

Fading indirect effects in a warming arctic tundra

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Abstract Indirect interactions in food webs can strongly influence the net effect of global change on ecological communities yet they are rarely quantified and hence remain poorly understood. Using a 22-year time series, we investigated climate-induced and predator-mediated indirect effects on grazing intensity in the tundra food web of Bylot Island, which experienced a warming trend over the last two decades. We evaluated the relative effects of environmental parameters on the proportion of plant biomass grazed by geese in wetlands and examined the temporal changes in the strength of these cascading effects. Migrating geese are the dominant herbivores on Bylot Island and can consume up to 60% of the annual production of wetland graminoids. Spring North Atlantic Oscillation, mid-summer temperatures and summer abundance of lemmings (prey sharing predators with geese) best-explained annual variation in grazing intensity. Goose grazing impact increased in years with high temperatures and high lemming abundance. However, the strength of these indirect effects on plants changed over time. Grazing intensity was weakly explained by environmental factors in recent years, which were marked by a sharp increase in plant primary production and steady decrease in grazing pressure. Indirect effects do not seem to be reversing the direct positive effect of warming on wetland plants. We suggest that cascading effects on plants may lag considerably behind direct effects in vertebrate dominated arctic communities, especially where key herbivore populations are strongly affected by factors outside of the Arctic [*Current Zoology* 60 (2): 189–202, 2014].

Keywords Climate change, Herbivore-mediated effects, Tundra food web, Trophic cascade, Grazing, Goose

Climate-induced and predator-mediated cascading effects can strongly influence ecosystem structure and functioning (Masters et al., 1998; Klanderud, 2005; Lensing and Wise, 2006). However, they are rarely quantified simultaneously in the field and hence remain poorly understood in most ecosystems (Meserve et al., 2003; Post 2013). In addition, controlled experiments of environmental conditions on a large scale are virtually impossible when studying vertebrate dominated terrestrial ecosystems. Hence, most progress in this field is achieved by observational science, and the use of mechanistic-based approaches to analyse time series is essential to understand cascading climate-induced effects or bottom-up vs. top-down biological processes in ecological systems (Krebs and Berteaux, 2006; Legagneux et al., 2012).

Climate change is expected to alter indirect effects within food webs. The sensitivity and response of higher and lower trophic levels to climate change can vary, thus cascading effects can either strengthen or weaken (Barton et al., 2009). In terrestrial ecosystems,

the effects of climate change on plants may be mediated by herbivory. Yet much research has been conducted to predict how plants will directly respond to warming (Hudson and Henry, 2009; Elmendorf et al., 2012) and few studies have investigated how indirect effects (e.g., climate-induced changes in herbivore abundance) could influence the net effect of climate change on ecological communities (Barton et al., 2009; Post, 2013).

Based on our current understanding of the mechanisms linking climate, plants, herbivores and predators (Gauthier et al., 2004, 2011), we examined how climatic factors and predator-mediated indirect effects can drive grazing intensity in the arctic tundra. Indirect effects can be pronounced in tundra ecosystems since they are characterized by relatively short food chains in which some key species can strongly and dynamically interact with several components of the food web (Ims and Fuglei, 2005). Moreover, polar regions are highly affected by climate change (ACIA, 2004) and identifying the key direct and indirect environmental effects is fundamental to predicting the response of the arctic eco-

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system (Le Roux et al., 2005; Post, 2013).

Since 1990, we studied primary production, herbivores and predator abundance on Bylot Island (Nunavut) in the Canadian High Arctic. This terrestrial ecosystem has experienced a rapid warming, with primary production of wetland vascular plants more than doubling over the past two decades (Gauthier et al., 2013). Similar to many sites in the arctic tundra (Ims and Fuglei, 2005), Bylot Island is characterized by high-amplitude lemming fluctuations (Gruyer et al., 2008) with peaks occurring every 3 to 4 years. Migrating greater snow geese *Anser caerulescens atlanticus* are the dominant herbivores on Bylot Island and can consume up to 60% of the annual production of graminoids (Gauthier et al., 1995; Massé et al., 2001; Valéry et al., 2010). Goose grazing can affect the production and composition of arctic plant communities, especially in wetlands (Gauthier et al., 2004; Van der Wal, 2006; Hillebrand et al., 2007), and can drive net ecosystem exchange of CO₂ (Sjogersten et al., 2008).

In this paper, we investigate climate-induced and predator-mediated indirect effects on grazing intensity in the tundra food web of Bylot Island by determining, for the first time, the relative effects of various environmental parameters on the amount of plant biomass removed by geese annually. We also examine the temporal changes in the strength of these indirect interactions in order to test the hypothesis that cascading effects are affected by the recent warming. Climatic conditions are known to strongly affect reproduction of arctic-nesting snow geese (Dickey et al., 2008; Morrissette et al., 2010), which should then generate cascading effects on plants. Moreover, fluctuations in small mammal populations indirectly affect breeding success of geese through shared predators (Bety et al., 2001; Bety et al., 2002). Based on such known mechanisms, we anticipated that climatic conditions (especially in spring) and lemming cycles would be the main drivers of the summer goose population size on Bylot Island (Bety et al., 2003; Reed et al., 2004; Dickey et al., 2008; Morrissette et al., 2010), and hence of the grazing intensity on wetland plants (Fig. 1). Finally, recent climate warming is expected to weaken herbivore-mediated effects in our study system because only primary production (not higher trophic levels) has strongly responded to rising temperatures (Gauthier et al., 2013).

1 Material and Methods

1.1 Study system

This long-term study was conducted on the south-

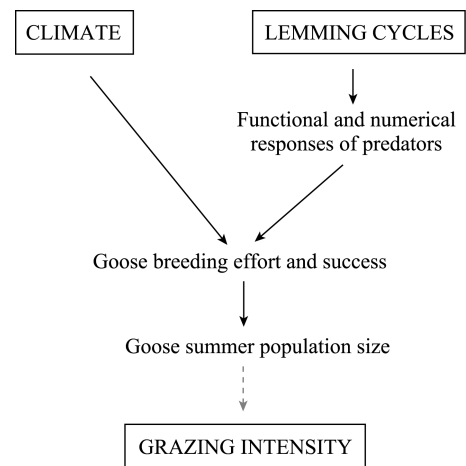


Fig.1 Potential cascading effects of climate and lemming cycles on goose grazing intensity

Upper case words indicate metrics used in this study and black arrows indicate mechanisms documented in previous studies (see Study System in Methods for details).

west plain of Bylot Island, Nunavut, Canada (73°N, 80°W) from 1990 to 2012. This area experienced a warming trend over the study period in both spring and summer (from 0.3°C per decade in June to 1.1°C per decade in May and August) and the average annual cumulative thawing degree-days (sum of the daily mean temperature above 0°C) increased by almost 40% (Gauthier et al., 2011; Gauthier et al., 2013).

The study area is dominated by mesic tundra in the upland and a mixture of mesic tundra and wetlands (primarily polygonal tundra) in the lowlands (Gauthier et al., 2013). Wetlands account for ca. 15% of the study area (Massé et al., 2001; Legagneux et al., 2012). The main features of Bylot Island are the absence of large mammalian herbivores (caribou *Rangifer tarandus* or muskoxen *Ovibos moschatus*) and the presence of a relatively large snow goose colony (> 15,000 breeding pairs each year), which showed no temporal change in nesting density during the study period (Gauthier et al., 2013). Wetlands, mostly polygon-patterned fens, are the preferred feeding habitat of geese and are dominated by sedges such as *Carex aquatilis* var. *stans*, *Eriophorum scheuchzeri* and *E. angustifolium*, and grasses such as *Dupontia fisheri*, *Pleuropogon sabinei* and *Arctagrostis latifolia* (Gauthier et al., 1995; Gauthier et al., 1996). Lemmings (brown and collared lemming *Lemmus sibiricus* and *Discrotonyx groenlandicus* respectively) also inhabit the study area but have little direct impact on the vegetation during the summer (Gauthier et al., 2004; Bilodeau, 2013), likely due to strong predation pressure (Legagneux et al., 2012; Therrien et al., 2014).

Predation is the main cause of nesting failure in geese at our study site (Bety et al., 2001; Lecomte et al., 2009). Goose predators (mostly on eggs and young) are, in decreasing order of importance, arctic foxes *Vulpes lagopus*, parasitic jaegers *Stercorarius parasiticus*, glaucous gulls *Larus hyperboreus* and common ravens (*Corvus corax*; see Bêty et al., 2001). The impact of predation on goose productivity is variable, but it can occasionally lead to almost complete nesting failure (Bety et al., 2001). Lemming cycles generate marked variations in predation pressure on goose eggs and goslings via shared predators (Bety et al., 2002; Lecomte et al., 2008).

Pre-nesting body condition and food availability upon arrival (late May/early June) are key proximate factors influencing females breeding propensity (the probability that a sexually mature female breeds in a given year) as well as laying date and clutch size (Bety et al., 2003; Reed et al., 2004). By affecting food and nest site availability during the critical pre-laying and laying periods, spring temperature and snow cover thus affect adult reproductive effort (Reed et al., 2004; Dickey et al., 2008; Morrissette et al., 2010).

Geese typically breed in colonies and use both wetland and mesic tundra to nest (Lecomte et al., 2008). In June, when geese are on the nest, grazing pressure is relatively light and feeding is dispersed (Reed et al., 1995). After hatching in early July, the goose population more than doubles with the addition of goslings, and families move to areas with high concentrations of wetlands (Mainguy et al., 2006). The grazing pressure is thus highest during the brood-rearing period (Gauthier et al., 1995).

The vast majority of non-breeders and failed nesting geese leave Bylot Island for molting (Reed et al., 2003). Therefore, annual variations in the size of the local summer goose population (i.e., number of birds grazing during the brood-rearing period) should depend mainly on variation in reproductive effort and success driven by fluctuations in climatic conditions and predation pressure (Fig. 1).

1.2 Plant production and biomass grazed

We estimated the grazing pressure exerted by geese in wetlands in all years but 1992. Methods are described in Valéry et al. (2010) and in Gauthier et al. (2011). Briefly, every year in late June, twelve 1-m² exclosures made of chicken wire (2.5-cm mesh, 50-cm high, with an open top) excluding geese only (and not lemmings) were spread over a ~1 km² area and set just after snow-melt (see Gauthier et al., 1995). The difference

between inside/outside exclosures is an accurate measure of the amount of plants consumed by geese (Gauthier et al., 1995; Beaulieu et al., 1996). Plant biomass was sampled at the end of the growing season (mid-August) by removing a 20 × 20 cm piece of turf. All live graminoids were removed, cut to the lowest leafing node, dried and weighed. The graminoid plant biomass grazed by geese (g/m²) was obtained by subtracting the biomass measured outside the exclosures (which corresponded to standing crop after goose grazing) from the biomass obtained inside (which provided an estimate of annual above-ground plant production; Gauthier et al., 1995). We then calculated the proportion of aboveground biomass of wetland graminoid plants removed by geese (plant biomass grazed/annual plant production).

Plant production in polygon fens varied considerably from 1990 to 2012 (3-fold fluctuation, from 21.8 to 78.4 g/m²) and was positively related to cumulative thawing degree-days and negatively to July-August NAO index (Gauthier et al., 2013).

1.3 Climatic Data

Dickey et al. (2008) showed that climate affects greater snow geese reproductive components during different periods of their breeding cycle; the pre-breeding (from 20 May to 20 June), the incubation (from 21 June to 15 July) and the rearing (from 16 July to 15 August) periods. The ending date corresponds to the date of plant sampling (see above). We retained the same periods and tested the importance of relevant climatic variables on the annual proportion of wetland plant biomass grazed by geese (Table 1).

For each period, two spatial scales (local and regional) were considered when examining the potential effects of climatic factors. At the local scale, air temperature and snow cover during snow-melt were recorded on the study area from 1994 to 2012 (see CEN 2013, Gauthier et al. 2013). Data recorded by Environment Canada in Pond Inlet, 60-km from the study area, were highly correlated and were used to extend the time series to 1990 (once properly adjusted and following the approach of Dickey et al. 2008). All covariates are presented in Table 1.

The North Atlantic Oscillation (NAO) influences weather conditions over eastern Canada and USA (Hurrell, 1995; Stenseth et al., 2002). Positive NAO values are associated with cold temperatures on Bylot Island and the northern part of the goose migration route (Morrissette et al. 2010). We obtained daily values of the NAO indices from the Climate Prediction Center of

the National Weather Service (<http://www.cpc.ncep.noaa.gov>).

1.4 Lemming abundance

Lemming abundance was estimated in mid-July (beginning of the goose brood-rearing period) using Museum special mammal traps ($\geq 1,000$ trap-nights each year). Traps were spaced every 15-m along 4 transects in wet polygon fens (17 stations per transect) and 2 transects in mesic upland habitat (34 stations per transect). Until 2006, each station had one trap set near burrows or runways (when possible) within a 2-m radius and trapping lasted 10 days (for more details see Gruyer et al. 2008). From 2007 onward, we set three traps per station and trapping lasted 3 or 4 days (Bilodeau et al., 2013). Both methods yielded similar results (G. Gauthier, unpublished data). No lemming estimates were recorded in 1990–1991. We extended the data back using two criteria. First, because snowy owls nest only in high lemming years at our study site (Therrien et al., 2014) and as no owls were found nesting in 1990–1991 (owls were found nesting in 1989, presumably a year of high lemming abundance, G. Gauthier, unpublished data), we assumed that neither of these two years were lemming peaks. To estimate lemming abundance in 1990 and 1991, we thus used the average abundance values observed from 1993 to 2012, excluding high lemming years that were confirmed by the high abundance of breeding predators (i.e., 1993, 1996, 2000, 2004, 2008, 2010, 2011; Legagneux et al., 2012; Therrien et al., 2014).

From 2004 to 2012, live trapping was also conducted in the same area in two 11-ha grids to obtain more accurate estimates of lemming density with capture-mark-recapture methods. Each grid had 144 traps laid out every 30 m in a 12×12 Cartesian plan (Gruyer et al., 2008, 2010). To extend the time series of annual lemming density, we used the relationship between annual

lemming density estimated from live recapture in July and the abundance index derived from snap-trapping (Legagneux et al., 2012; Gauthier et al., 2013).

Snap-trapping data were used to examine the effect of lemming cycles on plant biomass grazed by geese as these data were collected more consistently throughout the entire study period, and hence were better to investigate temporal changes in the strength of the relationship. Lemming density estimates obtained from capture-recapture are likely more accurate but live-trapping was conducted only during the second half of the study period. We nonetheless ran the analyses with lemming densities using live-trapping data (2004–2012) and derived densities from snap trapping data (1993–2003) to make comparison with results obtained with snap-trapping data only.

1.5 Statistical analyses

Statistical models linking environmental parameters to the proportion of wetland plant biomass grazed by geese were based on mechanisms previously proposed or documented in earlier studies (see references above; Table 1 and Fig. 1). We first examined the relative effects of these parameters to test the hypothesis that spring climatic conditions and lemming cycles are the main drivers of grazing intensity. Then, we used sliding windows analyses (see below) to test the hypothesis that cascading effects of environmental factors on grazing should weaken over time due to the quick response of plant production to recent warming (Gauthier et al., 2013). The proportion of biomass removed by geese tended to be lower in years of high plant production (Pearson = -0.34 , $n = 22$, $P = 0.12$) and, as primary production more than doubled over the past two decades (Gauthier et al., 2013), grazing intensity decreased over time (Fig. 2; see also Gauthier et al., 2013). We thus used residuals from a regression between the proportion of plant biomass grazed and time as dependent variable

Table 1 Periods of the greater snow goose breeding cycle and covariates included in statistical models used to investigate annual variation in grazing intensity on wetland plants

Periods (dates) and breeding stages	Covariates (label)	Description
<i>Spring (period 1)</i> (20 May to 20 June) Arrival and egg-laying	NAO index (NAO1) Mean temperatures (T1) Snow cover (Snow)	Mean of daily values Mean of daily values Date of 50% snow cover
<i>Early summer (period 2)</i> (21 June to 15 July) Incubation and hatching	NAO index (NAO2) Mean temperatures (T2)	Mean of daily values Mean of daily values
<i>Mid-summer (period 3)</i> (16 July to 15 August) Brood-rearing	NAO index (NAO3) Mean temperatures (T3)	Mean of daily values Mean of daily values
<i>Entire summer</i>	Lemming abundance index (Lemming) Lemming density ^a	Number caught per 100 trap-nights Number per ha (live-trapping)

^aAnalyses shown in the appendix only. See methods.

(i.e., de-trended data) to focus on the effects of environmental factors on inter-annual variation in goose grazing pressure. The de-trended proportion of biomass grazed was not correlated with annual plant production (Pearson $r = 0.16$, $n=22$, $P=0.47$). Some factors used in the models also showed temporal trends (especially mid-summer temperature; Fig. 2) but the use of de-trended covariates did not affect our main conclusions (analyses not shown). The proportion of biomass grazed by geese was arc-sin transformed and all covariates were standardized prior to analysis.

We ran multiple regressions and selected the most parsimonious model among the set of candidate models based on the Akaike Information Criterion corrected for small sample size (AICc). Models within 2 AICc values were considered as equivalent (Burnham and Anderson, 2002). We used parameter estimates averaged across these models using the AICcmodavg package in R to

account for uncertainty in model selection (Burnham and Anderson, 2002). The partial R^2 of a variable entered in the model was used to show its contribution and the R^2 was used to evaluate the global fit of the model. Local and regional predictors from all three time periods (goose pre-breeding, incubation and rearing periods) were included in the set of candidate models (Table 1). In order to avoid multicollinearity, we examined correlation matrices among variables and did not incorporate two variables with correlation coefficient >0.5 in the same model, which was the case for spring temperature and spring snow cover only. Moreover, no more than four co-variables were included in a model due to limited sample size (i.e., 22 years). All statistical analyses were performed in R 3.0.

To investigate temporal changes in the strength of the effects of environmental factors on plant biomass grazed by geese, we conducted analyses over 11 suc-

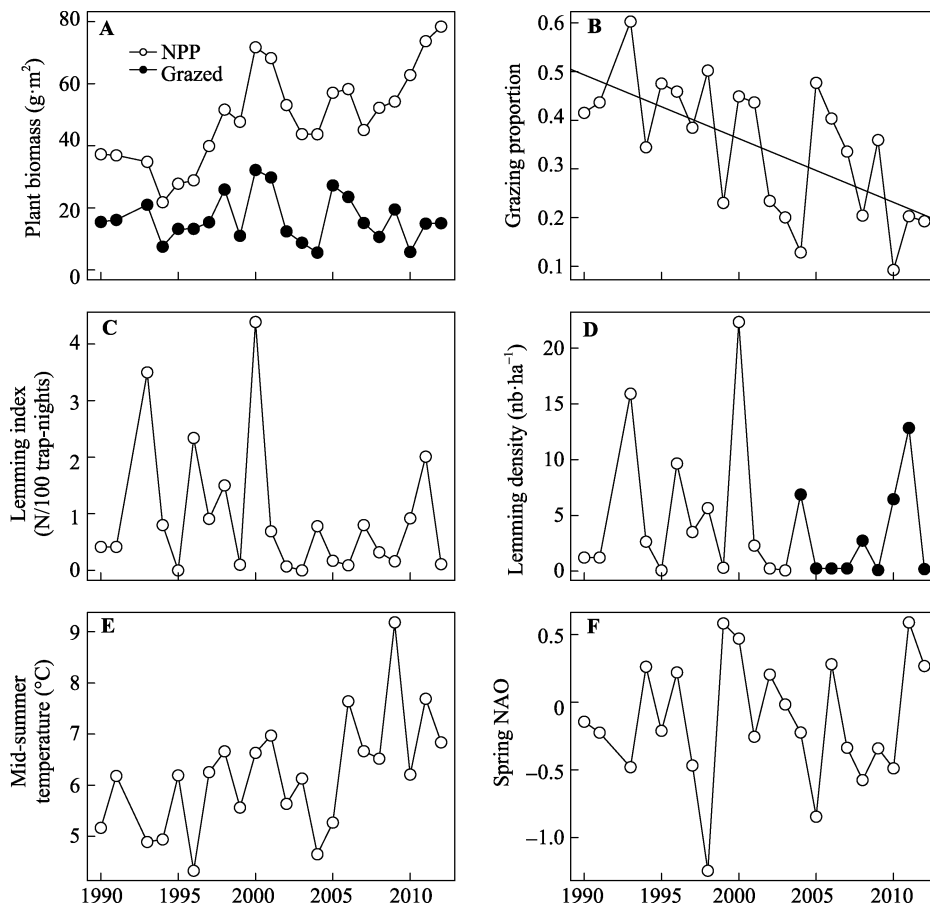


Fig. 2 A. Annual plant biomass produced (net primary production NPP) and biomass grazed by geese. B. Proportion of wetland plant biomass grazed by geese (grazed biomass/NPP). C. summer lemming abundance index obtained with snap-trapping, D. Summer lemming density from live-trapping, E. Air temperature in mid-summer in the Qarlikturvik Valley of Bylot Island, and F. Spring NAO index from 1990 to 2012

Lemming live-trapping was conducted from 2004 to 2012 (black circles, panel D) and the relationship between lemming density and lemming abundance index was used to extend the time series (see methods). The regression line in B) shows the temporal trend (1990 = year 1) in the proportion of wetland plant biomass grazed ($y = -1.31x + 50.2$, $R^2 = 0.39$). The year 1992 was excluded because grazing was not recorded in that year.

cessive 12-year windows moving along the time series by a 1-year step (t_1 to t_{12} , t_2 to t_{13} , ... t_{11} to t_{22} ; (Durant et al., 2004). A 12-year sliding window was a good trade-off between the number of successive windows available and the number of points in each window. Preliminary analyses indicated the persistence of the signal using smaller or larger windows. Obtaining a similar relationship between grazing intensity and a covariate for all windows would describe a single linear relationship over the entire study period. Otherwise, non-linear processes (i.e., change in the strength of the relationships over time) may be supported (Nevoux et al., 2008). We used hat-value to evaluate the leverage effect of specific data points in regression models (Belsley et al., 1980).

2 Results

We modelled the annual variation in the proportion of plant biomass grazed by geese (corrected for temporal decrease) to investigate the cascading effects of environmental factors on wetland plants. Spring NAO index (NAO1), summer lemming abundance and temperature in mid-summer (T3) best-explained variation in goose grazing pressure from 1990 to 2012 (Table 2). Each covariate explained between 14% and 18% of the variability in grazing intensity over the study period (Fig. 3). Negative values of spring NAO index (i.e., high spring temperature), high lemming abundance and high mid-summer temperatures were associated with high goose grazing intensity on plants (Table 2, Fig. 3).

Analyses performed over successive 12-year sliding

windows revealed important changes in the relative contribution of various covariates to annual variation in goose grazing intensity between successive time periods. A strong effect of spring NAO index and summer lemming abundance was detected during the early periods, each covariate explaining up to 23% and 47% of the variability in grazing intensity, respectively (Table 3, Fig. 3). However, these two covariates did not explain a significant part of the variation in grazing intensity in recent years (Table 3, Table 4 and Fig. 3). The effect of lemming abundance, which was strong initially, faded over time (decreasing slopes between successive windows; Fig. 3). On the other hand, mid-summer temperature had a significant effect on grazing only in the second half of the study period (i.e., increasing slope and partial R^2 ; Fig. 3, Table 3). Overall, the proportion of plant biomass grazed by geese was weakly explained by environmental factors in recent years (the null model was the most parsimonious among the top-3 models; Table 4). Similar patterns were obtained when using different lengths of sliding windows (from 10 to 14 years), or uncorrected (vs. de-trended data) proportion of plant biomass grazed, as well as lemming density estimates derived from live trapping data (vs. snap-trapping data; see Appendix). Some years had relatively high leverage effect in the regression models (i.e., hat value 3 to 5 times higher than the average hat value; 1998 for spring NAO, 2009 for mid-summer-temperature, and 1993 and 2000 for lemming; Fig. 2). However, for the two climatic parameters, the slope of the relationship remained similar after excluding these specific

Table 2 a) Variables, sign of the effect, number of estimated parameters (k), AICc score, Δ AICc, AICc weights and proportion of variation explained (R^2) by the most parsimonious candidate models relating environmental factors to the proportion of wetland plant biomass grazed by geese (using de-trended data) measured on Bylot Island (Nunavut) from 1990 to 2012. b) Model-averaged parameter estimate (β) and unconditional standard error (SE). All covariates are standardized.

a) Selected models					
Variables	k	AICc	Δ AICc	AICcWt	R^2
T3 + Lemming - NAO1	5	-32.42	0	0.24	0.42
Lemming - NAO1	4	-30.56	1.86	0.09	0.27
T3 + Lemming	4	-30.49	1.93	0.09	0.26
Lemming	3	-29.53	2.89	0.06	0.12
-NAO1	3	-29.52	2.9	0.06	0.12
Null	2	-29.46	2.96	0.05	
b) Parameter values					
	T3	NAO1	Lemming	Intercept	
β	0.04	-0.09	0.05	-0.01	
SE	0.02	0.05	0.02	0.02	

NAO1 = spring NAO index, T3 = mid-summer temperature, Lemming = summer lemming abundance index

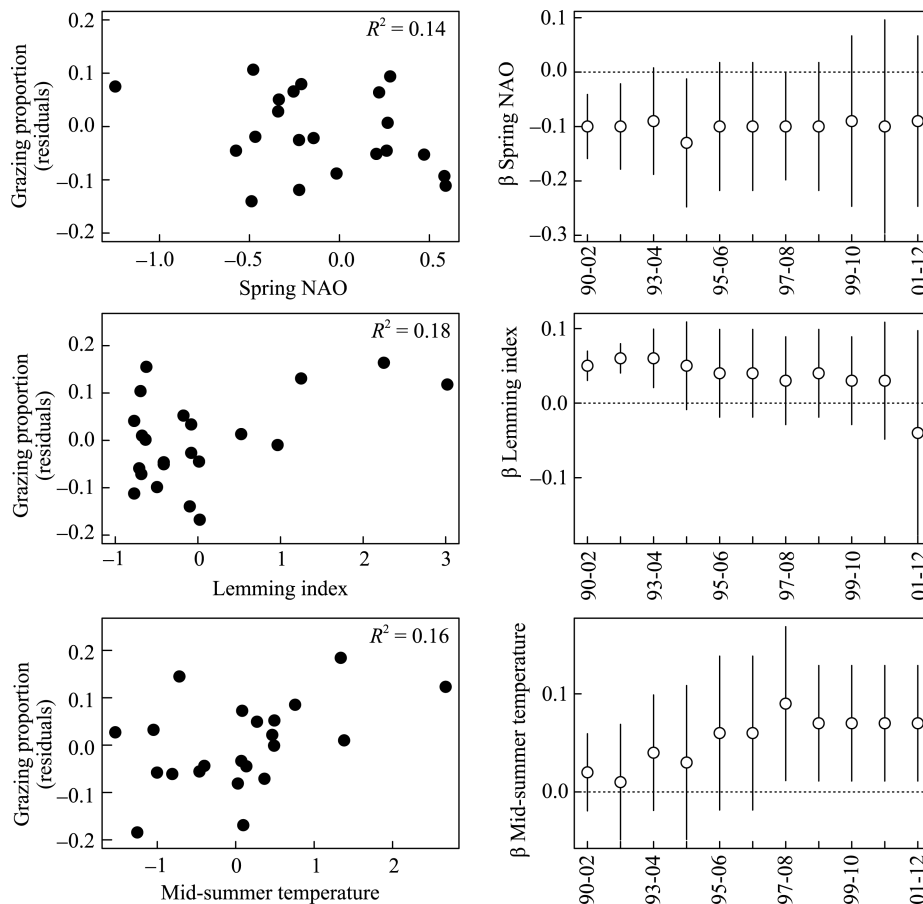


Fig. 3 Left panels: relationships between the three covariates (spring NAO index, summer lemming abundance and mid-summer temperature) and the proportion of plant biomass grazed by geese (residuals of a relationship between proportion of biomass grazed and time). Right panels: change in the relationship between grazing proportion and the covariates over the eleven successive 12-year sliding windows

Values of the slopes (β) of the relationships for each sliding window defined on the X-axis are shown (bars indicate ± 0.95 CI) and the horizontal dotted line indicates 0. All covariates are standardized.

Table 3 Partial R^2 of each covariate for different time periods (eleven successive 12-year windows and the entire study period)

Time period	NAO1	Lemming	T3	Global
1990-2002	0.23	0.47	0.02	0.78
1991-2003	0.23	0.47	0.01	0.78
1993-2004	0.13	0.44	0.08	0.70
1994-2005	0.29	0.19	0.03	0.54
1995-2006	0.19	0.12	0.17	0.45
1996-2007	0.19	0.14	0.17	0.47
1997-2008	0.19	0.06	0.27	0.54
1998-2009	0.18	0.09	0.29	0.55
1999-2010	0.09	0.07	0.31	0.42
2000-2011	0.10	0.06	0.30	0.34
2001-2012	0.07	0.03	0.32	0.37
1990-2012	0.15	0.18	0.16	0.42

Spring NAO index (NAO1), summer lemming abundance and mid-summer temperature (T3) best explained the annual proportion of plant biomass grazed by geese (see Table 2). The R^2 of the model including the three covariates (Global) is also presented. All covariates are standardized.

years (see sliding windows with or without those years in Fig. 3), indicating a limited effect on the whole regression. For lemming, the two years with high leverage corresponded to the highest abundance observed during our study and the removal of these biologically relevant data points had a clear effect on the regression (see period 2001–2012 in Fig. 3).

3 Discussion

As predicted, we found that climatic factors and predator-mediated interactions between herbivores can have significant cascading effects on wetland plants in the Bylot Island terrestrial ecosystem. Our approach, which relied on previously identified mechanisms, provides evidence that spring and mid-summer climatic conditions, as well as lemming cycles, indirectly affected grazing intensity by determining the breeding success of the geese and thus the size of the summer population on the island. However, the strength of these

indirect effects changed over the last two decades. Cascading effects weakly explained grazing intensity in recent years, which are marked by a sharp increase in plant primary production and steady decrease in grazing intensity.

The main environmental drivers of grazing pressure exerted on wetland plants (i.e., spring NAO, mid-summer temperature and summer lemming abundance) have also been identified as key factors determining annual breeding productivity of the greater snow goose population (Morrissette et al., 2010). The indirect effects of climate on grazing most likely reflect bottom-up processes (i.e., food availability in spring) affecting goose pre-breeding body condition and hence breeding effort (Bety et al., 2003; Reed et al., 2004; Dickey et al., 2008). In addition, higher temperatures in mid-summer decrease the costs of thermoregulation and exposure to cold, and consequently can have a direct positive effect on gosling growth and survival rates (Dickey et al., 2008). Finally, the cascading effects of lemmings on grazing intensity reflect processes occurring via shared predators (Bêty et al., 2001, 2002).

The lack of cascading effects of predators on plants is expected when predators have little influence on consumers that substantially impact vegetation (Maron and Pearson, 2011). However, when predators strongly affect the abundance of the main consumers, like snow geese on Bylot Island, factors generating marked numerical and functional responses of predators, such as lemming cycles, are strongly expected to cascade down on plants. Using a trophic mass balance model, Legagneux et al. (2012) also reported a positive indirect effect of lemming abundance on the proportion of vascular

plants consumed annually by geese on Bylot Island. However, their results were based on theoretical consumption rates and direct observation of grazing was not taken into consideration. Although the direct impact of lemmings grazing on plants can be important at some arctic and sub-arctic sites (Olofsson et al., 2012), this is not the case on Bylot Island (Gauthier et al., 2004; Bilodeau, 2013) and indirect effects of lemming abundance on wetland plants outweigh their direct effects. Indeed, predators can limit lemming populations during the summer (Therrien et al., 2014) and strong predator-mediated interactions are not surprising considering the dominant role of predation in this tundra food web (Legagneux et al., 2012), a situation also reported in a large portion of the arctic tundra (Reid et al., 1997; Krebs et al., 2003; Gilg et al., 2006).

The weak cascading impacts of lemming cycles and climatic conditions on plants in recent years coincide with a sharp increase in plant production due to warming and a declining grazing intensity (Gauthier et al., 2013). During the last decade, six years had the lowest grazing intensity recorded on Bylot Island since 1990 (Fig. 2). Such a low grazing regime may partly explain the temporal changes in the strength of indirect effects in the food web. Climate-induced and predator-mediated effects on plants, if present, are likely much harder to detect under such conditions. However, the sliding window analyses also revealed that the temporal changes in the strength of the relationships were not uniform for the three main environmental drivers of grazing intensity, suggesting that other mechanisms may be involved.

Lemming abundance indirectly affected grazing intensity but the relationship appeared non-linear over the

Table 4 Most parsimonious candidate models relating environmental factors to the proportion of wetland plant biomass grazed by geese for different time periods (eleven successive 12-year windows)

Period	Model 1	R ²	Model 2	ΔAICc	R ²	Model 3	ΔAICc	R ²
1990-2002	NAO1+Lemming	0.77	NAO1+Lemming+T3	5.33	0.78	Lemming	5.54	0.45
1991-2003	NAO1+Lemming	0.78	Lemming	5.67	0.47	NAO1+Lemming+T3	5.98	0.78
1993-2004	NAO1+Lemming	0.64	Lemming	0.97	0.42	Lemming+T3	2.25	0.56
1994-2005	NAO1	0.29	NAO1+Lemming	0.09	0.52	Null	0.44	0.00
1995-2006	Null	0.00	T3	1.29	0.18	NAO1	1.48	0.17
1996-2007	Null	0.00	T3	1.15	0.19	NAO1	1.40	0.17
1997-2008	T3	0.31	Null	0.74	0.00	NAO1+T3	1.26	0.48
1998-2009	T3	0.31	Null	0.70	0.00	NAO1+T3	1.61	0.46
1999-2010	T3	0.30	Null	0.61	0.00	NAO1	3.61	0.05
2000-2011	Null	0.00	T3	0.56	0.23	Lemming	3.49	0.01
2001-2012	Null	0.00	T3	0.43	0.24	NAO1	3.19	0.04

Only the top-3 models are shown here. R² are presented to compare models. All covariates are standardized.

study period, as indicated by the decreasing trend in the slope of the relationship (which became insignificant in recent years). Such a pattern may be partly explained by changes in lemming population cycles *per se*. Although we found little evidence of a negative temporal trend in lemming abundance, their abundance was nonetheless particularly low between 2002 and 2009, which corresponds to the second half of the study period (Gauthier et al., 2013). However, strong numerical and functional responses of predators to variations in lemming were still reported for those years (Gauthier et al., 2013; Therrien et al., 2014). Therefore, only a detailed analysis of temporal changes in lemming-geese relationships would allow us to fully explain the observed pattern.

Spring NAO also became a poor predictor of summer grazing intensity in the second half of the study but no evidence of non-linearity was found (i.e., decreasing R^2 but no apparent temporal trend in the slope of the relationship). Therefore, the effect of spring climatic conditions on goose reproduction likely remained similar over the study period but other factors affecting grazing intensity outweighed the cascading effect of NAO on plants in recent years. More favorable climatic conditions in spring and early summer observed during the second half of the study period (i.e., earlier snow melt and higher temperatures; Gauthier et al., 2013) likely generated lower annual variation in goose breeding effort and nesting success (Bety et al., 2003; Reed et al., 2004; Dickey et al., 2008). Hence, the relative effect of post-hatching environmental conditions on goose reproduction may have increased under such circumstances. Mid-summer temperature was indeed a better predictor of grazing intensity in recent years, suggesting that conditions encountered during the goose brood-rearing period more strongly influenced the summer goose population size in a warmer climate. Clearly, further investigations of the temporal changes in the relationships between goose reproduction and environmental factors would be needed to fully understand the observed temporal changes in the strength of herbivore-mediated interactions.

The nature and strength of the emergent effects of global change on ecological food webs remain poorly understood because they are the net result of multiple species responding to various changes in their environment (Suttle et al., 2007; Post 2013). Identifying the key direct and indirect environmental effects is fundamental to begin understanding potential ecological consequences (Le Roux et al., 2005). Very few studies have

investigated how indirect interactions may influence the net effect of climate change on ecological communities. In a system composed of herbaceous plants and invertebrates (grasshopper and spiders), Barton et al. (2009) found that plant production was not directly affected by temperature or precipitation, but the strength of top-down indirect effects on plants increased in warmer conditions. Hence, the net effect of climate change was to strengthen top-down control in this arthropod-dominated community.

On Bylot Island, the direct effect of warming on plants is apparently strong as primary production more than doubled over the past two decades in wetlands while no responses of higher trophic levels were detected (Gauthier et al., 2013). The proportion of above-ground biomass of wetland graminoid plants removed by the main herbivores is gradually decreasing and our results indicate that herbivore-mediated effects of climate on plants are fading over time. In our system, geese are a migratory, hunted species, and thus long-term changes in the size of this population have been mostly driven by events occurring during the non-breeding season (e.g. food subsidy in agricultural land and hunting regulations), when the birds are away from the Arctic (Gauthier et al., 2005). Our observations suggest that direct effects of warming on plants outweigh the indirect effects, and that the net effect of warming is positive for wetland plants at our study site.

Overall, our long-term ecological monitoring of the Bylot Island tundra food web allowed us i) to identify and quantify some key herbivore-mediated indirect effects on plants and ii) to reveal fading climate-induced and predator-mediated cascading effects on grazing intensity in a warming ecosystem. Although a better understanding of the temporal changes in the relationships between goose reproduction and environmental factors would be needed to fully explain the observed patterns, we can nonetheless conclude that indirect effects are not reversing the direct positive response of wetland plants to recent warming (Gauthier et al., 2013). While species interactions can offset short term responses of plants to changes in environmental conditions in invertebrate dominated systems (Suttle et al., 2007; Barton et al., 2009), indirect effects of climate on plants may lag considerably behind the direct effects in vertebrate dominated communities. Such time lags should be especially amplified in arctic ecosystems where key herbivores are long distance migrants strongly affected by environmental factors encountered away

from the Arctic.

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APPENDIX

Lemming live-trapping was conducted only during the second half of the study period. To extend the time series of annual lemming density, we used the relationship between annual lemming density estimated from live recapture and the abundance index derived from snap-trapping (see methods). The results presented below were obtained using the lemming density estimates.

Table S1 a) Variables, sign of the effect, number of estimated parameters (*k*), AICc score, Δ AICc, AICc weights and proportion of variation explained (R^2) by the most parsimonious candidate models relating environmental factors to the proportion of wetland plant biomass grazed by geese (using de-trended data) measured on Bylot Island (Nunavut) from 1990 to 2012. b) Model-averaged parameter estimate (β) and unconditional standard error (SE). All covariates are standardized.

a) Selected models					
Variable	<i>k</i>	AICc	Δ AICc	AICcWt	R2
-NAO1	3	-29.52	0	0.11	0.12
Null	2	-29.46	0.06	0.1	
T3 - NAO1	4	-29.36	0.16	0.1	0.23
T3 + Lemming - NAO1	5	-29.18	0.33	0.09	0.33
T3	3	-29.18	0.34	0.09	0.11
Lemming - NAO1	4	-28.5	1.02	0.06	0.19
-NAO3	3	-28.45	1.06	0.06	0.07
T3 + Lemming	4	-27.86	1.66	0.05	0.17
Lemming	3	-27.78	1.73	0.04	0.05
b) Parameter					
	T3	NAO1	Lemming	Intercept	
β	0.04	-0.09	0.03	-0.01	
SE	0.02	0.05	0.02	0.03	

NAO1 = spring NAO index, NAO3 = mid-summer NAO index, T3 = mid-summer temperature, Lemming = summer lemming density

Table S2 Similar to Table S1 except that the response variable is the uncorrected (i.e., not de-trended) grazing proportion and Lemming represents summer lemming abundance index.

a) Selected models					
Variable	<i>k</i>	AICc	Δ AICc	AICcWt	R2
-NAO1 + Lemming	4	-19.90	0	0.17	0.28
+ Lemming	3	-19.33	0.57	0.30	0.16
Null	2	-18.26	1.64	0.46	
b) Parameter					
	NAO1	Lemming	Intercept		
β	-0.11	0.06	0.35		
SE	0.02	0.03	0.03		

NAO1 = spring NAO index, Lemming = summer lemming abundance index.

Table S3 Partial R^2 of each covariate for different time periods (eleven successive 12-year windows and entire study period). Spring NAO index (NAO1), summer lemming density, and mid-summer temperature (T3) were included in the model to explain the annual proportion of plant biomass grazed by geese. The R^2 of the model including the three covariates (Global) is also presented. All covariates are standardized.

Time period	NAO1	Lemming	T3	Global
1990-2002	0.28	0.47	0.01	0.78
1991-2003	0.29	0.47	0.00	0.77
1993-2004	0.15	0.34	0.08	0.60
1994-2005	0.28	0.13	0.04	0.47
1995-2006	0.15	0.08	0.18	0.41
1996-2007	0.28	0.08	0.19	0.42
1997-2008	0.19	0.04	0.32	0.52
1998-2009	0.19	0.05	0.31	0.51
1999-2010	0.07	0.02	0.32	0.38
2000-2011	0.05	0.01	0.28	0.29
2001-2012	0.04	0.10	0.28	0.44
1990-2012	0.16	0.11	0.14	0.33

Table S4 Similar to Table S3 except that the response variable is the uncorrected (i.e., not de-trended) proportion of plant biomass grazed by geese and Lemming represents the summer lemming abundance index.

Time period	NAO1	Lemming	T3	Global
1990-2002	0.38	0.34	0.02	0.73
1991-2003	0.31	0.36	0.02	0.71
1993-2004	0.13	0.39	0.01	0.56
1994-2005	0.20	0.21	0.02	0.45
1995-2006	0.20	0.19	0.11	0.45
1996-2007	0.20	0.27	0.09	0.51
1997-2008	0.18	0.14	0.19	0.54
1998-2009	0.16	0.20	0.14	0.47
1999-2010	0.01	0.09	0.15	0.24
2000-2011	0.04	0.07	0.10	0.15
2001-2012	0.07	0.06	0.16	0.27
1990-2012	0.13	0.18	0.01	0.28

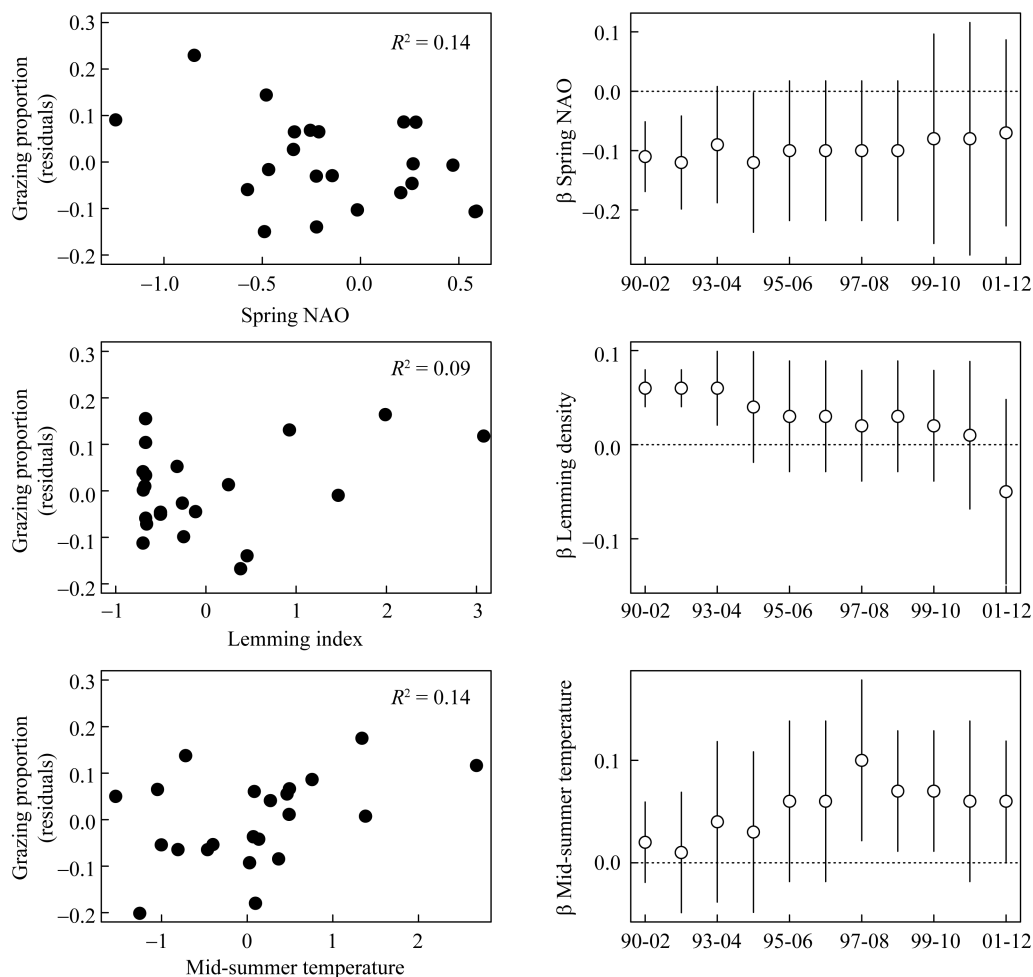


Fig. S1 Left panels: relationships between the three covariates (spring NAO index, summer lemming density based on live-trapping and mid-summer temperature) and the proportion of plant biomass grazed by geese (residuals from a regression between grazing proportion and time). Right panels: change in the relationship between grazing proportion and the different covariates over the eleven successive 12-year sliding windows. Values of the slopes (β) of the relationships for each sliding window defined on the X-axis are shown (bars indicate ± 0.95 CI) and the horizontal dotted line indicate 0. All covariates are standardized.

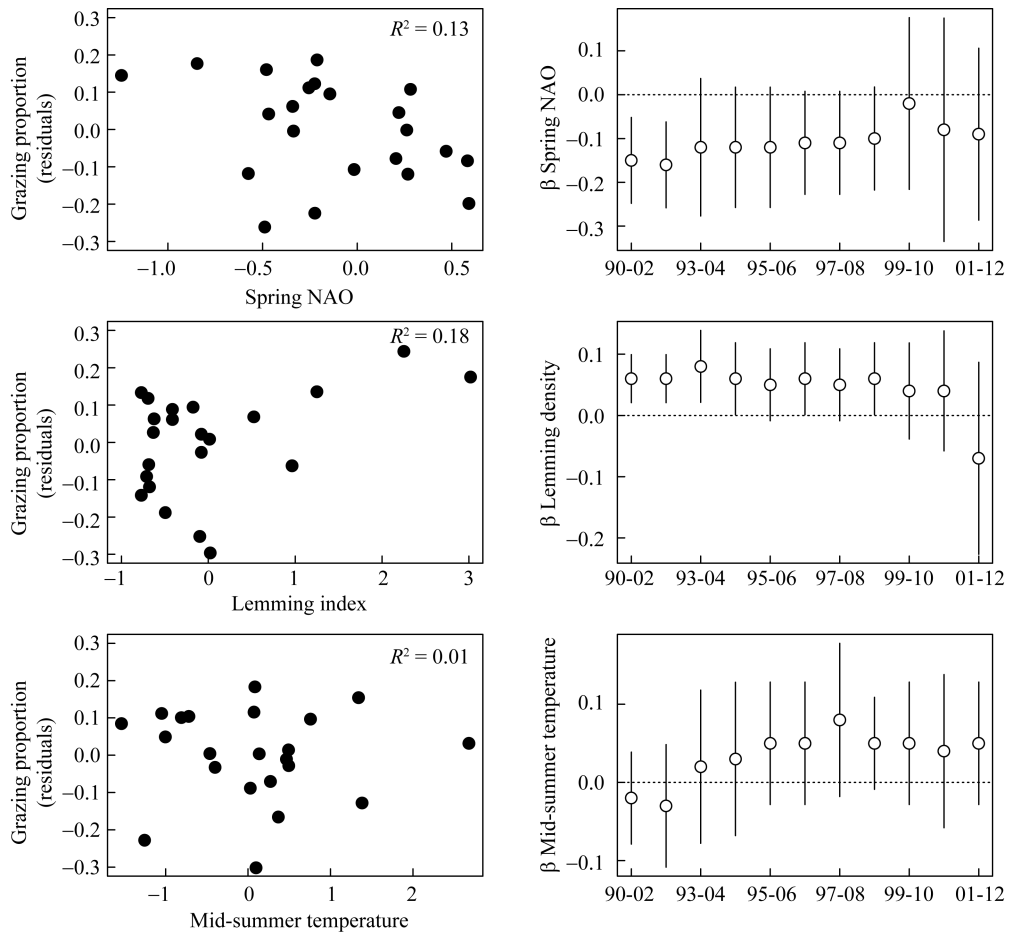


Fig. S2 Similar to Figure S1 except that the response variable is the uncorrected (i.e., not de-trended) proportion of plant biomass grazed by geese and Lemming represents the summer lemming abundance index.\