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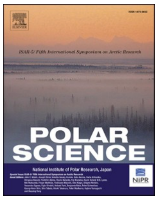

Long-term consequences of goose exclusion on nutrient cycles and plant communities in the High-Arctic

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ABSTRACT

Geese can profoundly affect arctic ecosystems directly (e.g., by grazing vegetation) and indirectly (e.g. by changing nutrient cycling resulting from faces inputs and by reducing plant litter). In the Arctic, behavior and abundance of geese have changed due to climate and land-use change. While the short-term effects of increased goose populations on tundra ecosystems are known, there is a knowledge gap for long-term consequences of goose population changes on nutrient cycling and plant communities, especially in the High-Arctic. Here, we compared wetland sites where geese have been almost absent for at least 50 years (Pond Inlet), and nearby sites where geese are abundant or sites where they have been excluded experimentally by cages and where the ground has been experimentally fertilized for over 16 years (Bylot Island). Long-term goose disappearance increased inorganic nutrients in wetlands through increased plant litter decomposition and changed community composition, likely by altering competitive relationships between three dominant vascular plant species that are different in terms of nutrient acquisition and use. In experimentally fertilized sites, inorganic nutrients were similarly increased, but fertilization had contrast effects on plant community composition compared with herbivory, released plant species from the nutrient limitation and converted wetland habitats to a dryer state. Overall, our results suggest that the direct effects of goose herbivory on vegetation are more profound than their indirect effects through an alternation of nutrient cycling even in nutrient-limited wetlands of the Arctic. These findings emphasize the need to assess long-term direct impacts of herbivores on vegetation.

1. Introduction

In recent years, the behavior and distribution of herbivores have substantially changed in response to anthropogenic drivers such as global warming and land-use changes. As herbivores can profoundly affect their environment (Côté et al., 2004) it is becoming increasingly apparent that recent changes in their behavior and distribution might modify ecosystems (Noy-Meir, 1975; Mayer and Rietkerk, 2004; Beisner et al., 2003; Van der Wal, 2006). Because of the low primary productivity and the relatively short food chains of the Arctic (Ims and Fuglei, 2005), the long-term influence of herbivores on these terrestrial ecosystems can be significant (Kaarlejärvi et al., 2015). Although changes in

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herbivore activity in these high-latitude ecosystems can be often considerable (Barrio et al., 2016), there is still a knowledge gap to be filled.

Goose abundance has increased worldwide (Fox and Madsen, 2017) in response to changes in, for example, intensified agricultural practices and warming climate (Gauthier et al., 2005; Kéry et al., 2006; Fox and Abraham, 2017). The profound effects of geese on high-latitude ecosystems have been frequently reported (Gauthier et al., 1995, 2004, 2006; Ganter et al., 1996; Jefferies et al., 2004; Abraham et al., 2005; Alisauskas et al., 2006; Jasmin et al., 2008). Geese migrate to northern region in summer to nest and rear young in graminoid-dominated nesting sites in mesic habitats surrounding ponds and lakes (Gauthier et al., 1995; Jantunen et al., 2015). In these sites, nesting density can be often high (Reed et al., 2002), substantially altering plant community composition. In extreme cases, vegetation-free ecosystem states can emerge (Ganter et al., 1996; Zacheis et al., 2001; Jefferies and Rockwell, 2002; Jefferies et al., 2006; Peterson et al., 2013, 2014).

Geese do not only defoliate vegetation directly, but they can indirectly influence plant communities by changing nutrient cycling and plant-soil interactions (Bazely and Jefferies 1985; Gauthier et al., 1996; Bardgett and Wardle, 2003). A well-known positive effect of geese via fecal material is an increase in soil soluble nutrients including N and P (Ruess et al., 1989; Jefferies et al., 1994; Gauthier et al., 1996). Goose feces contain approximately 2% Nitrogen (N) and 0.1% Phosphorous (P) in dry weight (Pouliot et al., 2009; Dessborn et al., 2016). In the Arctic, slow mineralization rates render soils poor in nutrients, so that the effects of nutrient enrichment by geese can be pronounced (Jonasson et al., 1999;Sørensen et al., 2008). In contrast to these positive influences of geese on the environment, their overabundance could have negative consequences. There is a rich body of evidence showing that vertebrate herbivores, including mammals and birds, can reduce photosynthetic activity and litter supply of plants through grazing and browsing. These top-down effects have cascading effects on carbon and nutrient cycling by reducing the supply of organic carbon to the soil and by decreasing abundance and activity of soil decomposers (Holt, 1997; Johnson and Matchett, 2001; Sankaran and Augustine, 2004). Negative effects of abundant herbivores such as geese could be especially severe in the nutrient-limited Arctic systems.

While goose populations have been increasing globally, their local disappearance has also been reported, especially near human settlements (Gagnon et al., 2009). Given the effects of decrease or disappearance of herbivores on plant diversity and ecosystem functioning reported for different herbivore species (Nishizawa et al., 2016; Stokely and Betts, 2019), understanding the consequences of goose absence is as important as is appreciating the impacts of their overabundance. This is especially true in the Arctic tundra, because of low nutrient availability to plants. Although several studies have simulated herbivore removal by establishing small-scale experimental exclosures, results are variable because of relatively short experimental duration. A serious knowledge gap exists for long-term effects of herbivore absence on nutrient cycling and resultantly plant community composition in the Arctic.

In this study, we examine the long-term impacts of geese on tundra ecosystems by contrasting plant communities and nutrients at sites where geese are abundant with those where they have been largely absent for at least 50 years. We further compare these sites with others where geese are abundant, but their effect on plant communities and nutrient cycling has been experimentally suppressed through the use of exclusion cages, and the soil has been experimentally fertilized for over 16 years. Together, these experiments offer an opportunity to improve our understanding of how geese influence plant communities and alter wetland nutrient conditions. Through comparing sites where geese have been virtually absent for at least 50 years with those where they were experimentally excluded by cages, we may also validate the effects at different time scales.

To more accurately assess possible processes behind plant community change, we analyze plant functional traits—that is, measurable features of plants that potentially affect individual performance or organism fitness (Violle et al., 2007; Cadotte et al., 2011). These traits provide information regarding the species phenotypic and genotypic response to environmental conditions including disturbance, resource availability and species interactions (Maire et al., 2012; Meihlac et al., 2020). Responses of community-level plant traits (e.g., leaf mass per area (LMA), leaf area (LA), leaf dry matter content (LDMC), N/C content or plant height) weighted by their relative abundances (CWM) reveal the effects of environmental change on plant communities (Bjorkman et al., 2018). By analyzing inorganic nutrient concentrations and plant functional traits among treatments, we can infer the effects of long-term absence of geese on plant communities, changes in nutrient cycles, and the mechanisms possibly responsible for these changes.

2. Materials and methods

2.1. Study sites

Our two study sites were located on two islands in the North Baffin Region, Nunavut, Canada. For site selection, we referred to goose distribution map in Reed et al. (2002) and Gagnon et al. (2009) (Fig. 1). The first site was on the southern plain of Bylot Island (73°08′N, 80°03′W), and the second at Pond Inlet (72°39′N, 78°03′W) on Baffin Island (Fig. 1). Bylot Island is the main breeding site of the Greater Snow Goose (*Anser caerulescens atlanticus*) and supports > 20 thousand goose pairs annually (Reed et al., 2002 Gauthier et al., 2013). High density of nesting geese during the summer results in intense herbivory and decrease in plant biomass, especially in wetlands. Up to 60% of the annual production of graminoids is consumed by geese in these wetland habitats (Gauthier et al., 1995; Massé et al., 2001; Valéry et al., 2010). Many long-term experiments since the 1980s have assessed the effects of high goose density on this ecosystem (Gauthier et al., 2004; March-and-Roy, 2009; Pouliot et al., 2009).

Pond Inlet (Inuit name: Mittimatalik) is a small village in northern Baffin Island with a 1600-strong population, about 92% of which are Inuit (Qikiqtani Inuit Association, 2014). Archaeological evidence indicates nomadic Inuit have lived in this area for almost 4000 years (Mary-Rousselière, 1985), but in the decade following establishment of a federal school in 1959, many Inuit families settled here in a permanent community. Following establishment of an airstrip in 1973–1974, the community developed rapidly (Qikiqtani Inuit Association, 2014). While goose nesting sites existed around Pond Inlet before the community development, density was likely very low because, during the first half of the 20th century, the total size of the greater snow goose population ranged from 0.5 to 3% of its size over the past 20 years (Gauthier et al., 2005). Since the establishment of the community, goose abundance around it has decreased to a near absence (Gagnon et al., 2009). Consequently, for at least 50 years, geese have been unintentionally excluded from this site.

Dominant vascular plant species in wetland used by nesting geese in these regions including *Dupontia fisheri*, *Eriophorum scheuchzeri*, and *Carex aquatilis* (Gauthier et al., 1995, 2013; Jasmin et al., 2008; Pouliot et al., 2009). Each site is also covered by a thick layer of brown mosses, dominated by the genus *Drepanocladus* (Pouliot et al., 2009). The greater snow goose is the most influential herbivore and other herbivores include brown (*Lemmus sibiricus*) and collared (*Dicrostonyx groenlandicus*) lemmings.

While Bylot and Pond Inlet sites are about 100 km apart, their climate is similar: the mean summer (June–August) temperature and precipitation at Bylot Island (southern plain) are 4.5 °C and 27.6 mm, while those at Baffin Island (Pond Inlet) are 4.7 °C and 26.8 mm, respectively (Duclos et al., 2006). These sites are also similar in geological age, being Mesozoic- and Tertiary-age sedimentary bedrock (Jackson et al., 1978; Miall et al., 1980) but present some differences in their geomorphology with a dominance of polygonal patterned ground on Bylot Island (Ellis and Rochefort 2004; Fortier et al., 2006).

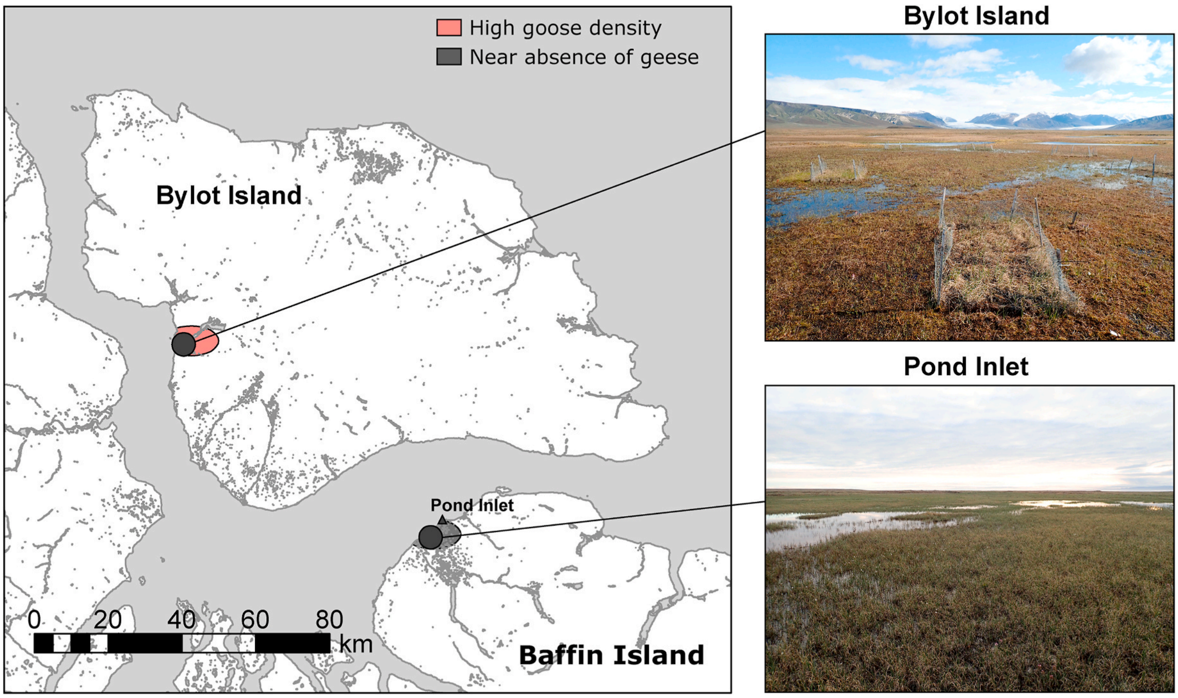

Fig. 1. Study sites, Bylot and Baffin islands. Relative abundance of greater snow geese around study sites from Reed et al. (2002) and Gagnon et al. (2009). Above right, Bylot Island wetland with 2 × 1 m goose exclusion cage; above left, Pond Inlet: graminoid-dominated wet meadows surrounding ponds.

2.2. *Experimental design*

Seven study sites were established at both Bylot Island and Pond Inlet. At Bylot Island, goose exclusion cages were established at all 7 sites, 3 sites had only goose exclusion treatment (2 exclusion treatments (grazed/ungrazed) × 3 sites) and the 4 remaining sites had combinations of goose exclusion treatment and five levels of fertilization, providing 10 treatment per study site (2 exclusion treatments (grazed/ungrazed) × 5 fertilization treatments × 4 sites). Fertilization treatments were established in 2 × 2 m squares, with half (2 × 1 m) exposed to goose herbivory (grazed) and half enclosed (ungrazed) within a 50 cm high chicken-wire fence (2.5-cm mesh). We set 80 × 80 cm vegetation survey plots in the central portion of each half (2 × 1 m) squares to avoid the edge effects. Although this mesh size did not prevent lemming movement, the effects of lemming herbivory on vegetation are likely to be limited here (Gauthier et al., 2004). Each 2 × 2 m square was located at least 5 m from the next to prevent cross-treatment contamination.

The five fertilization treatments at Bylot Island comprised: low N ($N_L = 1$ g m^{-2}), high N ($N_H = 5$ g m^{-2}), high P ($P_H = 3$ g m^{-2}), and high N and P ($N_HP = 5$ g m^{-2} of N + 1 g m^{-2} of P), and control (C_O) that received no fertilizer. These amounts exceed the amount of nutrients added to this ecosystem by goose droppings, which are around 0.6 g m^{-2} of N and 0.03 g m^{-2} of P in areas of high goose use (Pouliot et al., 2009). However, Pineau (1999) had shown that graminoid plants did not respond to the addition of 1 g m^{-2} g of N in this ecosystem. Since we wished to detect the potential change at the community level induced by goose feces in a context of increasing populations, we added higher level of nutrient than those encountered at current population level.

Fertilizers were applied in a single dose in late June each year; N was applied as ammonium nitrate (NH_4NO_3), and P as superphosphate phosphoric acid (H_3PO_4). While N was dissolved in 2 L of water before application, P was scattered uniformly over the moss surface before watering (2 L by experimental unit). For consistency, control treatments also received 2 L water. Water was obtained from an open source near experimental sites (Pouliot et al., 2009). Goose exclusion cages were set up in 2002 and fertilization experiments have been performed from 2002 to 2019.

Seven study sites were established near Pond Inlet in wetlands similar to those encountered on Bylot Island (Fig. 1, photos). According to local knowledge, these areas were reported to be used as nesting sites by geese in the past but geese are rarely encountered in those areas nowadays (Gagnon et al., 2009; G. Gauthier pers. obs.; Appendix. 1). To minimize human effects, each wetland site was located at least 5 km from the village, and was separated by at least 500 m. Three replicate 80 × 80 cm vegetation survey plots were established at each site.

2.3. *Field data collection*

Regarding plant community data, the number of vascular plant tillers per species was counted from four randomly selected subplots (10 × 10 cm) within each 80 × 80 cm vegetation survey plot, and pooled. The relative abundance of each species was calculated as the ratio between the number of tillers of the species and the total number of tillers of all species encountered in the four subplots. We also measured the above-ground biomass of vascular plants (g) per plot by clipping vegetation, drying samples and weighting them. Above-ground parts included green leaves and white parts of the tiller above the last leafing node.

The water table lies at or above the surface through most of the plant growing season in wetland. Graminoid plants grow in organic soils formed by mosses (e.g. Madsen and Mortensen, 1987; Gauthier et al., 2006). As vascular plants mainly absorb nutrients from water around bryophytes, we measured PO_4^{2-}, NH_4^+, NO_3^- and dissolved organic carbon concentrations (DOC) in wetland water; water samples were collected from the water table and immediately frozen until analysis. After thawing, water samples were filtered through 0.2 μm membrane filter (DISMIC-25CS, Advantec, Japan); PO_4^-, NH_4^+, NO_3^- concentrations were determined colorimetrically using a TRACCS-800 Autoanalyzer (Technico, Japan; Tanabe et al., 2010). DOC was measured with a Sievers 5310 C TOC Analyzer (GE Analytical Instrument, USA) in a two-stage process commonly referred to as T–IC; IC (inorganic carbon) was oxidized by sample acidification (pH2) and TC (total carbon) by ultraviolet lamp. DOC was calculated by subtracting sample IC from TC. Measurements of DOC were replicated three times; mean values are used in analysis.

Six plant functional traits were measured: leaf dry matter content (LDMC, g g $^{-1}$), leaf mass per area (LMA, g cm^{-2}), plant height (Height, cm), leaf nitrogen content (N, %), leaf carbon content (C, %), and leaf C–N ratio (C/N). Fresh leaves were immediately scanned and weighed, then dried for 72 h at 70 °C to obtain leaf dry weight. LA was calculated from leaf scan data using Image-J (Rasband, 1997–2008). SLA and LDMC were calculated using LA and leaf weight data (LMA = dry weight/LA; LDMC = dry weight/fresh weight). Leaf N and C were measured by NC analyzer (Sumigraph NCH–22 F, Sumika Chemical Analysis Service, Japan). Plant height was measured from the ground to the highest photosynthetic structure. These trait data were taken at each combinations of treatments (Pond inlet and 10 treatments in Bylot island (2 exclusion treatments (grazed/ungrazed) × 5 fertilization treatments)) and averaged values were used in analysis.

All data and samples were collected during the peak plant growth in this region, between mid-July and early August 2018. Time and logistical constraints (e.g., helicopter schedules changing with weather) precluded sampling environmental data at 1 of 3 fertilization sites, and plant community data at 5 of 8 low N (N_L) plots (2 grazed and 1 exclosure) on Bylot Island.

2.4. Data analysis

The relative abundance of plant species per study plot, which we used to describe community composition, was determined from tiller numbers. Environmental and trait data were log-transformed to follow a normal distribution.

To detect changes in community composition, principal component analysis (PCA) was performed on plant community composition data (relative abundance). To evaluate communities by plant features, we calculated community-weighted mean (CWM) trait values for each plot—the mean trait value of all species in a community weighted by their relative abundance (Garnier et al., 2004). Trait data used for CWM correspond to the sites and treatments (Fertilization and exclusion) to accommodate intraspecific variability (e. g. CWM in "Roc8/Exclosure/High N treatment" was calculated by using averaged trait values obtained from four "Exclosure/High N treatment" quadrat). Species richness was the number of the species at each plot.

Two types of multiple regression analysis were performed. First, to detect treatment effect (Goose exclusion and Fertilization (addition of P and N)) on wetland water quality, we constructed linear models. Response variables included any of four indices of wetland water quality (PO_4^{2-}, NH_4^+, NO_3^- and DOC); treatments (Goose exclusion, and level of addition of P (g m^{-2}), and N (g m^{-2})) were used as explanatory variables. The variable of goose exclusion was treated as categorical variables here with the levels Grazed (= grazed site on Bylot Island), Exclosure (=goose exclosure on Bylot Island) and Near absence (= near Pond Inlet) due to the uncertainty of goose exclusion duration around Pond Inlet (50 years in minimum). Values for P were quantity of fertilizer ($C_O = 0$, $P = 1$, and $P_H = 3$). Since we only have three low N (N_L) plots (2 grazed and 1 exclosure), we removed low N treatment from the linear models and values for N were treated as binomial variable ($C_O = 0$, $N_H = 1$). Second, to detect effects of environmental change on plant communities, generalized linear models were constructed. Response variables were any of eight indices represented by the species or trait composition in communities (PC1, PC2, species richness, total biomass and 6 of CWM (Leaf N, C, C/N ratio, LDMC, SLA, plant height)). Treatments (Goose exclusion, and levels of addition of N and P; see above) and wetland water quality (PO_4^{2-}, NH_4^+, NO_3^- and DOC concentrations) were taken as multiple experimental variables after standardization. We used both treatments and water quality in the models such as N addition and NH_4^+ since the treatments do not necessarily represent the snapshot inorganic data. For both models, we assumed a Gaussian distribution for response variables to fit linear regressions except for Species richness where we used a Poisson distribution. The model with lowest Akaike information criterion (AIC) was identified as the best model. We considered that a variable had a significant effect when the 95% confidence interval of the slope parameter excluded. All statistical tests were performed in R version 3.5.2 (http://www.R-project.org; R Development Core Team).

3. Results

We recorded 29 vascular plant species (Table A.2) from our study sites, with a mean species richness per plot of 4.4 (mean alpha diversity = 3.7 (Pond Inlet) and 4.8 (Bylot Island)). The three dominant species, *D. fisheri, E. scheuchzeri* and *C. aquatilis* were present in most plots. Other highly abundant species were *Hierochloe pauciflora*, *Poa arctica*, and *Stellaria longipes*, which were especially abundant in plots with a high fertilization level (Table A.2).

PC1 explained 44.8% and PC2 26.8% (71.6% in total) of the variance in community structure. Factor loadings of each species onto the principal components were given in Table A.3. We infer that PC1 reflects the duration of goose exclusion (Fig. 2 (a), positive loading associated with increasing duration of goose exclusion) and PC2 reflects fertilization treatment intensity (Fig. 2 (b), negative loading associated with increasing fertilization intensity). Results indicate that both long-term goose exclusion and nutrient addition have had considerable effects on plant community composition. As the duration of goose exclusion increased (Table A.2), *C. aquatilis* and *E. scheuchzeri* increased in abundance, and *D. fisheri* decreased. As the quantity of fertilizer increased, *H. pauciflora* and *P. arctica* increased their abundance and *C. aquatilis*, *E. scheuchzeri* and *D. fisheri* decreased (Table A.2).

The duration of goose exclusion considerably increased PO_4^{2-}, while P (H_3PO_4) addition contributed to increased PO_4^{2-}, and addition of N (NH_4NO_3) contributed to increased NH_4^+ but there were no effects on NO_3^- (Table 1). DOC was positively affected by P and N additions.

Plant community composition indices were explained by treatments (goose exclusion and fertilization) and water quality (Table 2). PC1 was mainly explained by the goose exclusion, while PC2 was mainly explained by the amount of P and N added to a treatment. Their results are consistent with the patterns seen in Fig. 2. Fertilization (both N and P addition) increased species richness. Plant biomass and CWM of plant height showed a similar pattern with PC1, with the duration of goose exclusion positively related to increased plant biomass accumulation (Table 2). Results of CWM of leaf C and N content and C/N ratio responded well to all treatments (Exclusion and addition of N and P). More carbon rich and nutrient poor plant species, and increased C/N ratios were positively related with increased duration of goose exclusion (Fig. 3). Although addition of P decreased plants high in N and C, the C/N ratio increased significantly and LMA was increased (Fig. 4). These results indicate that addition of P increased species with high C/N ratio and with thick tissues. Conversely, addition of N increased plant N content and decreased C/N ratio, indicating nitrogen-rich species increased in abundance (Fig. 4). The effects of wetland water quality on plant community indices were rarely detected (Table 2).

4. Discussion

In arctic wetlands, geese have been recognized to affect nutrient cycling through intense herbivory and fecal input (Van der Wal, 2006; Hillebrand et al., 2007; Pouliot et al., 2009). We compare sites with and without geese to those in which geese have been excluded but soils have been experimentally fertilized, to assess the long-term effects of geese on arctic wetland ecosystems.

4.1. Change in nutrient conditions

Sites exposed to goose grazing lacked high nutrient concentrations, indicating fertilization through goose feces was limited. These results were consistent with previous studies. At moss dominated freshwater wetlands in the Arctic, it is known that nutrients released from goose

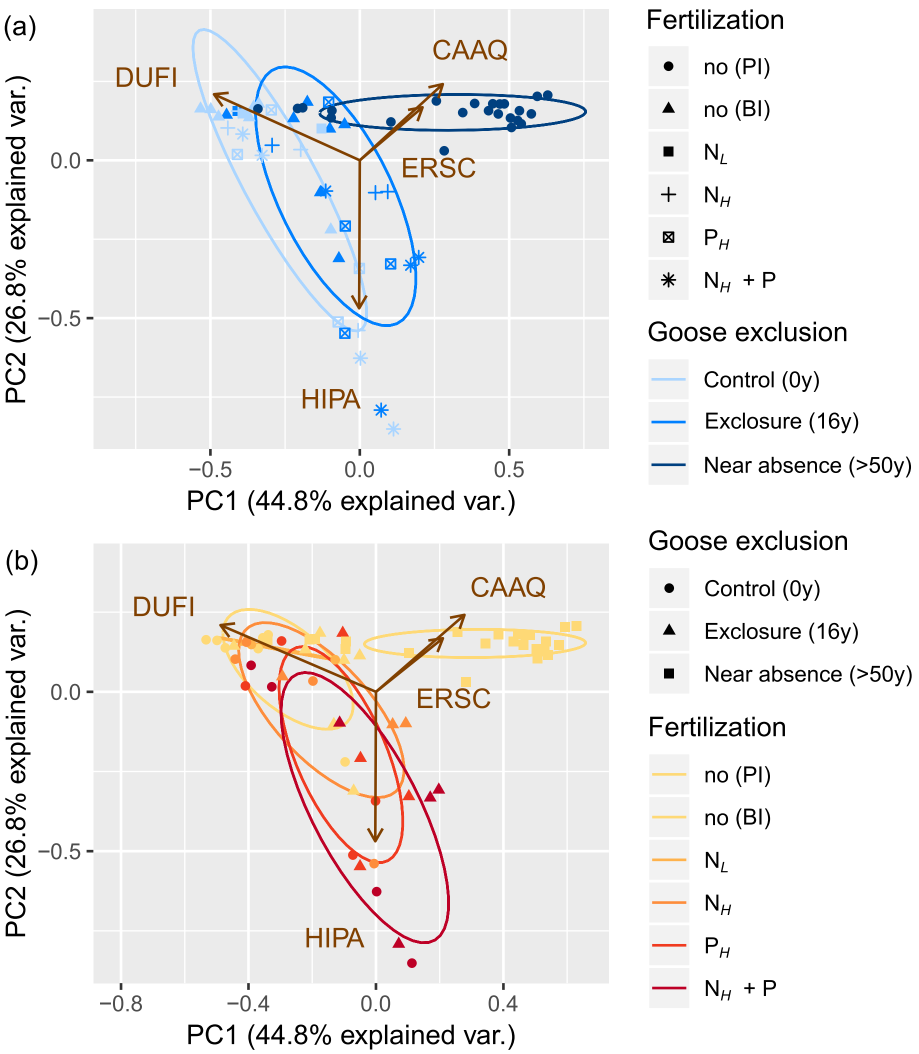

Fig. 2. Principal component analysis (PCA) of plant community compositions. Colored ellipses in A and B represent 68% (1σ) confidence intervals for each treatment, goose exclusion (Grazed (0 years) on Bylot, Exclosure (16 years) on Bylot, or Near absence (>50 years) around Pond Inlet) and fertilization (no (PI) (Pond Inlet), no (BI), N_L, N_H, P_H, N_H + P), respectively. Solid lines show the direction and loadings of four dominant species (CAAQ = *Carex aquatilis*, DUFI = *Dupontia fisheri*, ERSC = *Eriophorum scheuchzeri*, HIPA = *Hierochloe pauciflora*). Each point represents vegetation survey plot (n = 61, 40 in Bylot Island and 21 in Pond Inlet).

feces leach quickly into water where they can be quickly absorbed by thick moss cover (Kotanen et al., 2002; Pouliot et al., 2009). Conversely, sites at which geese were absent had high concentrations of PO_4^{2-}. Since PO_4^{2-} input is mainly from herbivore feces and plant litter decomposition, increased PO_4^{2-} in this habitat is most likely the result of increased plant decomposition. We infer from Sorensen et al. (2008) that accumulated leaf litter and increased biomass in areas where geese are absent released the decomposer from the resource limitation (plant litter), consequently facilitates decomposition, improving plant-soil interactions.

The effect of fertilization on wetland water conditions was straightforward. Addition of P increased PO_4^{2-}, and addition of N significantly increased NH_4^+. The effects of sustained fertilization on water quality was detected despite the presence of a thick moss cover and the flow of wetland water (Pouliot et al., 2009). It is possible that the sustained, long-term addition of N and P exceeded the capacity of absorption by mosses and ultimately changed water quality. Conversely, addition of N did not change NO_3^- concentration, possibly because NO_3^- has chemical characteristics conducive to denitrification and leaching, especially in wetlands (Borman and Likens, 1979; Lin et al., 2001). Since the water sampling was 2 months later from the fertilization, the nutrients in wetland water should be diluted. In aquatic and terrestrial systems, studies reported that fertilization often increases DOC (Gale et al., 2003) as also found in our N and P addition treatments, likely due to a resulting from microbial responses to carbon and nutrient availability (Findlay 2003). As a consequence, we found some plant species atypical in wetlands at the fertilized plots (Duclos et al., 2006).

4.2. Change in plant community

PCA showed differences in plant communities among sites exposed to goose grazing were characterized by high abundance of *D. fisheri*, a small-sized pioneer plant highly abundant in young wetlands (Billings and Peterson, 1980), but as the duration of goose exclusion increased, *E. scheuchzeri* and *C. aquatilis* increased in abundance. Both *E. scheuchzeri* and *C. aquatilis* are larger, and dominate in undisturbed wetlands, with *C. aquatilis* being a particularly strong competitor that can outcompete other species, including *E. scheuchzeri* in older arctic wetlands (Billings and Peterson, 1980). *E. scheuchzeri*, a plant preferred by snow geese in Arctic wetlands, has also been reported to increase following short-term goose exclusion (Gauthier et al., 2004). In sum, our results suggest a substantial impacts of goose absence/presence on vegetation. However, careful interpretations are needed here, because geomorphological processes – other major determinants of structure and composition of tundra vegetation – are not necessarily equivalent between Bylot Island and Baffin Island. For instance, Bylot Island wetlands may be more geomorphologically active than those around Pond Inlet due to the presence of polygonal patterned ground, which may contribute to a reduced long-term stability of wetlands at the former site (Ellis and Rochefort; 2004; Fortier et al., 2006).

Community weighted means (CWM) of functional traits support the interpretation that goose herbivory has a dominant role in this

Table 1

Best linear models. Response variables include wetland water quality (PO_4^{2-}, NH_4^+, NO_3^- and DOC (dissolved organic carbon) concentrations); explanatory variables include treatment data (goose exclusion (dummy variables; Exclosure (16 years) and Near absence (>50 years)), and level of N and P addition). The values in the rows of explanatory variables represent the slop of the regression coefficients for selected explanatory variables (with 95% confidence interval).

	Response variables:			
	PO_4^{2-}	NO_3^-	NH_4^+	DOC
Exclosure (16 y)	1.02 (0.46, 1.58)	0.32 (-0.49, 1.14)		0.22 (-0.50, 0.94)
Near absence (>50 y)	1.75 (1.24, 2.27)	0.46 (-1.14, 0.22)		0.76 (0.07, 1.45)
N addition			0.46 (1.14, 0.22)	1.51 (0.71, 2.31)
P addition	1.74 (1.10, 2.38)		1.14 (0.38, 1.90)	1.51 (0.71, 2.31)
Intercept	−1.45 (-1.88, −1.01)	0.20 (-0.35, 0.75)	−0.26 (-0.55, 0.02)	−0.74 (-1.34, −0.15)
AIC Best model	85.16	115.17	104.77	105.46
AIC Null model	119.26	116.18	118.10	117.58

ecosystem. Dominant plant species at sites where geese are absent were taller and had high C/N ratios. Relationships between plant height and duration of goose exclusion may indicate the existence of competitive relationships between plant species through the community assembly process. Height is a fundamental characteristic of plants and is associated with their competitive ability to intercept light. In general, competition for light intensifies as aboveground biomass or plant stature increases (Hautier et al., 2009). Here, with prolonged absence from goose herbivory, plant biomass increased and competition between plants intensified. In Arctic wetlands, almost all plants are summer green perennial herbs where plant height depends largely on accumulation of carbohydrates in rhizomes stored from previous years. Grazing can reduce carbohydrate accumulation in rhizomes (Beaulieu et al., 1996) and geese can even feed directly on rhizomes, especially early and late in the season (Gauthier, 1993; Hupp and Robertson, 1998). Thus, the compound effects of competition and grazing impact likely contributed to a gradual change in plant community height.

The C/N ratio reflects plant growth strategies (Wright et al., 2004; Freschet et al., 2010). Generally, species with high N and low C/N ratio are described as having a resource acquisitive strategy, using a high amount of resources to rapidly acquire C. This strategy may benefit plants under high-resource conditions; however, due to excess respiratory costs, it is likely disadvantageous for plants under low-resource conditions. Species with low N and high C/N ratios are described as

Table 2

Best generalized linear models. Response variables include PC1, PC2, Species richness (Sp rich), aboveground biomass of vascular plants (Biomass), and community-weighted mean (CWM) of six traits (leaf nitrogen (N), carbon (C), carbon/nitrogen ratio (C/N), leaf mass per area (LMA), and leaf dry matter contents (LDMC), and plant height (Height)). Explanatory variables in treatments include goose exclusion (dummy variables; Exclosure (16 years) and Near absence (>50 years), and addition of N and P; wetland water quality data include PO_4^{2-}, NH_4^+, NO_3^- and DOC (dissolved organic carbon) concentrations. The values in the rows of explanatory variables represent the multiple regression coefficients for selected explanatory variables (with 95% confidence interval).

	Response variables:									
	PC1	PC2	Sp rich	Biomass	N	C	C/N	LMA	LDMC	Height
Exclosure (16 y)	0.08 (-0.14, 0.30)			0.17 (-0.19, 0.52)	−0.36 (-0.71, −0.01)	−0.49 (-0.80, −0.18)	0.47 (0.03, 0.91)		1.42 (0.72, 2.12)	0.92 (0.34, 1.50)
Near absence (>50 y)	0.47 (0.28, 0.66)			1.92 (1.63, 2.21)	−0.86 (-1.20, −0.51)	0.32 (-0.01, 0.65)	1.31 (0.88, 1.74)		1.13 (0.51, 1.74)	1.64 (1.16, 2.12)
N addition		−0.05 (-0.08, −0.02)	0.08 (0.00, 0.15)		1.35 (0.97, 1.73)		−1.02 (-1.50, −0.55)			
P addition		−0.12 (-0.16, −0.07)	0.15 (0.01, 0.29)		−0.45 (-0.60, −0.30)	−0.76 (-0.91, −0.61)	0.55 (0.36, 0.73)	0.33 (0.02, 0.64)	0.46 (0.15, 0.76)	
PO_4^{2-}	0.11 (0.03, 0.19)					0.15 (0.01, 0.29)				
DOC		−0.06 (-0.11, −0.002)		−0.14 (-0.27, −0.01)					−0.31 (-0.56, −0.05)	
NH_4^+										
NO_3^-										
Intercept	−0.22 (-0.36, −0.07)	0.13 (0.08, 0.18)	1.37 (1.20, 1.55)	−0.71 (-0.95, −0.48)	0.23 (-0.07, 0.52)	0.51 (0.25, 0.78)	−0.55 (-0.93, −0.18)	−0.35 (-0.66, −0.05)	−1.11 (-1.63, −0.60)	−0.87 (-1.26, −0.48)
Akaike Inf. Crit.	6.21	−39.28	162.41	47.00	46.46	30.11	64.41	113.36	103.86	87.33
AIC Null model	37.28	−4.08	166.77	121.40	104.64	110.35	113.88	115.58	120.02	115.26

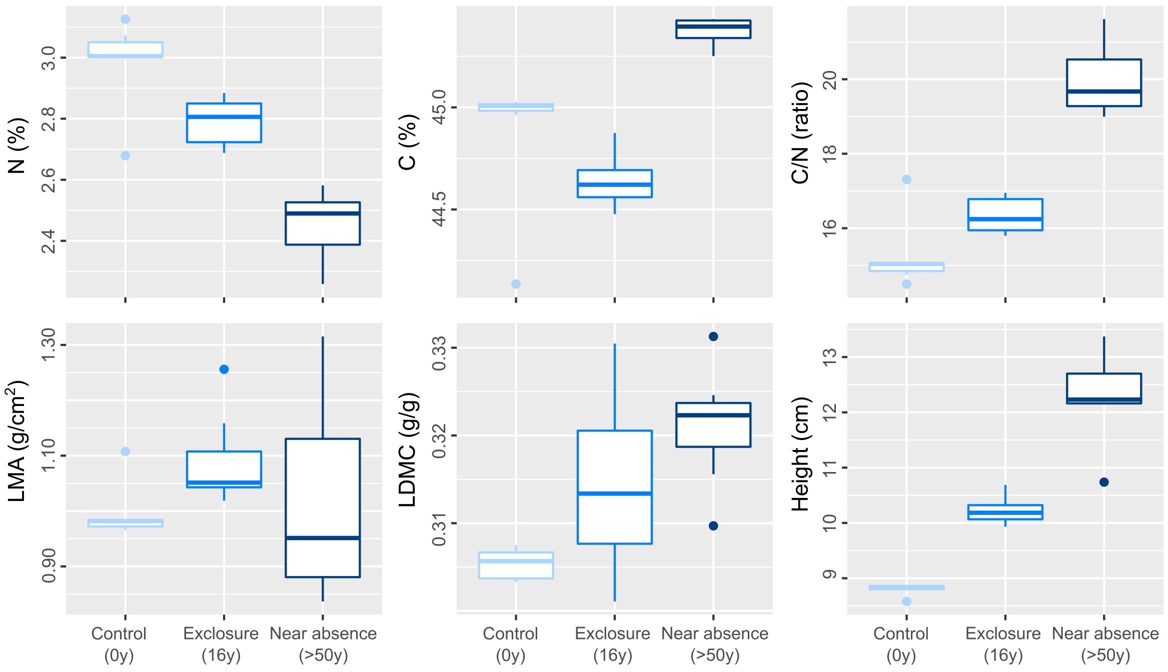

Fig. 3. Boxplots showing median (central lines), 25 and 75% quartile ranges around the median (box width). Comparison of CWM of six plant traits (leaf nitrogen (N), carbon (C), carbon/nitrogen ratio (C/N), mass per area (LMA), and dry matter (LDMC) contents, and plant height (Height)) in treatments where geese have been excluded for 0 years (Grazed (0 years on Bylot)), 16 years (Exclosure (16 years)on Bylot), and Near absence (>50 years) on Pond Inlet. These boxplots contain only unfertilized plots in Bylot Island (7 grazed and 7 exclosure plots) and 7 plots in Pond Inlet (random selection of 1 plot per site) to visualize the patterns more clearly.

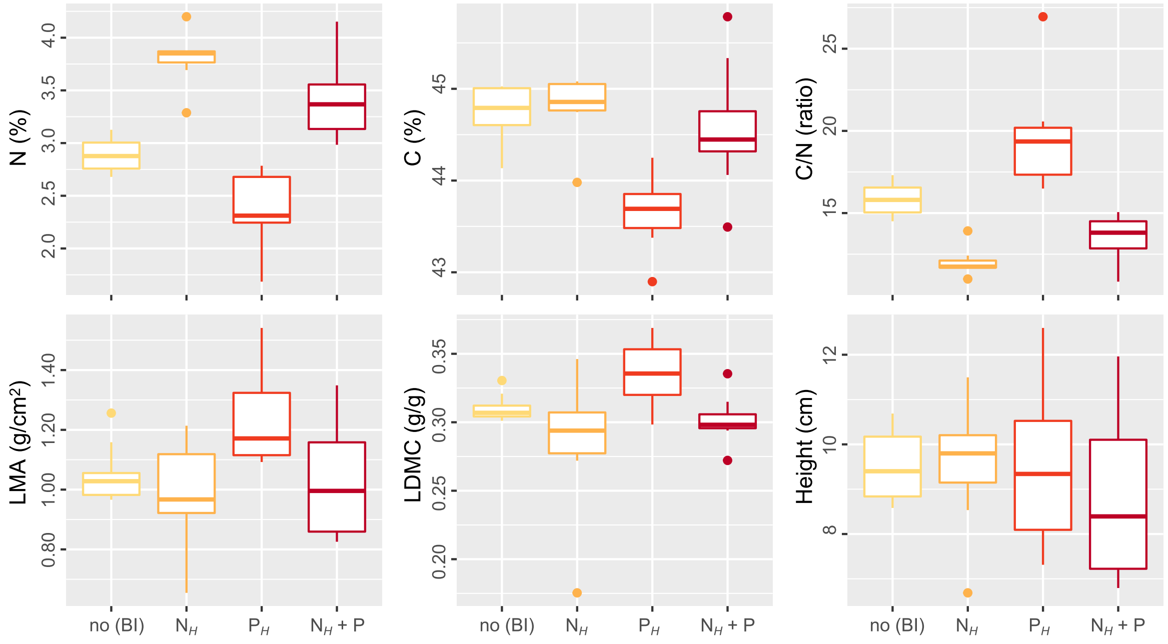

Fig. 4. Boxplots showing median (central lines), 25 and 75% quartile ranges around the median (box width). Comparison of CWM of six plant traits (Leaf nitrogen (N), carbon (C), carbon/nitrogen ratio (C/N), mass per area (LMA), and dry matter (LDMC) contents, and plant height (Height)) among four fertilization treatments (except for N_L) at Bylot Island (Co, N_H, P_H, N_H + P). These boxplots contain only four fertilized study sites (Roc 3, Roc 6, Roc 7, Roc8).

having a resource conservative strategy, which is advantageous to plant species in low-resource conditions (Reich, 2014). Here, plant species with conservative strategy were more abundant in sites where geese were absent, where low temperatures of Arctic limit the bioavailability of nutrients to plants (Shaver and Chapin, 1995). This diminution of nitrogen in plant tissue might result from a dilution of nitrogen with the observed accumulation of plant biomass, which is a well-known phenomenon in grassland ecosystem (Maire et al., 2013), but has not been already described in tundra ecosystems to our knowledge.

Long-term fertilization substantially changed plant community composition in our study, in a different way to that of long-term goose exclusion. Species like *H. pauciflora* and *P. arctica*, which are more typical of drier habitat than wetlands (Duclos et al., 2006) increased whereas typical wetland species (*C. aquatilis*, *E. scheuchzeri* and *D. fisheri*) decreased. These recruitments of non-wetland species suggest that fertilized sites may become drier over time and could contribute to the higher species richness at both N and P addition sites.

While the effect of adding P and N was compounded in PCA results, CWM trait values revealed contrasting patterns between addition of these two fertilizers. Addition of N increased species typical of resource acquisitive taxa (high N content and low C/N ratios). Here, the increase in non-graminoid species such as *S. longipes* might contribute to this trend. This indicates that addition of N may have released plants from nutrient limitations, enabling resource acquisitive strategy species to increase their abundance. On the contrary, addition of P reduced more strongly N than C content and increased high C/N and LMA. This suggests that addition of P was advantageous for resource conservative species with thicker leaf tissues, perhaps reflected by the increased number of species in the family Poaceae, such as *H. pauciflora* and *P. arctica*. Despite the $N_H + P$ addition treatment being most dissimilar to all other communities in the PCA, the CWM of N and C/N ratio in this treatment was half-way between the values of the N_H and P addition alone (Fig. 4) treatments. Thus, we speculate that these plots contain features of both N and P addition plots alone. The greater impact of treatments (goose exclusion and fertilization) on plant community composition than nutrients in water could be because nutrients were immediately absorbed by plants and mosses after treatment.

5. Conclusion

Our study was based on a unique opportunity to compare plant communities between two nearby sites that differ greatly in their historic use by geese (Pond Inlet and Bylot Island) to assess the long-term effects of geese on Arctic vegetation. Long-term goose exclusion likely changed plant community composition by altering competitive relationships between dominant plant species. Interestingly, fertilization experiments released plant species from the nutrient limitation and converted wetland habitats to a dryer state. Even after 50 years of goose absence, changes in plant community structure were not comparable to those found for the fertilization treatments. While we found PO_4^{2-} improvement at both goose exclusion and P-addition sites, results of plant community composition and traits were dissimilar between the sites. This finding indicates that the direct effects by goose herbivory on vegetation are more profound than their indirect effects through alteration of nutrient cycling even in nutrient-limited wetlands of the Arctic.

To date, a substantial number of herbivore exclusion experiments exists to evaluate the impacts of herbivory on vegetation but inferences gained from these studies are still limited, especially for a longer time horizon. By combining planned and unplanned goose exclusion, we have addressed this issue. Nutrient conditions and vascular plant community composition encountered in sites which are virtually free from geese for more than a half century could represent conditions in the future in our experimental exclosure sites if the high abundance of geese persist. Avian and mammal herbivores are often ecosystem engineer, and thus the consequences of their population changes are far from negligible. Although challenging, we emphasize the need of studies that can quantify the long-term impacts of these engineers on composition, structure and functions of ecological systems.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix 1. Photos of goose feces on a xeric ridge near the study wetlands. Goose feces often last for >1 yr when deposited on xeric ridges along wetlands. There were abundant faces around the study sites in Bylot Island (photo above). In contrast, feces were very few in Pond Inlet and rarely found near the study sites in Pond Inlet (photo below)

Table A2

Heat map of the relative abundance of each vascular plant species per plot, species order reflects abundances, 0 represents trace (value less than 0.01).

Area	Site ID	Fertilization	Goose exclusion	*Dupontia fisheri*	*Carex aquatilis*	*Eriophorum scheuchzeri*	*Hierochloe pauciflora*	*Poa arctica*	*Stellaria longipes*	*Eriophorum angustifolium*	*Festuca brachyphylla*	*Cardamine pratensis*	*Pedicularis albolabiata*	*Saxigraga hirculus*	*Saxifraga foliolosa*	*Pleuropogon sabinei*	*Poaceae_sp1*	*Equisetum arvense*	*Salix herbacea*	*Salix richardsonii*	*Poaceae_sp2*	*Salix arctica*	*Bistorta vivipara*	*Unknown_2*	*Arctagrostis latifolia*	*Poaceae_sp3*	*Unknown_1*	*Salix reticulata*	*Ranunculus hyperboreus*	*Lycopodium annotium*	*Vaccinium uliginosum*	*Luzula confusa*
Pond Inlet	PA1	-	Absence		0.87	0.13																										
Pond Inlet	PA2	-	Absence	0.55	0.16	0.29																										
Pond Inlet	PA3	-	Absence	0.64	0.18	0.18																										
Pond Inlet	PB1	-	Absence	0.13	0.66	0.18														0.04												
Pond Inlet	PB2	-	Absence	0.03	0.82	0.15																										
Pond Inlet	PB3	-	Absence	0.01	0.46	0.41							0.06		0.05																	
Pond Inlet	PC1	-	Absence	0.05	0.25	0.71																										
Pond Inlet	PC2	-	Absence	0.04	0.44	0.52																										
Pond Inlet	PC3	-	Absence	0.11	0.58	0.32																										
Pond Inlet	PD1	-	Absence	0.09	0.46	0.4							0.06																			
Pond Inlet	PD2	-	Absence	0.12	0.42	0.44							0.01																			
Pond Inlet	PD3	-	Absence	0.29	0.6	0.1							0.02																			
Pond Inlet	PE1	-	Absence	0.65	0.16	0.19																										
Pond Inlet	PE2	-	Absence		0.38	0.62																										
Pond Inlet	PE3	-	Absence	0.53	0.17	0.22		0.01					0.06																			
Pond Inlet	PF1	-	Absence		0.24	0.71							0.01						0.04													
Pond Inlet	PF2	-	Absence	0.1	0.59	0.32																										
Pond Inlet	PF3	-	Absence	0.18	0.6	0.2							0.02																			
Pond Inlet	PG1	-	Absence	0.36	0.22	0.32				0.1																						
Pond Inlet	PG2	-	Absence	0.12	0.23	0.28				0.32								0.05														
Pond Inlet	PG3	-	Absence	0.33	0.08	0.29	0.19			0.11																						
Bylot	R33	Co	Exclosure	0.46	0.07	0.09	0.16		0.07	0.14												0.01						0.01				
Bylot	R33	Co	Control	0.89		0.11																										
Bylot	R35	Co	Exclosure	0.54	0.19	0.2	0.05																	0.01								
Bylot	R35	Co	Control	0.77	0.13	0.1																										
Bylot	R36	Co	Exclosure	0.63	0.18	0.08				0.08		0.02														0.01						
Bylot	R36	Co	Control	0.75	0.05	0.11										0.08																
Bylot	ROC3	Co	Exclosure	0.35		0.11	0.36			0.15			0.02																			
Bylot	ROC3	Co	Control	0.43	0.11	0.07	0.32			0.07																						
Bylot	ROC6	Co	Exclosure	0.83		0.13			0.02			0.02																				
Bylot	ROC6	Co	Control	0.91		0.09																										
Bylot	ROC7	Co	Exclosure	0.5	0.13	0.32	0.03	0.01																								
Bylot	ROC7	Co	Control	0.84		0.09						0.02	0.05																			
Bylot	ROC8	Co	Exclosure	0.64	0.33	0.03																										
Bylot	ROC8	Co	Control	0.77	0.21	0.02																										
Bylot	ROC7	NL	Control	0.56	0.12	0.26	0.04			0.01												0.01										
Bylot	ROC8	NL	Exclosure	0.81		0.19																										
Bylot	ROC8	NL	Control	0.78	0.09	0.07				0.02											0.02						0.01					
Bylot	ROC3	NH	Exclosure	0.6	0.08	0.2	0.11			0.02																						
Bylot	ROC3	NH	Control	0.61	0.02	0.04			0.1	0.07				0.15	0.01																	
Bylot	ROC6	NH	Exclosure	0.78		0.04				0.1		0.08			0																	
Bylot	ROC6	NH	Control	0.27	0.01	0.08	0.62						0.01																			
Bylot	ROC7	NH	Control	0.18	0.04	0.14			0.57			0.07																				
Bylot	ROC8	NH	Exclosure	0.81		0.19																										
Bylot	ROC8	NH	Control	0.31	0.05		0.63			0.01																						
Bylot	ROC3	P	Exclosure	0.34	0.05		0.6			0.01																						
Bylot	ROC3	P	Control	0.11		0.01	0.2			0.01	0.66	0																				
Bylot	ROC6	P	Exclosure	0.74		0.03	0.08	0.08		0.07		0.01																				
Bylot	ROC6	P	Control	0.35	0.05	0.08	0.21	0.18	0.13																							
Bylot	ROC7	P	Exclosure	0.28	0.01	0.1	0.33	0.23	0.02						0.03																	
Bylot	ROC7	P	Control	0.58	0.36	0.06																										
Bylot	ROC8	P	Exclosure	0.71	0.22	0.01						0.06																				
Bylot	ROC8	P	Control	0.14	0.01		0.85																		0.01							
Bylot	ROC3	NH+P	Exclosure	0.22	0		0.66		0.1			0.01	0																			0.01
Bylot	ROC3	NH+P	Control				0.01	0.73	0.26																							
Bylot	ROC6	NH+P	Exclosure	0.63		0.02	0.03		0.11	0.01		0.12					0.07												0.01			
Bylot	ROC6	NH+P	Control	0.07	0	0.07	0.12	0.71	0.02						0																	
Bylot	ROC7	NH+P	Exclosure	0.08		0	0.89	0.02					0																			
Bylot	ROC7	NH+P	Control	0.37	0.01			0.13	0.49																							
Bylot	ROC8	NH+P	Exclosure	0.73	0.05			0.09	0.03			0.1																				
Bylot	ROC8	NH+P	Control	0.02	0.2	0.71							0.03						0.01				0.02							0.01	0.01	

Table A3

Factor loadings of each species onto the PC1, PC2, PC3, PC4 in PCA analysis. The values of most important component per axis are written in bold.

	Principal component loadings			
	PC1	PC2	PC3	PC4
Arctagrostis latifolia	0.00	0.00	0.00	0.00
Bistorta vivipara	0.00	0.00	0.00	0.00
Cardamine pratensis	−0.01	0.00	0.00	0.00
Carex aquatilis	0.16	0.11	**−0.09**	−0.06
Dupontia fisheri	**−0.27**	0.09	−0.03	0.01
Equisetum arvense	0.00	0.00	0.00	0.00
Eriophorum angustifolium	0.00	0.00	0.00	0.01
Eriophorum scheuchzeri	0.12	0.07	0.04	**0.11**
Festuca brachyphylla	0.00	−0.01	0.00	0.00
Hierochloe pauciflora	0.00	**−0.20**	−0.07	0.03
Luzula confusa	0.00	0.00	0.00	0.00
Lycopodium annotium	0.00	0.00	0.00	0.00
Pedicularis albolabiata	0.00	0.00	0.00	0.00
Pleuropogon sabinei	0.00	0.00	0.00	0.00
Poa arctica	0.01	−0.04	0.09	−0.07
Poaceae_sp1	0.00	0.00	0.00	0.00
Poaceae_sp2	0.00	0.00	0.00	0.00
Poaceae_sp3	0.00	0.00	0.00	0.00
Ranunculus hyperboreus	0.00	0.00	0.00	0.00
Salix arctica	0.00	0.00	0.00	0.00
Salix herbacea	0.00	0.00	0.00	0.00
Salix reticulata	0.00	0.00	0.00	0.00
Salix richardsonii	0.00	0.00	0.00	0.00
Saxifraga foliolosa	0.00	0.00	0.00	0.00
Saxigraga hirculus	0.00	0.00	0.00	0.00
Stellaria longipes	0.00	−0.02	0.05	−0.04
Vaccinium uliginosum	0.00	0.00	0.00	0.00
Unknown_1	0.00	0.00	0.00	0.00
Unknown_2	0.00	0.00	0.00	0.00
% of variance	0.45	0.27	0.11	0.09
Cumulative %	0.45	0.72	0.82	0.91

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