be explained 355 by the senescence of Cyperaceae tillers that are highly abundant at these locations (Fig. 5); 356 (iv) goose feces were mainly associated with older disturbed and mesic environments. While 357 this may suggest a higher use of these habitats by geese, the slower degradation of feces in 358 dryer habitats cannot be ruled out; this has yet to be tested.

359 The shift in vegetation composition in disturbed polygons was accompanied by 360 significant changes in biomass. Above-ground biomass of graminoids was the greatest in wet 361 polygons, which is concordant with the fact that wetlands are the most productive habitats of 362 forage plants in the Arctic (Sheard and Geale, 1983; Duclos, 2002; Doiron, 2014). It gradually 363 decreased in disturbed polygons as conditions became closer to those of mesic environments. 364 Compared to the immediate change in environmental conditions, we nonetheless observed a 365 lag-time in vegetation response to thermo-erosion related disturbance as graminoid biomass 366 differed significantly between recently and older disturbed polygons. In our study, graminoid 367 above-ground biomass of wet polygons was 35 % lower than what Cadieux et al. (2008) 368 found via a long-term plant monitoring on Bylot Island (45.2 g/m²), and 62.7 % lower than 369 what Gauthier et al. (2012) measured in the most productive wetlands of the Qarlikturvik 370 Valley (78.4 \pm 10.5 g/m²). These contrasts may be explained by varying species composition 371 and to a lesser extent by earlier plant harvesting in our case. Indeed, while we focused on wet 372 polygons dominated by *Carex aquatilis*, Cadieux et al. (2008) and Gauthier et al. (2012) 373 worked on wet polygons dominated by Dupontia fisheri and Eriophorum scheuchzeri. 374 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. 375 376 graminoids) biomass and did not sample forbs or shrubs. Since above-ground biomass of 377 graminoids account for more than 90 per cent of vascular plant biomass in wetlands (Gauthier 378 et al., 1995), we provide here an accurate estimate of the total above-ground biomass that can 379 be found in these habitats. However, the total above-ground biomass in mesic environments 380 was probably underestimated. For instance, biomass of shrubs and forbs respectively ranged between 22 and 48 g.m⁻² and between 6 and 20 g.m⁻² in the mesic environments adjacent to 381 382 our study area (E. Lévesque, unpublished data). Overall, total above-ground biomass in wetlands and mesic environments is of similar order of magnitude (50.5 g.m⁻² \pm 2.8 SE in 383 wetlands and 44.2 g.m⁻² \pm 6.8 SE in mesic tundra for the period 2007-2009; Legagneux et al., 384 385 2012).

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387 **4.3 Impacts on ecosystems**

388 It is likely that the replacement of hydrophilic plants by mesic vegetation will severely impact 389 wildlife biology. The Qarlikturvik valley of Bylot Island represents an important summer 390 habitat for greater snow geese (Legagneux et al., 2012). It is well documented that this species 391 mostly relies on wetlands for food resources (Gauthier et al., 1995, 2011), especially because 392 graminoids are easily digested due to their low fiber concentration and rich nutritive elements 393 (Sedinger and Raveling, 1989; Manseau and Gauthier, 1993; Audet et al., 2007). For instance, 394 geese removed respectively 40 % and 31 % of the total annual production of Dupontia fisheri 395 and Eriophorum scheuchzeri during the period 1990-2007 (Cadieux et al., 2008). It remains to 396 quantify the extent to which gullying alters wetland carrying capacity. In addition, the 397 presence of ponds in wetlands provides geese refuges from predators such as arctic fox 398 (Hughes et al., 1994; Lecomte et al., 2009), and their disappearance might also change 399 predator-prey interactions.

400 Effects of gullying-induced vegetation changes may finally be visible on variations of 401 greenhouse gas emissions. There is evidence for a strong vegetation control on methane 402 emission from wetlands (Olefeldt et al., 2013; Lara et al., 2015; McEwing et al., 2015; Tveit 403 et al., 2015). In wet polygonal tundra of Northern Siberia, Kutzbach et al. (2004) found for 404 instance that dense Carex aquatilis stands emitted more methane than sites with low Carex 405 densities. Overall, wetland and lake expansion are thought to increase methane emission but 406 also carbon storage (Myers-Smith, 2005; Nauta et al., 2015; Treat et al., 2015; Bouchard et 407 al., 2015). We can therefore expect that the reverse transition from wet to mesic environments 408 observed within our low-centered polygon landscape would lead to reduced methane emission 409 and increased CO₂ emission through enhanced decomposition. However, no general pattern 410 on ecosystem responses to decreased water table position and subsequent gas emissions has 411 emerged to date (see Grosse et al., 2011 for review). It will thus be crucial to determine in the 412 near future the specific evolution of Salix and Luzula spp primary production in mesic 413 environments in order to accurately predict the effects of wetland retreat on methane and soil 414 organic carbon cycles.

415 **5 Conclusions**

416 This study illustrates that changes in the hydrological and thermal regimes following the 417 inception of thermo-erosion gullies boost landscape transformation from wet to mesic 418 habitats, providing evidence that permafrost disturbance is a critical component of ecosystem 419 modification at high latitudes. Ecological studies should consequently start using an approach 420 that integrates disturbed permafrost monitoring if one wants to more efficiently document 421 climate change effects on arctic terrestrial ecosystems. In addition, our latest field 422 observations showed that hydrology and thaw regimes of breached polygons have yet to reach 423 equilibrium with new conditions. Similarly, vegetation remains in transition given that, ten 424 years after disturbance, the cover of dominant shrubs and mesic bryophytes in disturbed 425 polygons is still lower than in adjacent mesic environments. It is currently not possible to 426 predict how long these species would take to out compete declining species and cryptogamic 427 crust and reach a new mesic environment equilibrium. This current state underscores the 428 importance of long-term monitoring of permafrost and its associated vegetation. In addition, 429 while surface warming is expected to alter the ground's thermal regime (Couture and Pollard, 430 2007), more work should be devoted to the feedback effects of plant communities and 431 vegetation succession on thermal and mechanical stabilization dynamics of disturbed 432 permafrost terrains. This is especially needed since plant community differences between 433 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 \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	$24.9\pm0.8b$	5	$9.3 \pm 4.0b$
Mesic environments	46	$19.6 \pm 1.3b$	50	$28.4 \pm 1.4b$	44	$27.6 \pm 1.1b$	48	$26.5\pm0.7b$	5	$5.9 \pm 2.6b$

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).

441

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.

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⁴⁴³ ^a *Draba* sp. was not counted as a distinct species because it is probably one of the five species already mentioned.

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	Habitats					
Gullies	Wet polygons	< 5-year disturbed polygons	> 5-year disturbed polygons	Mesic environments	Total	
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 1. Distribution of the sampling sites per habitat type and per gully.

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 habitat types studied in the Qarlikturvik valley, 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	Disturbe	Mesic		
	polygons	< 5 years	> 5 years	environments	
	(n = 62)	(n = 44)	(n = 43)	(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)	Ő	0	<<	<<	
Rosaceae (2)	ů 0	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	0.2	<	<	
Non-vascular taxa	0.7	0.5			
Lichens	<	<	1.9	6.6	
Live mosses	53.1	26.6	1.9	44.6	
Drepanocladus spp.	39.9	20.0 21.4	5.1	44.0 0	
Aulocomnium spp.	7.5	3.2	5.1 1.4	39.3	
Dried mosses	2.9	3.2 29.6	1.4	0.9	
Fungi	<	0.2	0.1	0.9 <	
•	<	0.2	0.1	<	
<i>Nostoc</i> spp. Cryptogamic crust	<<	<	14.6	5.1	

Table 3. Canonical Correspondence Analysis of the vegetation and environmental data gathered in four habitat types in the Qarlikturvik valley, Bylot Island, Nunavut. 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 of the vegetation sampled along three gullies in the Qarlikturvik valley, Bylot Island, Nunavut, and biplot scores for environmental variables. 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	Р	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				

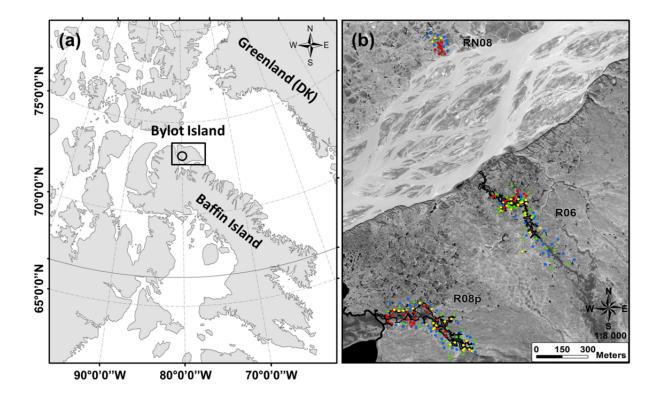


Figure 1. Location of the study area. (a) The Qarlikturvik valley (black circle), Bylot Island (black rectangle), Nunavut. (b) the 197 sampling sites located along the three selected gullies (wet polygons (n = 62): blue circles; < 5-year disturbed polygons (n = 44): yellow circles; > 5-year disturbed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

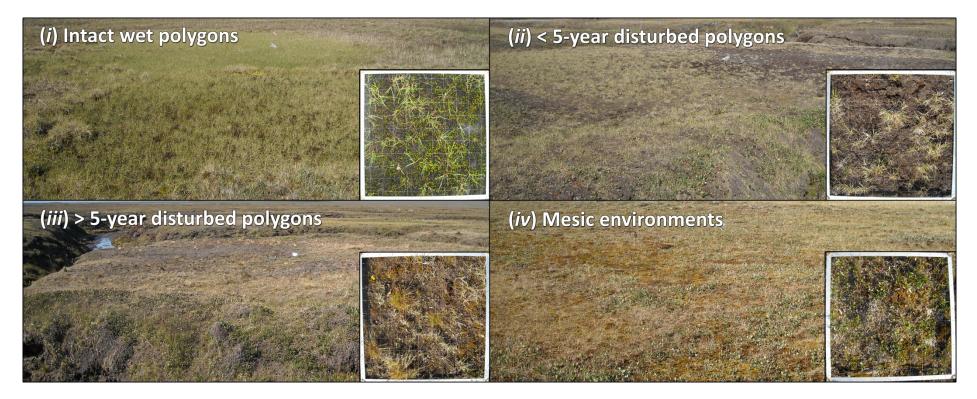


Figure 2. The four habitat types studied in the Qarlikturvik valley, Bylot Island, Nunavut. The close view at the bottom right of each picture represents the 70 cm x 70 cm quadrats that were used to determine species richness and abundance in each sampling site.

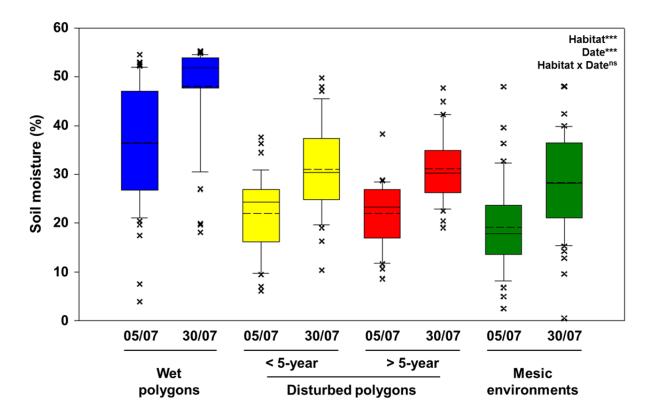


Figure 3. Soil moisture monitored early and late July 2010 in the four habitat types studied in the Qarlikturvik valley, Bylot Island, Nunavut. 10^{th} percentiles, lower quartile, median, mean (dash line), upper quartile and 90th percentiles are shown. See Table A1 for sample sizes and post-hoc contrasts.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

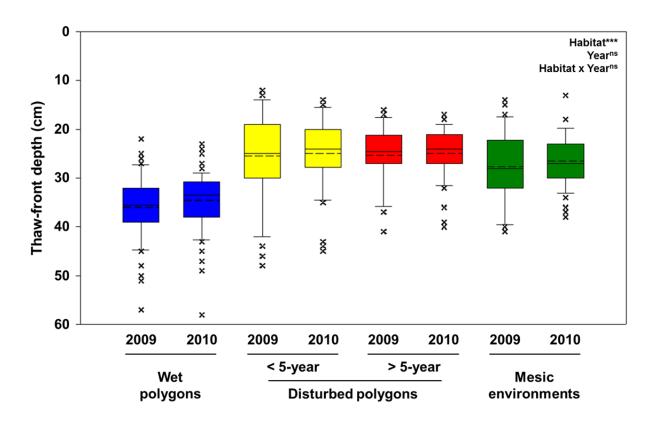


Figure 4. Thaw-front depth monitored in July 2009 and 2010 in the four habitat types studied in the Qarlikturvik valley, Bylot Island, Nunavut. 10^{th} percentiles, lower quartile, median, mean (dash line), upper quartile and 90th percentiles are shown. See Table A1 for sample sizes and post-hoc contrasts.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

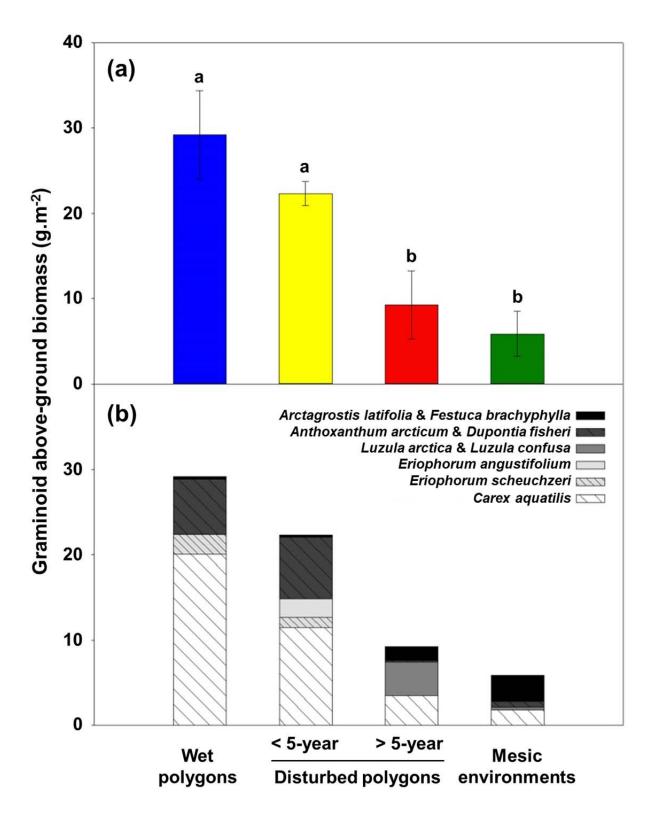


Figure 5. Above-ground biomass of graminoids growing in the four habitat types studied in the Qarlikturvik valley, Bylot Island, Nunavut. (a) Mean total biomass (\pm SE), and (b) mean biomass per species. In panel (b), dashes represent hydrophilic species. n = 5 per habitat. Species aforementioned belong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

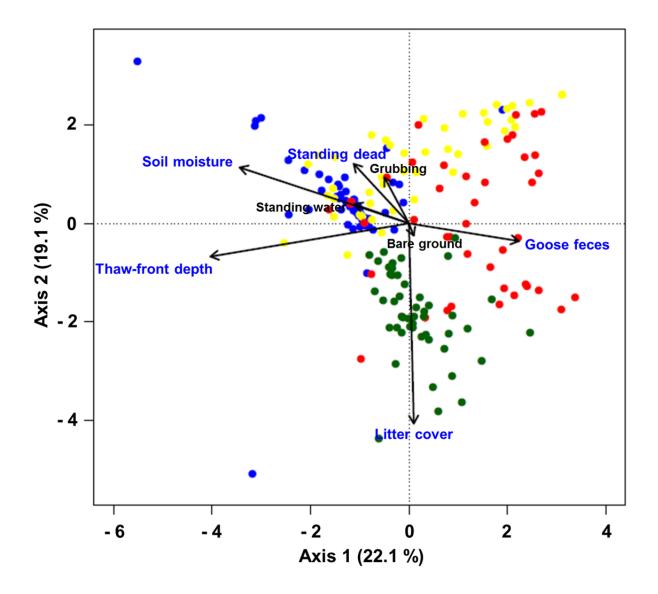


Figure 6. Canonical Correspondence Analysis ordination diagram of the 197 sites sampled in the Qarlikturvik valley, Bylot Island, Nunavut. Wet polygons (n = 62): blue circles; < 5-year disturbed polygons (n = 44): yellow circles; > 5-year disturbed polygons (n = 43): red circles; mesic environments (n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