Chapitre 4

Does lemming winter grazing impact vegetation in the Canadian Arctic?

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Résumé

Dans les environnements comme la toundra, où la productivité est faible, il a été proposé que les cycles de population multi-annuels des lemmings soient causés par l'épuisement des ressources alimentaires pendant l'hiver lors des années de pics d'abondance. Si la dynamique de population de lemming est contrôlée par les ressources alimentaires, nous prédisons (1) que le broutement hivernal devrait avoir un impact négatif sur l'abondance des plantes consommées, (2) que cet impact devrait être proportionnel à la densité de lemming et (3) que la forte pression exercée par un broutement hivernal élevé devrait se traduire dans une réduction de la croissance des plantes lors de l'été subséquent. Nous avons testé ces prédictions à l'île Bylot, Nunavut, Canada, où deux espèces de lemming sont présentes, le lemming brun (*Lemmus trimucronatus*) et le variable (*Dicrostonyx groenlandicus*). Nous avons installé 16 exclos dans leurs habitats hivernaux préférés (combes à neige) et échantillonné annuellement la biomasse des plantes vasculaires et des mousses à l'intérieur et à l'extérieur des exclos directement après la fonte de la neige et à la fin de la saison de croissance durant les étés 2009-2012, couvrant un cycle de population complet. Les plantes ont été exposées aux densités de lemming les plus élevées au cours des hivers 2009-2010 et 2010-2011, d'après l'abondance de nids d'hiver; les populations avaient chuté à l'hiver 2011-2012. Le broutement hivernal n'a eu aucun impact sur la biomasse totale de plantes vasculaires ou de mousses à la fonte de la neige. Seulement deux familles de plantes, les Polygonacées et les Caryophyllacées, deux plantes peu communes, ont montré un déclin. Aucun effet n'a été détecté sur les Salicacées, Poacées et Juncacées. Pour les mousses, un effet négatif a été détecté sur les *Polytrichum* mais seulement une année sur trois. Dans l'ensemble, la croissance des plantes durant l'été a montré peu de variation annuelle et n'a pas été réduite lors des années de fortes abondances de lemmings. Seulement la croissance des Polygonacées et des Caryophyllacées semble avoir été réduite par le broutement des lemmings. Nos résultats suggèrent qu'il est peu probable que l'épuisement de la nourriture durant l'hiver soit la cause du déclin des populations de lemming suite au pic d'abondance. D'autres facteurs limitent probablement les populations de lemmings et les empêchent d'atteindre des densités assez élevées pour épuiser leurs ressources alimentaires.

Abstract

In low productivity environments such as the tundra, it has been proposed that regular multi-annual population cycles of lemmings are driven by winter food depletion in years of peak abundance. If lemming population dynamics is controlled by food resources, we predict that (1) winter grazing should negatively impact the abundance of food plants, (2) this impact should be proportional to lemming density and (3) high lemming winter grazing pressure should result in a reduction of plant growth in the subsequent summer. We tested these predictions on Bylot Island, Nunavut, Canada, where two species of lemmings are present, the brown (*Lemmus trimucronatus*) and collared lemming (*Dicrostonyx groenlandicus*). We installed 16 exclosures in their preferred wintering habitat (snow beds) and sampled annually vascular and moss plant biomass inside and outside exclosures at snow-melt and at peak growth during the summer from 2009-2012, covering a full population cycle. Plants were exposed to the highest lemming densities during winter 2009-10 and 2010-11, as judged by winter nest abundance; populations had crashed by winter 2011-2012. Winter grazing had no impact on total vascular plant or moss biomass at snow-melt. Among plant families, only Caryophyllaceae, an uncommon plant, showed a decline. No effect was found on Salicaceae, Poaceae and Juncaceae. In moss taxa, a negative effect was found on *Polythichum* in only one year out of three. Overall, plant regrowth during the summer showed little annual variation and was not reduced in years of high lemming abundance. Only the summer regrowth of Polygonaceae and Caryophyllaceae appeared to be reduced by lemming grazing. Our results suggest that it is unlikely that food depletion during winter was the cause of the decline in lemming abundance following peak abundance. Other factors probably limit lemming populations and may prevent them from reaching densities high enough to exhaust their food resources.

Introduction

The relative importance of bottom-up (i.e. resources) vs top-down (i.e. predators) forces in controlling small mammal populations in northern ecosystems is still debated (Stenseth 1999, Oksanen et al. 2008, Gauthier et al. 2009, Oksanen et al. 2009). According to the bottom-up hypothesis, herbivore abundance is primarily influenced by the abundance and availability of their food resources (i.e. plants) (Polis and Strong 1996, Polis 1999). The exploitation ecosystem hypothesis (EEH) attempts to reconcile the latter view with a top-down control by stating that, although primary production determines the length of food chains and thus ultimately the abundance of higher trophic levels, in the absence of predators, herbivore populations can be high enough to negatively impact plant abundance (Oksanen et al. 1981, Oksanen and Oksanen 2000). In temperate and desert areas, small mammals can sometimes exert a significant impact on plant production and species composition (Bowers 1993, Hulme 1996, Howe and Brown 1999, Curtin et al. 2000, Howe et al. 2006, Fraser and Madson 2008), though not always (Báez et al. 2006; see also Moen 1990).

According to the EEH, in low productivity environments such as the Arctic, predator abundance should be too low to control herbivores and thus food webs should be dominated by plant-herbivore interactions (Oksanen 1983, Oksanen and Oksanen 2000). Support for this view comes from Fennoscandia and Alaska where small mammals can have a strong impact on plant production (Moen et al. 1993, Moen and Oksanen 1998, Huitu et al. 2003, Pitelka and Batzli 2007, Olofsson et al. 2012). Therefore, it has been proposed that regular, multi-annual population cycles of lemmings, the dominant small mammals of the tundra, are driven by food limitation in years of peak abundance in those areas (Oksanen and Oksanen 1992, Turchin et al. 2000, Turchin and Batzli 2001, Pitelka and Batzli 2007, Oksanen et al. 2008).

Lemming populations often reach their highest densities during late winter (Henttonen and Kaikusalo 1993, Reid et al. 1997, Gilg 2002, Kausrud et al. 2008) because reproduction starts under the snow (MacLean et al. 1974, Negus and Berger 1998, Duchesne et al. 2011b). However, lemmings have access to low-quality food during winter because photosynthetic activity and plant growth stops under the snow, a period that can last for up to 9 months in the High Arctic (Hansson 2002). Wintering lemmings show a strong selection for areas with deep snow and a heterogeneous micro-topography (Duchesne et al. 2011b), and thus will concentrate their foraging activity in those areas. Access to plants may sometimes be limited by snow conditions, for instance when their food becomes encapsulated in ice during melt-freeze or freezing-rain events (Callaghan et al. 2004, Korslund and Steen 2006). Therefore, it is during winter that food limitation should be most severe for lemmings.

If bottom up forces are the main factors controlling lemming population cycles, it is then during winter that the impact of lemming grazing on plants should be greatest, especially when densities are at their highest. A strong impact of lemmings on their winter food may not be sufficient to conclude that lemming population dynamic is controlled by resources, but it is a necessary condition to accept the hypothesis of a bottom-up control. Thus, according to the latter hypothesis, we predicted that (1) winter grazing by lemmings should negatively impact the abundance of food plants in their preferred habitats, (2) this impact should be proportional to lemming density and (3) high lemming winter grazing pressure should result in a reduction of plant growth in the subsequent summer. We tested these predictions in the Canadian High Arctic where two species of lemmings coexist, the brown (*Lemmus trimucronatus*) and collared lemming (*Dicrostonyx groenlandicus*). When they occur in sympatry, both species have relatively synchronous multiannual population cycles, with the brown lemming showing cyclic fluctuations of abundance of much greater amplitude than the collared (Batzli et al. 1983, Negus and Berger 1998, Gruyer et al. 2008).

Methods

The study site was located in the Qarlikturvik glacial valley (73° 08 'N, 80°00' W) on Bylot Island, Sirmilik National Park, Nunavut Territory. The study area (70 km^2) consisted of tundra polygons, thaw lakes and ponds forming wetlands at the bottom of the valley and is surrounded by drier mesic tundra on the nearby slopes and hills, which account for 90% of the landscape on the south plain of Bylot Island. The wetlands form grass/sedge meadows dominated by mosses and graminoids (*Dupontia fisheri*, *Eriophorum scheuchzeri* and *Carex aquatilis*; Gauthier et al. 1996). The mesic tundra is dominated by prostrate shrubs (*Salix* spp., *Dryas integrifolia*, *Cassiope tetragona*) with a sparse cover of forbs (*Saxifraga* spp., *Potentilla* spp., *Ranunculus* spp., *Pedicularis* spp.), graminoids (*Arctagrostis latifolia*, *Alopecurus alpinus*, *Poa* spp., *Luzula* spp.), mosses and lichens. Small, intermittent streams running through upland areas were also often located at the bottom of small gullies and were characterized by a thin band of wetland vegetation surrounded by mesic tundra. These sites were especially important for lemmings during winter.

The most important herbivores present on the island are the two lemming species, which are present throughout the year, and the greater snow goose (*Chen caerulescens atlantica*), which is present only in summer. No other small mammal species are present and large mammalian herbivores are absent. Other herbivores such as the rock ptarmigan (*Lagopus mutus*) and arctic hare (*Lepus arcticus*) are present at low densities. The two lemming species show some segregation in their summer habitat, with brown lemmings preferring wetter and collared drier habitats (MacLean et al. 1974, Batzli et al. 1983, Morris et al. 2011). During winter, both species share the same habitats and concentrate in mesic tundra and especially in small gullies along streams which are conducive to deep snow accumulation (Duchesne et al. 2011b, Reid et al. 2012). According to the literature, the two species have divergent diets, with brown lemmings preferring monocotyledons and mosses and collared lemmings preferring dicotyledons (Batzli and Jung 1980, Rodgers and Lewis 1985, 1986, Negus and Berger 1998). However, recent data based on DNA barcoding (Soininen et al. 2009) suggests that brown lemmings may actually be concentrating on dicotyledons (primarily *Salix* spp.) and mosses and eat little monocotyledons during winter at our study site (E. Soininen and G. Gauthier, unpublished data).

Lemming exclosures

In late May and early June 2009, before snow-melt, we systematically measured snow depth in 95 sites of high snow accumulation, mostly snow drifts caused by topography. We retained sites showing snow depth >60 cm, which are preferred by lemmings during winter at our study site (Duchesne et al. 2011b). These sites were visited after snowmelt and those showing signs of lemming use (winter nests or piles of faeces) were noted. We randomly selected 16 of those sites (8 in mesic tundra and 8 in stream gullies) to set lemming exclosures in August 2009. Exclosures consisted of galvanized, welded wire fence (1.25-cm mesh size) attached to wooden stakes in each corner and were separated by at least 50 m. Each exclosure was 0.75 x 0.75 m, 1 m high, and the fence was driven 15 cm into the ground to prevent lemmings from digging under. In subsequent years, at the same time that vegetation was sampled in August (see below), exclosures were moved by at least 10 m to a new site showing signs of winter use by lemmings to avoid sampling the same site twice.

Plant biomass was sampled in quadrats twice a year: at the end of the growing season in early August and at snow melt in June (or early July in a few sites where snow persisted late). In August, a vegetation sample was taken at ~2 m from where the exclosure was set. At snow-melt, a first sample was taken inside the exclosure and a second one outside, again within 2 m of the exclosure. If the sample collected outside did not show any sign of lemming activity (e.g. shoot clipping, pile of faeces, etc.), we searched for these signs within a 5 m radius around the exclosure and collected a third sample at such site. Positions of quadrats outside exclosures were chosen randomly except for the third sample at snow-melt, when no signs of lemming activity had been found in the random quadrat. For the third quadrat, we sampled the first area where signs of lemming activity were detected. Vascular plants were sampled in 20x50 cm quadrats and mosses in a 10x10 cm sub-quadrat inside the previous one. All above ground vascular plants were clipped at the ground level. Dead material was removed and the remaining live material was sorted by family, genus or species, dried to constant mass at 45^{o} C, and weighed. *Salix* were sorted into two categories, woody parts and leaves. Buds were included with leaves. Mosses were identified by genus or species on the 10x10 cm quadrat. Proportion cover of each genus or species was visually estimated in the field to the nearest 5 % before all above ground live (i.e. green) material was clipped (Pouliot et al. 2009). Clipped material was dried to constant mass at 45°C and weighed. Total weight was then divided by the proportion estimated for all genus or species.

We analysed the standing crop of each taxa (family, genus or species) of vascular plants and mosses using generalised linear models to test if we could detect a difference between (1) ungrazed (i.e. inside exclosure) and random plots outside exclosures and (2) ungrazed and grazed plots (i.e. those showing signs of lemming use outside exclosure) at snow-melt. We ran these two analyses separately because not all sites had both a random and a grazed plot. We hereafter refer to grazed and random plots as the treatment effects as both were potentially exposed to lemmings. Habitat (mesic tundra and stream gullies) and year were additional factors entered into the analysis and two-way interactions between those variables and the treatment effect were also examined (interactions are only reported when significant, i.e. $P < 0.05$). We further tested if biomass of each taxa at the end of the growing season remained stable throughout the study years, including habitat and its interaction with year, using a generalised linear model. All plant biomass data was transformed using natural logarithm to respect normality for analyses. We used Tukey's test to compare individual means (or Least Square Means, LSM when there was a significant interaction). Statistical analyses were performed with R statistical software (http://cran.r-project.org/).

Lemming density

Lemming density was estimated each summer. We live trapped rodents on two 11-ha grids (330 x 330 m), one set out in wetlands and one in mesic tundra, to obtain mark-recapture estimation of abundance. The trapping grids were laid out in a Cartesian plane of rows and columns, with numbered stakes spaced every 30 m. At each stake, we set out a Longworth trap baited with apple near signs of lemming use or active burrows. Trapping occurred over 3 consecutive days 3 times during the summer (mid-June, mid-July and mid-August) and traps were checked twice a day. All individuals captured were identified to the species, marked with PIT tags (when unmarked) and released. We considered the lemming population closed within our trapping sessions. All density estimates were carried out in DENSITY 4.4 (http://www.otago.ac.nz/density) using Efford's maximum likelihood method (Efford et al. 2004, Borchers and Efford 2008; see Bilodeau et al. 2013d for details).

Lemming winter nests provided us with an index of winter density (Krebs et al. 2012). We estimated nest density each spring, shortly after snow-melt, on 60 transects distributed randomly across the study area and equally in our 3 habitats (20 each in wetlands, mesic tundra and stream gullies). Transects were 500 m long and the same transects were used each year. All winter nests found while walking along the transect line were removed, their exact position and perpendicular distance to the transect noted, and the species using it identified (see Duchesne et al. 2011b for details). Nest density was estimated using line transect method (Buckland et al. 2001) and was carried out in Distance 6.0 (http://www.ruwpa.st-and.ac.uk/distance/), a software for distance sampling analysis (Thomas et al. 2009).

Results

Lemming population dynamic

The combination of winter nest and summer density data (Figs. 1 and 2) indicates that both species of lemmings had declined from high densities in summer 2008 to a near absence during the winter 2008-2009. Populations were extremely low during the summer 2009 but both species increased during winter 2009-2010 to reach high densities during summer 2010. Populations of both species remained high during the winter 2010-2011 but showed a divergent dynamic during summer 2011. Whereas brown lemmings reached very high densities during that summer, the collared lemming population had apparently crashed by the time snow had disappeared. By winter 2011-2012, brown lemmings had also declined to low numbers and densities of both species were low during summer 2012.

Impact of lemmings on plants during winter

The dominant vascular plants were the same in both habitats (Table 1), with Ericaceae and Salicaceae being the most abundant, followed by Juncaceae and Poaceae. In spring 2010, 12 out of 16 random quadrats had signs of lemming use, 14 out of 16 in spring 2011, but none in spring 2012. We found no differences in total vascular plant biomass between random sites outside the exclosures and ungrazed sites inside ($F_{1,86} = 0.34$, $P = 0.561$) nor between sites showing signs of lemming grazing and ungrazed sites ($F_{1,86} = 0.92$, $P = 0.339$; Fig. 3). There was more biomass in 2012 compared to 2010 and 2011 (random vs ungrazed: $F_{2,86} = 4.25$, $P = 0.017$; grazed vs ungrazed: $F_{2,86} = 7.19$, $P = 0.001$). This effect is mostly due to the high biomass of *Cassiope tetragona* (an Ericaceae) in and around our exclosures in spring 2012 (Fig. 4). Grazed sites tended to have less *Cassiope* in 2012 compared to ungrazed sites ($P = 0.084$), probably because these plants tend to overgrow other plants when present and are not eaten by lemmings.

Among 17 individual plant families, only four showed some evidence of an effect of lemmings' winter grazing (for the others, $P > 0.32$ in all comparisons; see Annexe 3). There was no treatment effect on Salicaceae woody parts (random vs ungrazed: $F_{1,86} = 0.23$, $P = 0.629$; grazed vs ungrazed: $F_{1,86} = 0.43$, $P = 0.515$; Fig. 4) but biomass was higher in 2012 than in other years ($F_{2,86} = 6.17$, $P = 0.003$). Similarly, no treatment effect was detected on Salicaceae leaves (random vs ungrazed: $F_{1,86} = 0.83$, $P = 0.364$; grazed vs ungrazed: $F_{1,86} = 0.10$, $P = 0.749$) although leaf biomass was lower in 2011 than in the other 2 years ($F_{2,86} = 13.5$, $P < 0.001$; Fig. 4). The large annual difference is possibly due to later sampling dates in 2010 and 2012 when *Salix* had already started to grow before snow on quadrats had completely melted. Biomass of Juncacea did not differ between inside and outside exclosures (random vs ungrazed: $F_{1,86} = 0.07$, $P = 0.799$; grazed vs ungrazed: $F_{1,86} = 0.51$, $P = 0.476$) nor that of Poaceae (random vs ungrazed: $F_{1,86} = 0.75$, $P = 0.390$; grazed vs ungrazed: $F_{1,86} = 0.80$, $P = 0.375$ Fig. 4). Caryophyllaceae biomass was reduced by 33 % in grazed sites compared to ungrazed sites ($F_{1,86} = 5.97$, $P = 0.017$; Fig. 4) but not in random sites ($F_{1,86} = 0.73$, $P = 0.395$). Papaveraceae, a rare family, showed inconsistent trends, its biomass being significantly lower in random compared to ungrazed sites but higher in grazed sites.

Dominant mosses were similar in both habitats (Table 2), with the genus *Drepanocladus*, *Hylocomium*, *Polytrichum* and *Scapania* being the most abundant. We found no differences in total live moss biomass between random sites and ungrazed sites within exclosures ($F_{1,86} < 0.001$, $P = 0.984$), nor between sites showing signs of lemming grazing and ungrazed sites ($F_{1,86} < 0.001$, $P = 0.989$; Fig. 3). The apparent decline in spring moss biomass over the years ($F_{2,86} = 4.34$, $P = 0.016$) is probably related to the high prevalence of Ericaceae in 2012, as explained above, because this decline was not apparent at the end of the growing season (see below). Evidence for an effect of lemming grazing was detected for 3 out of 32 individual moss species or genus. The effect on *Polytrichum* tended to vary among years with random plots (treatment x year: $F_{2,86} = 2.48$, $P = 0.089$). In grazed plots, biomass varied according to year ($F_{2,86} = 3.59$, $P = 0.032$) and tended to differ among treatments ($F_{2,86} = 3.10$, $P = 0.082$). *Polytrichum* biomass in random and grazed sites was about 57% lower than in ungrazed sites in 2010 but not in 2011 and 2012 (Fig. 4). The effect of grazing on *Drepanocladus* biomass varied with habitat but was inconsistent. Biomass was 9% lower in random than in ungrazed sites in mesic tundra but not in stream gullies (treatment x habitat; $F_{2,86} = 3.33$, $P = 0.072$) whereas biomass was 51% higher in grazed than in ungrazed sites in the stream gullies but not in the mesic tundra (treatment x habitat: $F_{2,86} = 4.50$, $P = 0.037$). Finally, *Ptilidium* biomass was also 56 % lower in grazed than in ungrazed sites but this time only in the stream gullies (treatment x habitat: $F_{2,86} = 6.49$, $P = 0.013$).

Annual variation in plant growth

Aboveground live vascular plant biomass at the end of the growing season tended to increase over the years ($F_{3,56} = 2.07$, $P = 0.114$) and was significantly higher in 2012 than in 2010 (Fig. 5). For individual vascular plant families, there were few differences among years, and trends were not always consistent (see Annexe 3 for details). The biomass of Salicaceae did not vary significantly among years (leaves: $F_{3,55} = 0.76$, $P = 0.523$; wood: $F_{3,55} = 0.78$, $P = 0.509$) although biomass appeared much higher in 2012 than in other years (Fig. 6). This was partly due to one exclosure showing an extremely high biomass (leaves: 101.5 g/m^2; wood: 177.2 g/m^2). Excluding this outlier, Salicaceae biomass in 2012 was 27.7 ± 6.3 g/m^2 for leaves and 30.5 ± 6.3 g/m^2 for wood. Poaceae biomass tended to differ among years ($F_{3,56} = 2.71$, $P = 0.054$; Fig. 6) as there was more biomass in 2012 compared to 2010 (Fig. 6). The biomass of Juncaceae did not vary among years ($F_{3,56} = 0.21$, $P = 0.888$). The biomass of Caryophyllaceae and Polygonaceae varied among years ($F_{3,56} = 4.03$, $P = 0.012$ and $F_{3,56} = 4.17$, $P = 0.010$; respectively) as the biomass was higher in 2009 than in 2010, 2011 (both species) and 2012 (Polygonaceae only; Fig. 6).

Total moss biomass at the end of the growing season did not vary significantly among years ($F_{3,56} = 0.97$, $P = 0.415$; Fig. 5). Analysis of individual taxa revealed variable effects across species and sometimes also habitats. *Aulacomnium* tended to have higher biomass in 2012 than in other years ($F_{3,56} = 2.23$, $P = 0.095$), *Cinclidium* had higher biomass in 2009 than in other years ($F_{3,56} = 3.50$, $P = 0.021$) and *Scapania* had lower biomass in 2009 than in other years ($F_{3,56} = 7.86$, $P < 0.001$). Finally, annual change in biomass of *Ditrichum flexicaule* and *Hylocomnium* varied among habitats (interaction year x habitat: $F_{3,56} = 3.30$, $P = 0.027$ and $F_{3,56} = 2.66$, $P = 0.057$, respectively).

Discussion

During winter, plant growth stops under the snow and a large proportion of plant biomass is lost to senescence (Hansson 2002). Therefore, if small mammal populations are controlled by their resources, they should be particularly vulnerable to food shortage during winter, and years of high population densities should result in detectable signs of food depletion at snow melt. This is especially true for lemmings that can breed and show population growth under the snow, which would put even more pressure on their winter food supply.

We found weak evidence to support the hypothesis that winter grazing by lemmings reduced plant biomass in their preferred habitat and no support for the hypothesis that this impact should be highest during the winter of peak abundance (2010-2011 at our study site). Even when we selected sites with signs of lemming grazing, differences in biomass between these sites and those protected from grazing were small or absent. A significant but slight impact of winter grazing was detected on a few mosses known to be important food items for brown lemmings (Batzli et al. 1983), the most abundant lemming species at our site, and no effect was detected on Poaceae and Juncaceae. Similarly, no effect on Salicaceae and Rosaceae was detected, two plants known to be preferred by collared lemmings (Batzli et al. 1983, Rodgers and Lewis 1985). The only dicotyledon plants showing a substantial impact were the Caryophyllaceae, which compose a very small proportion of total plant biomass at our site. We must point out that, contrarily to what was reported elsewhere (Batzli and Jung 1980, Rodgers and Lewis 1985, 1986), Soininen and Gauthier (unpublished data) recently found that Salicaceae was the dominant vascular plant eaten by brown lemmings during winter at our study site (up to 55% of their diet), though data came from only one year (2011). These results were based on DNA barcoding analysis of fecal material (Soininen et al. 2009). Thus, even though *Salix* may be the most important food item for both lemming species, the impact of grazing was non-detectable, probably because this plant is extremely abundant at our study site. It could be argued that brown lemmings used *Salix* because their putative preferred food resources (graminoids and mosses) were depleted, but we found no evidence for that. Moreover, we stress that we measured grazing impact in their preferred winter habitat (i.e. areas with the deepest snow pack; Duchesne et al. 2011b, Reid et al. 2012) where lemming densities are highest. Lemmings also use areas outside snowdrifts, which compose the majority of the study area and where densities are generally lower. Even less impact on vegetation should be expected in those areas.

Plants were exposed to the highest lemming densities during winter 2009-10 and 2010-11 as judged by winter nest abundance. If lemming grazing has a negative impact on plant growth, we should have observed a marked decline in plant and moss biomass in summer 2010 and 2011 compared to 2009. We did not observe such pattern in total vascular and moss biomass in late summer as vascular biomass was generally higher in 2011 and 2012 than in 2009 and 2010, and moss biomass did not show annual variations. Annual variation in vascular plant biomass may be best explained by climatic factors, which are a strong driver of plant growth (Gauthier et al. 2011). At individual taxa level, we did find evidence for a reduction in the biomass of some species at the end of the summer in the two years of high lemming abundance. Caryophyllaceae, Polygonaceae and to a lesser extent Salicaceae and Poaceae biomass were lower in the two years of high lemming abundances. However, considering that the reduction in biomass during the winter was generally weak or absent, especially for important families such as Salicaceae and Poaceae, it is possible that the reduction in biomass observed in late summer was partly a consequence of summer grazing as the plots sampled in August had not been protected from grazing. If food resources were controlling lemming populations, plant biomass should have been lowest by the end of the

2011 growing season, after two winters of high densities, which was not the case. If high grazing pressure during the lemming peak years had damaged these plants, we would have expected a carry-over effect during the following growth season. However, in 2012, Salicaceae, Poaceae and Caryophyllaceae growth was high and comparable to 2009. Therefore, the Polygonaceae appears to be the only plant family that consistently suffered from lemming grazing.

At our study site, lemmings show regular 3 to 4 years cycles of high amplitude (Gruyer er al. 2008, Legagneux et al. 2012) and 2010 and 2011 were two consecutive years of high lemming abundance. Both lemming species increased in densities from 2009 to 2010, but while brown lemmings, the most abundant species, continued to increase during the following winter to reach peak densities in 2011, collared lemmings started decreasing in late summer 2010 and had crashed by spring 2011. Considering that the two species can eat the same food plants during winter (E. Soininen and G. Gauthier, unpublished data), it appears unlikely that food depletion during winter was the cause of the decline in collared lemmings.

Our results do not provide evidence that a lack of plant food during winter may have caused the crash of lemming populations on Bylot Island. Nonetheless, it is still possible that exceptional environmental conditions such as the extensive formation of ground ice or an extremely hard and compacted snowpack, could severely limit food availability for lemmings during some winters. Episodes of ground icing have been reported in Fennoscandia and Svalbard and appear to be relatively common in those areas (Callaghan et al. 2004, Korslund and Steen 2006, Stien et al. 2012). Moreover, changes in the quality of the snow cover have been invoked as a possible cause of the collapse of lemming cycles in some areas (Kausrud et al. 2008, Gilg et al. 2009). Snow cover in the Canadian Arctic is generally much drier than in Fennoscandia and is subject to more consistent cold temperatures, allowing the formation of a stable subnivean space for lemmings to move under the snow (Reid et al. 2012, Bilodeau et al. 2013b). Signs of lemming use (e.g. travel paths in the moss, piles of faeces, winter nests) were easy to find and were common around our exclosures and throughout the study area in peak years, suggesting that lemmings were not restricted in their movements and had easy access to their preferred winter habitats.

It has been suggested that plant quality, mostly through the presence of secondary compounds, could limit population growth of small mammals more than does available biomass (Seldal et al. 1994, Berg 2003, Hogstedt et al. 2005). Because we did not look at plant nutritive quality during this study, we cannot rule out a possible role of this factor in the population dynamic of lemmings at our study site. However, since we investigated winter grazing when plants are metabolically inactive, we believe that it is unlikely that secondary compounds played a major role, especially for fast growing plants such as graminoids, which allocate a very small proportion of their resources to defences (Coley et al. 1985).

Even though we found some impact of winter grazing on a few vascular plant and moss taxa in preferred lemming habitat, these effects were relatively modest and short-lived. In order to reduce the carrying capacity and maintain a cyclic dynamic, the impact on food resources must be sufficiently strong and sustained to have a long-lasting effect on plants, i.e. plants must take more than one year to recover (Turchin and Batzli 2001, Ims and Fuglei 2005). Our results show that these conditions were not met in our system, which suggests that resources are unlikely to control the population dynamic. It appears that other factors may be limiting lemming populations and prevent them from reaching densities high enough to deplete their food resources and cause a crash. On Bylot Island, recent evidence suggests that predators could play that role and perhaps regulate lemming populations (Legagneux et al. 2012, Therrien 2012).

Table 1. Percentage of aboveground biomass of the different vascular plant families found at the peak of growth in the two lemming winter habitats in late summer.

Vascular plant family or group	Mesic tundra	Stream gullies
Ericacea [a]	47.2	59.8
Salicaceae [b]	38.2 (18.2) [k]	31.7 (15.2) [k]
Juncaceae [c]	6.0	3.7
Poaceae [d]	4.0	2.5
Fabaceae [e]	0.8	1.0
Caryophyllaceae [f]	0.8	0.3
Pyrolaceae [g]	1.0	0.1
Rosaceae [h]	0.4	0.6
Polygonaceae [i]	0.4	0.1
Others [j]	1.2	0.2

[a] *Cassiope tetragona*

[b] Mostly *Salix arctica*

[c] Mostly *Luzula confusa* and *Luzula nivalis*

[d] Mostly *Arctagrostis latifolia* and *Poa arctica*

[e] Mostly *Astragalus alpinus*

[f] Mostly *Stellaria longipes* and *Cerastium regelii*

[g] *Pyrola grandiflora*

[h] Mostly *Dryas integrifolia* and *Potentilla nivea*

[i] *Oxyria digyna* and *Polygonum viviparum*

[j] Others includes the following families, which represent ≤0.5 % of total biomass in the two habitats: Brassicaceae, Cyperaceae, Equiseraceae, Papaveraceae, Ranunculaceae, Saxifragaceae and Scrophulariaceae

[k] percentage of leaves and buds in parenthesis

Table 2. Percentage of green biomass of the different mosses genus or species found at the peak of growth in the two lemming winter habitats in late summer.

Moss genus or species	Mesic tundra	Stream gullies
Drepanocladus [a]	16.4	27.0
Hylocomium splendens	18.4	19.8
Polytrichum [b]	17.2	14.4
Scapania simmonsii	18.4	12.2
Ditrichum flexicaule	9.3	9.2
Ptilidium ciliare	7.1	0.4
Aulacomnium [c]	5.1	5.8
Tomenthypnum nitens	3.5	5.2
Dicranum [d]	2.1	3.3
Philonotis fontana	0.3	1.3
Gymnommitrion concinnatum	0.8	0.00
Others [e]	1.4	1.4

[a] *Drepanocladus uncinatus* and *D. brevifolius*

[b] *Polytrichum juniperinum*, *P. piliferum*, *P. strictum* and *P. swartzii*

[c] *Aulacomnium turgidum* and *A. palustre*

[d] *Dicranum angustum* and *D. acutifolium*

[e] Others includes the following species, which represent individually ≤0.5 % of total biomass in the two habitats: *Bartramia ithyphylla*, *Blindia acuta*, *Campylium stellatum*, *Ceratodon purpureus*, *Cinclidium stygium*, *Dicranoweisia crispula, Encalypta alpina*, *Hypnum revolutum*, *Meesia triquetra*, *Oncophorus wahlenbergii*, *Orthotrichum speciosum*, *Plagiomnium ellipticum*, *Pohlia cruda* and *Racomitrium anuginosum*

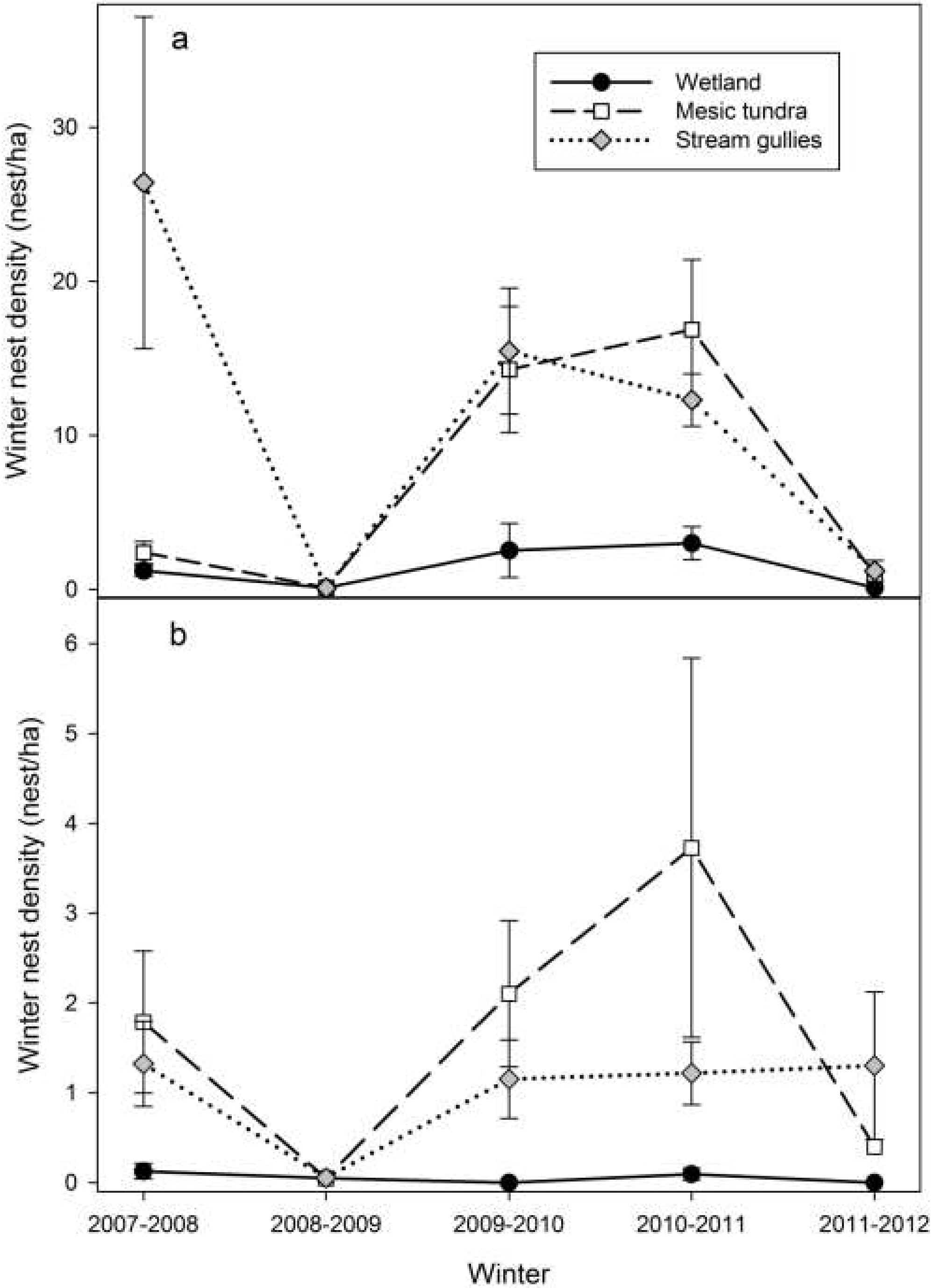

Figure 1. Winter nests densities for brown (a) and collared (b) lemmings from 2008-2012 in wetlands, mesic tundra and in stream gullies.

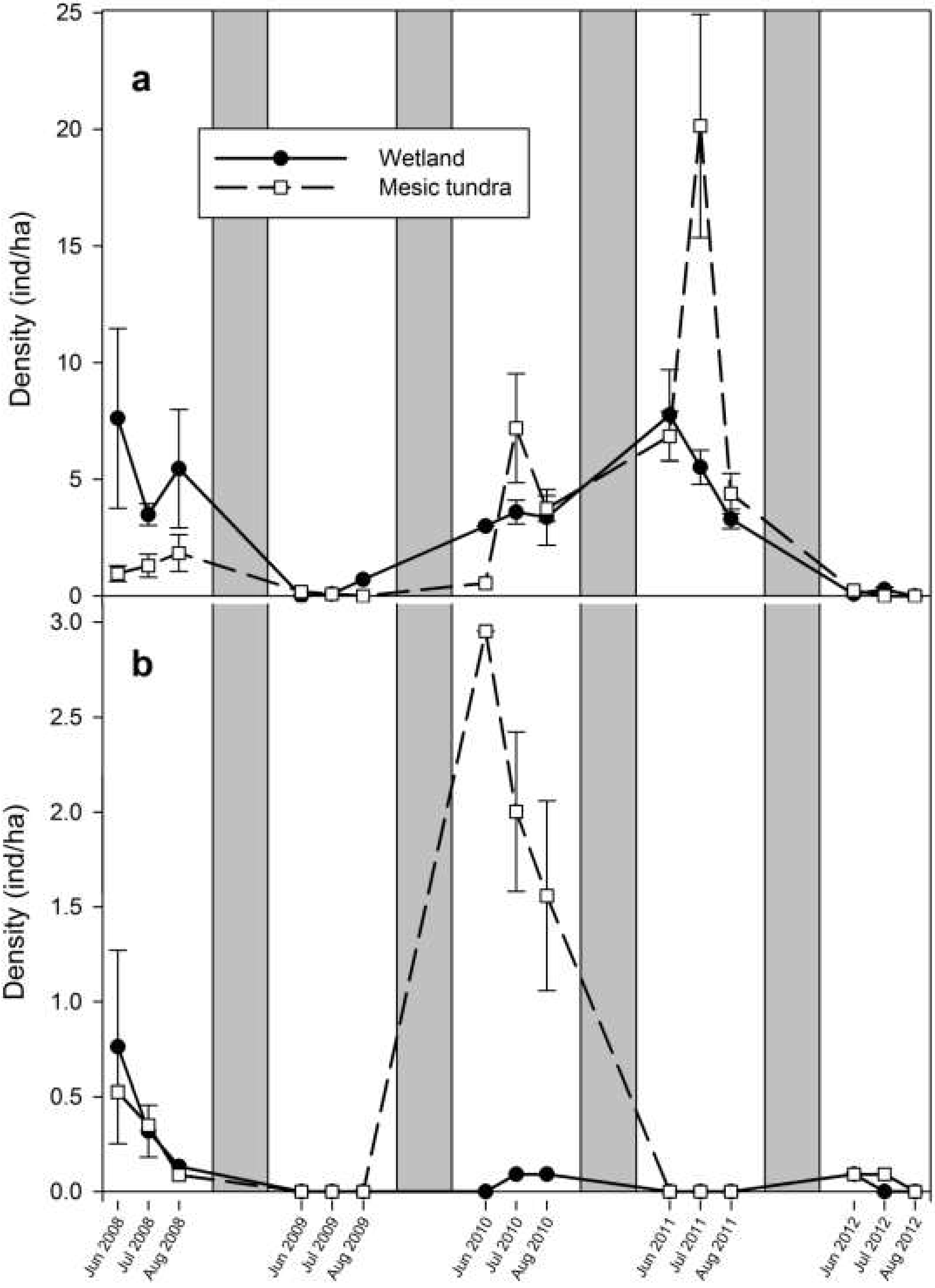

Figure 2. Brown (a) and collared (b) summer densities estimated by capture-mark-recapture using Efford's maximum likelihood method from 2008-2012 in the wetland and mesic tundra grids.

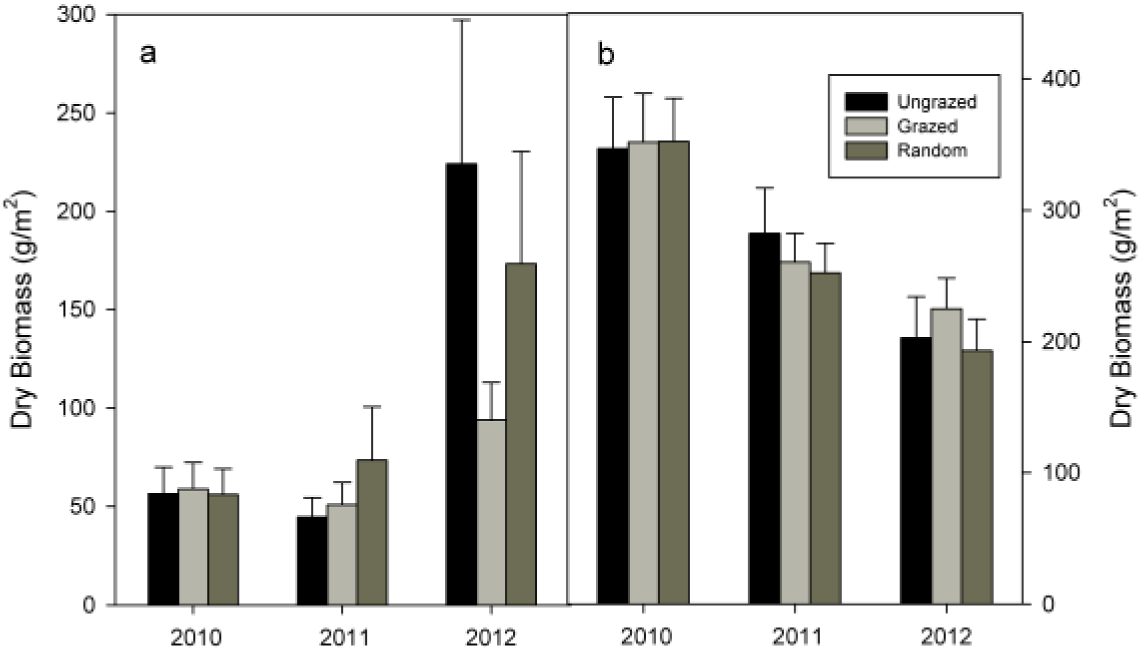

Figure 3. Aboveground live biomass (dried biomass in g/m^2) of vascular plants (a) and mosses (b) shortly after snowmelt in spring 2010-2012 in ungrazed (inside exclosures), grazed and random quadrats (outside exclosures). Error bars represent SE. N = 16 in each treatment and year.

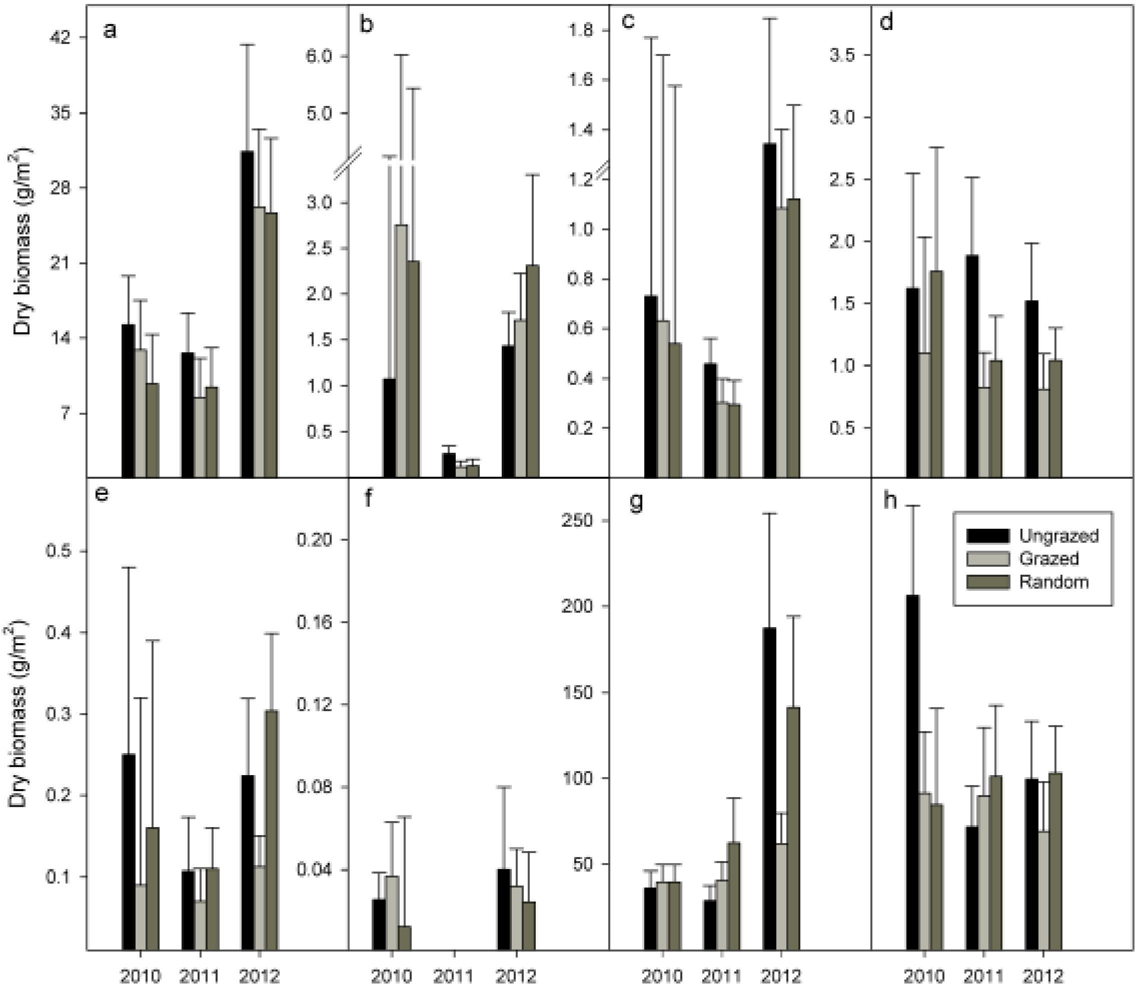

Figure 4. Aboveground live biomass (dried biomass in g/m^2) of Salicaceae wood (a) and leaves (b), Poaceae (c), Juncaceae (d), Caryophyllaceae (e), Polygonaceae (f), Ericaceae (g) and of the moss genus *Polytrichum* (h) shortly after snowmelt in spring 2010-2012 in ungrazed (inside exclosures), grazed and random quadrats (outside exclosures). Error bars represent SE. N = 16 in each treatment and year.

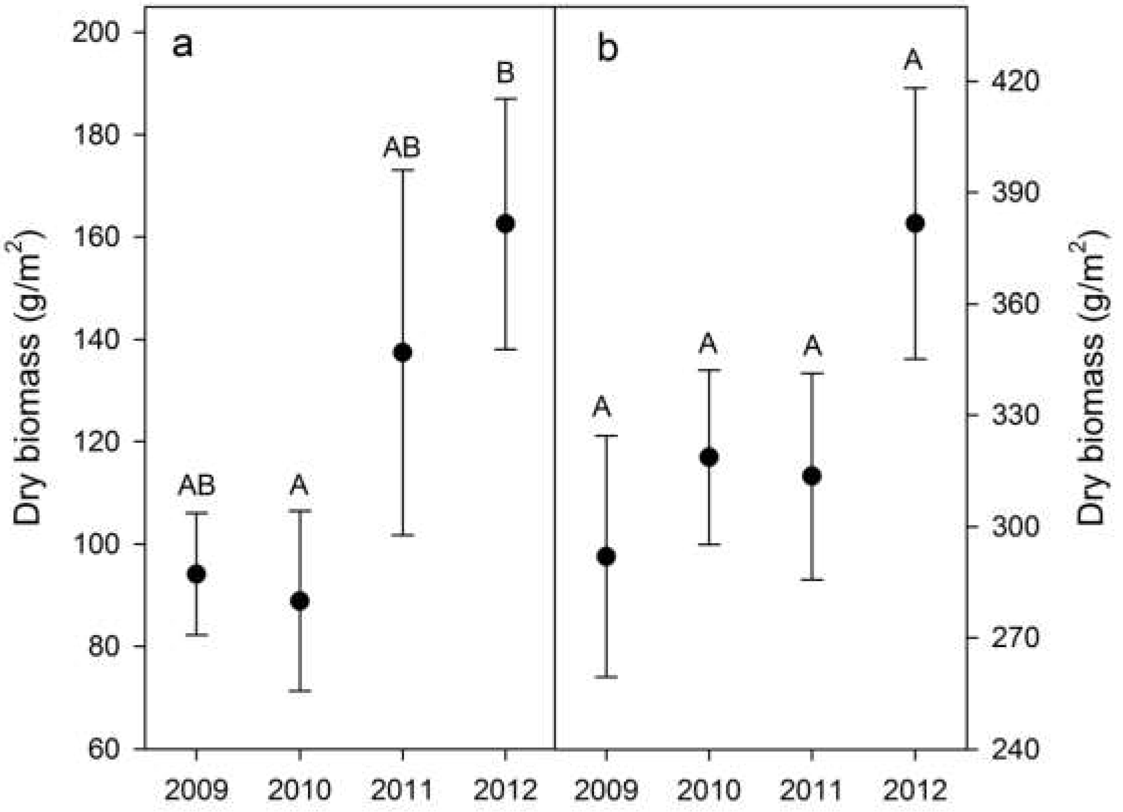

Figure 5. Aboveground live biomass (dried biomass in g/m^2) of vascular plants (a) and mosses (b) at the end of the growing season in August 2009-2012. N = 16 in each treatment and year. Values with the same letter are not significantly different ($P < 0.1$; Least Square Means or Tukey's test).

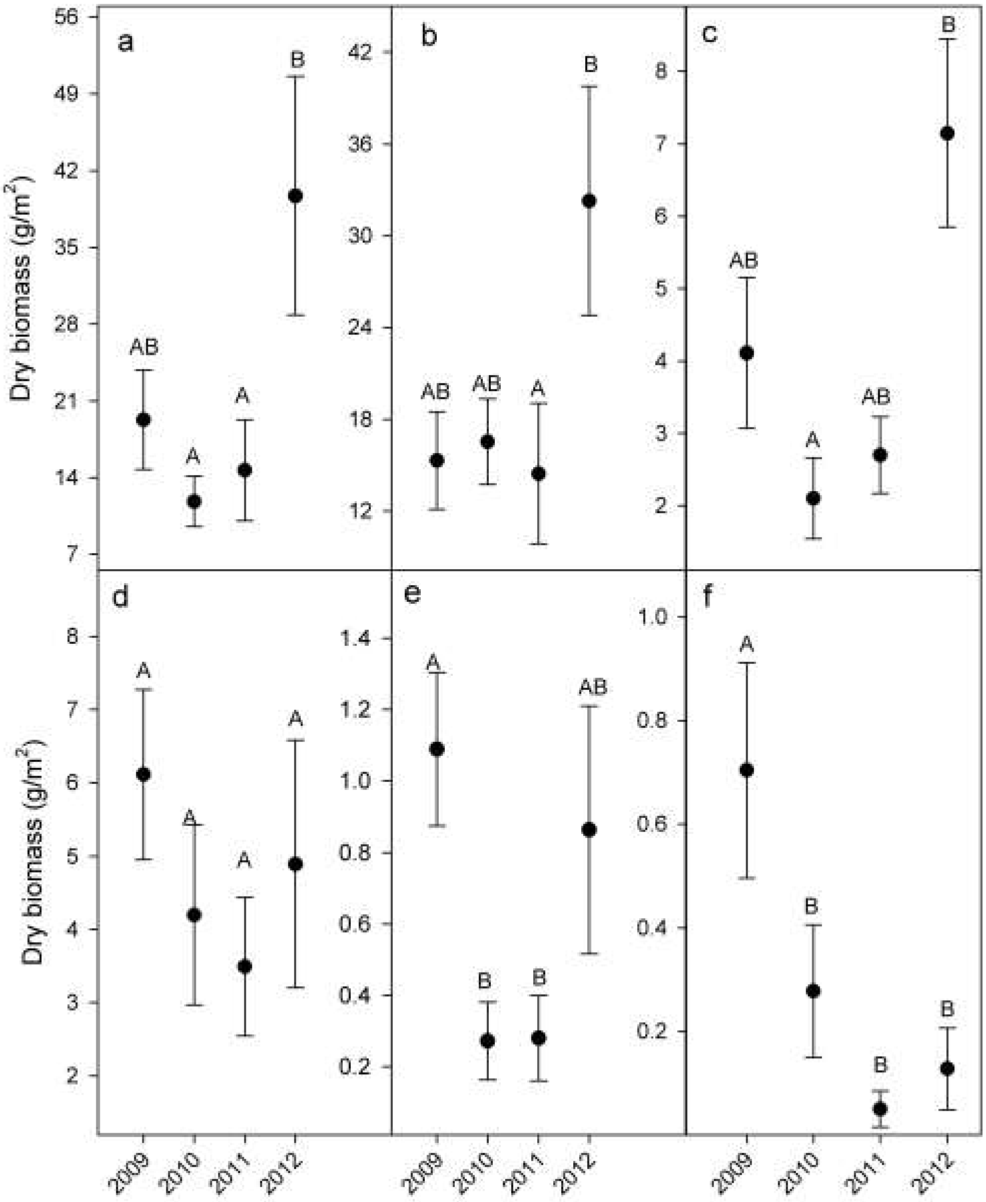

Figure 6. Available live biomass (dried biomass in g/m^2) of Salicaceae wood (a) and leaves (b), Poaceae (c), Juncaceae (d), Caryophyllaceae (e) and Polygonaceae (f) at the end of the growing season in August 2009-2012. N = 16 in each treatment and year. Values with the same letter are not significantly different (P < 0.1; Least Square Means or Tukey's test).