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ORIGINAL PAPER

# Goose grazing influences the fine-scale structure of a bryophyte community in arctic wetlands

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**Abstract** Herbivores can shape plant communities, especially in the Arctic. We tested the role of geese for structuring bryophyte communities at fine spatial scales in the arctic tundra by excluding them from 4 × 4 m areas. We surveyed the presence and absence of bryophyte species in quadrats (10 × 10 cm) divided into 25 cells outside and inside these exclosures, after 5 and 11 years of treatment. Species richness per cell (4 $\text{cm}^2$) was higher in the presence of geese, especially after 11 years of treatment, while geese had little effect on richness at larger scales (i.e. quadrat and whole exclosure). The slope of the species–area relationship within quadrats was consequently shallower outside exclosures. Our results further suggest that the community outside the exclosures was more variable in space and time than that inside the exclosures. We conclude that goose foraging activity promotes the coexistence of bryophyte species at the centimetre scale.

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## Introduction

Herbivores can influence several aspects of plant communities, including species diversity. For example, herbivores have been shown to change species relative abundance due to spatially structured or selective grazing (Pacala and Crawley 1992; Adler et al. 2001; Côté et al. 2004; van der Wal 2006; Hansen et al. 2007) and to promote species diversity by creating disturbances and opening regeneration niches (Grubb 1977; Kimmerer and Young 1996). The role of herbivores for the structure of plant communities remains controversial, however, as experiments often reveal contrasting patterns (Olff and Ritchie 1998; Austrheim and Eriksson 2001). This has prompted us to examine the influence of the Greater Snow Goose (*Chen caerulescens atlantica*) on the structure of the bryophyte community at a major breeding site located in wet polygon fens of the arctic tundra.

The Greater Snow Goose is a medium-sized herbivore whose population size has increased markedly in the second half of the last century, mostly because of intensified foraging on agricultural lands in its wintering habitat (Menu et al. 2002; Gauthier et al. 2005). This population expansion has increased foraging pressure on their breeding habitat located in the Arctic, a biome apparently prone to strong herbivore control (Oksanen and Oksanen 2000; van der Wal 2006). In polygon fens of the Arctic, the preferred feeding area of Greater Snow Geese on the breeding grounds, goose grazing activity changes the standing crop, production, and relative abundance of graminoid plant species (Gauthier et al. 1995, 2004, 2006), which indirectly leads to a high bryophyte biomass (Gauthier et al. 2004). Although geese do not feed on mosses at our study site (Gauthier et al. 2004), they disturb physically the moss carpet when feeding on graminoid rhizomes, a foraging mode called grubbing. When grubbing, geese typically tear apart the moss carpet to reach the below-ground rhizomes of sedges and grasses and drop the mosses that they dug up to reach the rhizomes (Gauthier 1993). This foraging behaviour led us to hypothesize that geese are breaking monospecific patches of bryophytes and indirectly structuring the bryophyte community at the scale of the size of a goose bill, i.e. a few centimetres.

To assess the effect of geese on the fine-scale bryophyte community structure, we performed a long-term exclosure experiment. We measured common community structure metrics inside and outside goose exclosures, 5 and 11 years after the exclusion of geese. Five aspects of the bryophyte community were analysed: the species frequency, the species richness and its coefficient of variation at multiple scales, the species–area power law (Scheiner 2003), and the species evenness. Our sampling focused on fine spatial scales (4–100 $\mathrm{cm}^2$) because these are the scales at which geese directly perturb the moss carpet through foraging, which makes them appropriate scales to examine the coexistence of neighboring individual bryophyte shoots of different species in a common environment. Overall, our analyses revealed changes in the community structure that are consistent with the hypothesis that geese tend to increase species diversity at the centimetre scale.

## Materials and methods

### Study area

This study was carried out in a 70 $\mathrm{km}^2$ glacial valley located on the south plain of Bylot Island, Nunavut, Canada (73°N, 80°W). During the summer, Greater Snow Geese forage mostly on graminoids, dominated by *Dupontia fisheri*, *Eriophorum scheuchzeri* and *Carex aquatilis* var. *stans* in the polygon fens we studied. Exclosures were located in this habitat, which covers $30.2 \pm 2.0$ $\mathrm{km}^2$ of the 1,600 $\mathrm{km}^2$ south plain of Bylot Island (Massé et al. 2001). Other significant herbivores on the island include the brown lemming (*Lemmus sibiricus*) and the collared lemming (*Dicrostonyx groenlandicus*) and the mesh size of our exclosures did not prevent lemming movement. *L. sibiricus* is known to forage on graminoids in wetlands and on bryophytes during winter (Virtanen 2000); however, lemming abundance in our area was low in most years (Gruyer 2007).

The 24 bryophyte species and genera sampled in our study are, in the order of decreasing abundance indicated in parentheses (expressed as the mean number of 4 $\mathrm{cm}^2$ cells occupied in a 5 × 5 cells quadrat across all samples), *Drepanocladus* spp. (19, mostly *D. cossinii*), *Campylium arcticum* (17), *Calliergon giganteum* (11), *Cinclidium arcticum* (9), *Bryum cryophilum* (9), *Aulacomnium palustre* (6.3), *Polytrichum strictum* (5.8), *Pohlia nutans* (4.5), *Aulacomunium turgidum* (4.3), *Brachythecium turgidum* (3.8), *Meesia triquetra* (3.5), *Tomenthypnum nitens* (3.3), *Bryum algovicum* (2.8), *Sphagnum* spp. (2.8, mostly *S. subsecundum*), *Polytrichum swartzii* (2.3), *Aneura pinguis* (1.8, liverwort), *Oncophorus wahlenbergii* (0.8), *Dicranum elongatum* (0.5), *Tritomaria quinquedentata* (0.3, liverwort), *Pohlia cruda* (0.3), *Amblystegium serpens* (0.2), *Pleurozium* spp. (0.2), *Odontoschisma macounii* (0.1), and *Distichium capillaceum* (0.05). The botanical authority names follow Anderson et al. (1990) for mosses and Scoggan (1979) for vascular plants.

### Experimental design and analyses

Early during the 1994 growing season, 17 goose exclosures (4 × 4 m) made of 2.5-cm mesh chicken wire and covered with light nylon netting were set in the central area of as many polygon fens to initiate a study on the impact of snow goose grazing on its preferential food plants (essentially graminoid plants, see Gauthier et al. 2004). Exclosures were randomly located within 3 km from our main camp in one of the largest concentration of polygon fens in the island. Field observations by L. Rochefort in 1996–1997 revealed an unusual mixing of moss species at the centimetre scale. Hence, we decided to use these permanent exclosures to test whether the fine-scale mixture of bryophyte species was caused by geese activities. Due to time constraints, sampling was limited to seven of the 17 exclosures dispersed over the valley. The seven exclosures were surveyed 5 years (1998) and 11 years (2004) after they were erected. The experimental design is a complete random block with replication and measurements repeated in time. We surveyed the presence and absence of all species in each of 25 cells (2 × 2 cm) in a quadrat (10 × 10 cm) and sampled five quadrats inside and five quadrats outside the exclosures at both sampling periods. Quadrats sampled outside exclosures were placed in the central part of the same polygon (margins were avoided) and all sampling was done no closer than 30 cm from a chicken-wire fence. For both treatments, quadrats were thrown purposely where bryophytes were present, i.e. standing water and areas lacking bryophytes, which always comprised less than ~10% of the sampled polygons, were avoided. Our sampling effort focused on areas containing bryophytes rather than being completely random because we were interested in fine-scale community patterns inside moss carpets. This procedure is conservative as it compares similar zones, in the sense that they all contain bryophytes, inside and outside the exclosures.

Species richness, defined as the number of species occurring in a given area (whether a cell, a quadrat, or an exclosure), and species frequency, defined as the number of cells out of 25 in which a species occurs in a quadrat, were calculated from the presence–absence of data collected in the surveys as described earlier. Diversity pattern was analysed through (1) the species richness at three scales (cell, quadrat and exclosure), (2) the slope of the species–area power function in a quadrat (Scheiner 2003), (3) the frequency of a species, (4) the evenness index $E_{\mathrm{var}}$ (Smith and Wilson 1996), and (5) the coefficient of variation of species richness between cells within a quadrat and between quadrats in a treatment/year. The slopes of the log species–log area relationships were calculated for each quadrat from the mean richness per cell and the total richness of the quadrat. We used the coefficient of variation (CV = standard deviation/mean) to measure the variability in richness inside a quadrat or an exclosure because CV is independent from the mean.

We calculated the mean species frequency of a community as the mean frequency of all species in a quadrat. To account for the fact that differences in mean frequencies among communities may be due to a small number of species each having a large effect or to many species each having a small effect, we used an evenness index as a measure of the variability of relative frequencies. We used Smith and Wilson's (1996) evenness index $E_{\mathrm{var}}$ because these authors' work has shown that it is independent from the species richness. $E_{\mathrm{var}}$ is calculated as

$$E_{\mathrm{var}} = 1 - \frac{2}{\pi}\arctan\left\{\sum_{x=1}^{s}\left(\ln(x_s) - \sum_{x=1}^{t}[\ln(x_t)/S]\right)^2 \Bigg/ S\right\}$$

where $x_s$ and $x_t$ are the abundance of the $s$th and $t$th species, respectively, and $S$ is the total species richness in the sample. We used the species frequency to estimate the abundance ($x$).

To test for a main effect of goose exclusion on the community structure aspects defined at the quadrat scale, we performed an analysis of variance (ANOVA) with "exclusion" and "sampling year" as fixed and ordinal factors, "exclosure" as a random and nominal factor, and the quadrat-level data formed the residuals. The analysis of richness within cell also included a random factor for "quadrat nested within exclosure", while the residuals were now formed by data from each cell, and the analysis of CV in species richness at the exclosure-scale only comprised the "exclusion" and "sampling year" effects and their interaction. These analyses allowed us to test for treatment and sampling period effects, as well as for their interaction. Mean values in the text are reported with ± 1 standard error. All statistical analyses were performed using the EMS procedure in JMP 7.0 (SAS Institute Inc., Cary, NC, USA).

### Geese abundance

We counted goose faeces along 12 randomly located transects (1 × 10 m; new location each year) marked with small pegs. These transects were placed in the same habitat and the same general location as the permanent exclosures (typically within 10–100 m) and were part of an annual sampling effort to assess intensity of use of the area by geese (see Gauthier et al. 1995 for details). Faeces already present on transects were removed after snowmelt in mid-June, and all faeces were counted and removed from transects at 2-weeks intervals until mid-August. Cumulative faeces density at the end of the summer provided an annual index of local abundance of geese on the study area.

## Results

Fewer species occurred inside the exclosures for both sampling periods at the scale of a single cell (4 $\mathrm{cm}^2$) (Table 1, Fig. 1a), but not at the scales of a quadrat or an exclosure ($P > 0.4$ for all factors at both larger scales). The effect of exclusion on the cell-level species richness was much stronger after 11 years of treatment, as supported by a significant exclusion × year interaction (Table 1). After 11 years of treatment, there were on average 4.12 ± 0.05 species per cell (4 $\mathrm{cm}^2$) where geese were removed against 4.91 ± 0.06 species where they were present, a difference of 19% (Fig. 1a). The number of species in a quadrat (100 $\mathrm{cm}^2$), the largest contiguous area sampled, ranged from 3 to 16 across all samples and treatments, with 9.1 ± 0.3 species counted on average. The total number of species observed inside the exclosures was comparable to the number observed outside: on average, 12.6 ± 0.6 species were found inside the exclosures versus 12.4 ± 0.5 species outside (in a total area sampled equal to 500 $\mathrm{cm}^2$).

The effect of exclusion on the rate of accumulation of bryophyte species with area (i.e. the slope of the log species–log area relationship) also depended on the sampling year (Table 1, Fig. 1b). After 11 years of goose exclusion, the mean slope was steeper inside the exclosures ($P < 0.001$; inside 0.24 ± 0.01; outside 0.18 ± 0.01 species $\mathrm{cm}^{-2}$, see Fig. 1b), which implies that the number of species recorded with increasing area increases faster inside than outside the exclosures. Five years after

**Table 1** The effect of goose exclusion and sampling year on the species richness per cell and on the slope of the log species–log area relationship, the mean species frequency, and the species evenness index ($E_{\mathrm{var}}$) at the scale of a quadrat

| Factor | d*f* | Richness | | | d*f* | Species–area | | | Frequency | | | $E_{var}$ | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | SS | *F* | *P* | | SS | *F* | *P* | SS | *F* | *P* | SS | *F* | *P* |
| Exclusion | 1 | 8.51 | 4.20 | **0.041** | 1 | 0.004 | 1.1 | 0.30 | 22.5 | 3.41 | 0.067 | 0.052 | 3.1 | 0.08 |
| Year | 1 | 10.7 | 5.30 | **0.021** | 1 | 0.008 | 2.2 | 0.14 | 14.4 | 2.17 | 0.143 | 0.004 | 0.2 | 0.63 |
| Exclusion × year | 1 | 91.5 | 45.2 | <**0.001** | 1 | 0.022 | 5.8 | **0.018** | 18.0 | 2.73 | 0.101 | 0.120 | 7.2 | **0.008** |
| Error | 3,462 | 7,011 | | | 130 | 0.491 | | | 858 | | | 2.17 | | |

*SS* sum-of-squares, *F F* ratio

*P* values lower than 0.05 are shown in bold

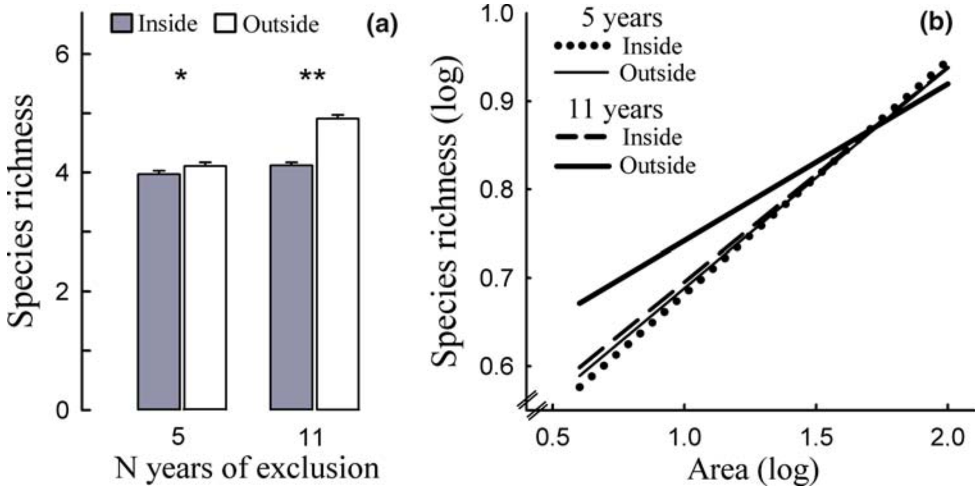

**Fig. 1** Species richness patterns of the bryophyte community inside and outside the exclosures, 5 and 11 years after goose exclusion. **a** Mean (±SE) species richness per cell (4 $cm^2$). *Asterisk* and *double asterisk* indicate a statistically significant difference with $P < 0.05$ and $P < 0.001$, respectively. **b** Log species–log area relationship within quadrats (from species richness in 4 and 10 $cm^2$ areas)

exclusion the slopes were both equally steep ($P = 0.28$; inside $0.26 \pm 0.01$; outside $0.25 \pm 0.01$ species $cm^{-2}$). It is noteworthy that the largest temporal change that we detected in the richness patterns occurred where geese were present (Fig. 1), as indicated by significant exclusion × year interactions for both the species richness and the species–area slopes (Table 1).

Species frequency tended to be lower in quadrats inside than outside the exclosures for both sampling periods, a marginally significant difference (Table 1, Fig. 2a). Species thus tended to occur in fewer cells per quadrat in areas without geese when compared to areas with geese. Changes in frequency can result from a general trend across most species in the community or from major changes in a few species. Figure 2c suggests that the lower mean species frequency inside exclosures after 11 years of exclusion was apparently due to lower frequencies of several abundant species rather than to highly species-specific effects. Finally, the effect of exclusion on the evenness index $E_{\mathrm{var}}$ changed with the year of sampling as indicated by a significant exclusion × year interaction (Table 1, Fig. 2b). Species frequencies were more even inside the exclosures after 5 years of goose exclusion ($P = 0.025$), whereas the converse was true after 11 years, although the latter effect was only marginally significant ($P = 0.093$). Figure 2b further suggests that $E_{\mathrm{var}}$ was also more variable through time in the presence of geese.

Excluding geese increased the spatial variability of species richness at larger scales (i.e. meters): the coefficient of variation (CV) of species richness between quadrats was about 30% higher inside than outside exclosures (Fig. 3b), with little variation between sampling periods (exclusion, $P = 0.02$; year, $P = 0.78$; interaction, $P = 0.63$). However, there was no consistent effect of goose exclusion between sampling period on the spatial variability of species richness at a smaller scale, i.e. among cells within a quadrat (CV, $P > 0.17$ for all factors; Fig. 3a).

Annual faeces density varied considerably through time at our study site since 1994, when the exclosures were erected (Fig. 4). These data suggest that goose abundance was very low in 1999, especially high in 2000 and 2001, and intermediate in all other years.

## Discussion

We hypothesized that the foraging activity of geese may facilitate the coexistence of bryophyte species at small

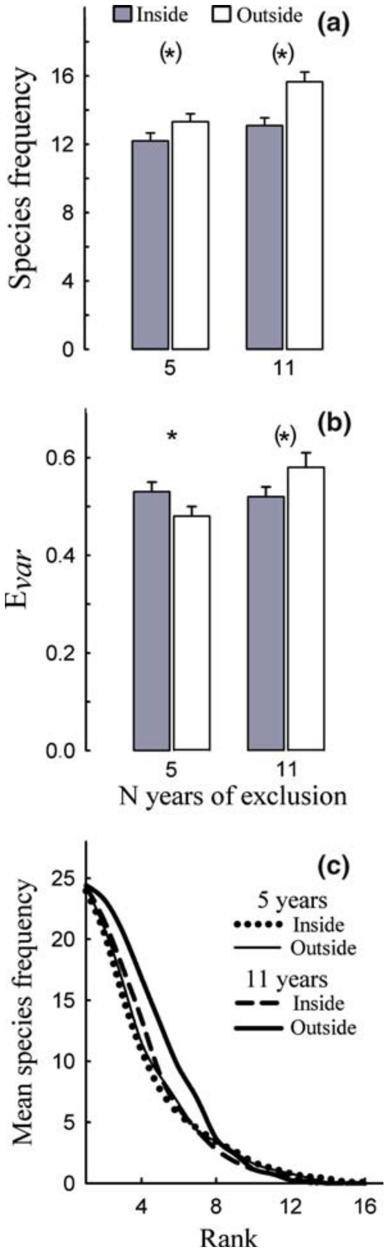

**Fig. 2** Species frequency patterns of the bryophyte community within quadrats inside and outside the exclosures, 5 and 11 years after goose exclusion. **a** Mean (±SE) species frequency. **b** Mean (±SE) evenness index $E_{var}$. *Asterisk* and *asterisk in brackets* indicate, respectively, $P < 0.05$ and $0.05 < P < 0.10$ from an ANOVA within each year. **c** Distribution of species frequencies by rank, from the most frequent (rank 1) to the least frequent species (up to rank 16). The frequency distributions were obtained by ranking species from the most to the least frequent independently for each sampling period and treatment, consequently each rank does not represent the same species across treatments/year

spatial scales in polygon fens of the tundra. We tested this idea by sampling seven exclosures that prevented geese from walking, grazing, grubbing and defecating for an 11-year period. In comparison to fenced areas, those exposed to geese showed (1) marginally higher species frequencies, (2) higher fine-scale species richness, (3) shallower species–area relationships, and (4) low spatial variability in species richness between areas 1–4 m apart (Figs. 1, 2, 3). Those results tended to be more pronounced after 11 years of goose exclusion but this was more the outcome of temporal changes in the community impacted by geese than changes inside the exclosures. These observations lend support to the hypothesis that geese promote the fine-scale coexistence of bryophyte species.

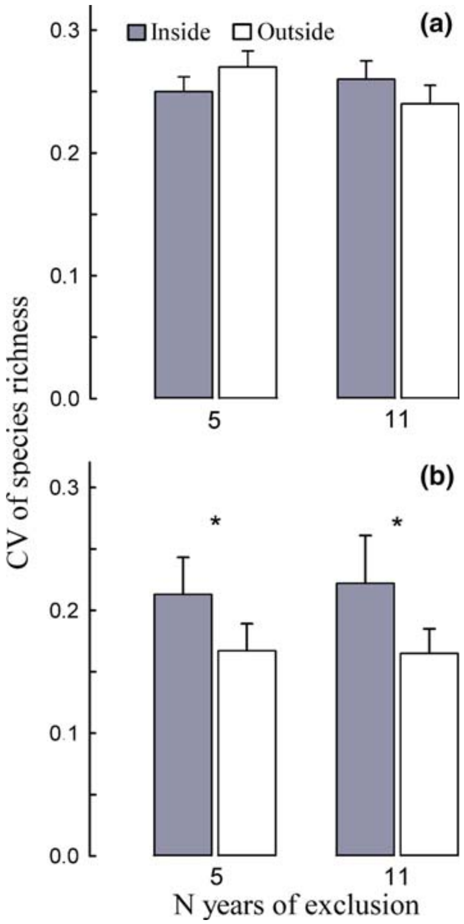

**Fig. 3** Mean (±SE) coefficient of variation of species richness between **a** cells and **b** quadrats inside and outside the exclosures, 5 and 11 years after goose exclusion. *Asterisks* indicate statistically significant differences with $P < 0.05$

Species richness in 4-cm$^2$ cells was higher outside the exclosures, especially after 11 years, but differed little at larger spatial scales (Fig. 1). This higher species richness is associated with the tendency for species frequency to also be higher outside exclosures (Fig. 2a), and it explains the shallow species–area slope observed in the presence of geese (see Lawrey 1992 for a similar observation in a different context). These effects are consistent with our hypothesis and can be summarized by a single general process; geese contribute to the spreading of individual

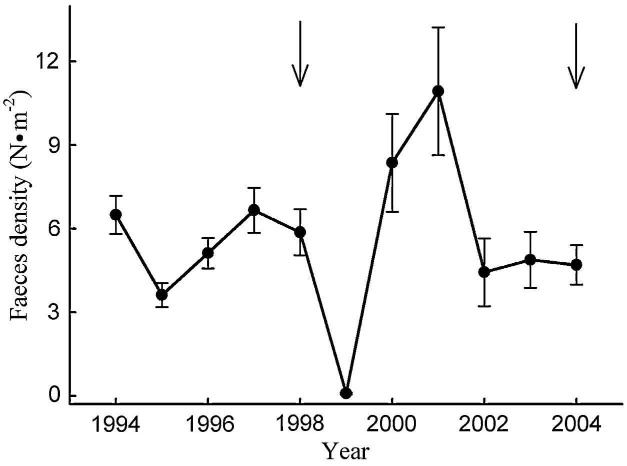

**Fig. 4** Mean (±SE) faeces density on the study site at the end of the growing season, an index of local of goose abundance. *Arrows* indicate the two bryophyte sampling periods

bryophyte species at small spatial scales, i.e. in the order of a few centimetres. To the best of our knowledge, this is the first report of such fine-scale effects of herbivory on tundra plant communities. Experiments and surveys performed at larger spatial scales generally find a positive effect of herbivory on plant diversity (Austrheim and Eriksson 2001; Pykälä 2004); however, this outcome is far from being ubiquitous (Austrheim et al. 2006 and references therein).

When geese grub for rhizomes, they typically grab a piece of moss with their bill and tear it apart before reaching for the rhizomes exposed in the hole that they just created. These holes, which are about 2–5 cm in diameter, create small perturbations in the moss carpet that may be colonized by various moss species, thereby leading to high small-scale species diversity. Our results provide evidence that this effect is transient: after a few years of goose exclusion, small scale species diversity is lower than in areas where geese remained, presumably because hole-colonizing species are excluded by their neighbors (Jonsson and Esseen 1990; Kimmerer and Young 1996). Moreover, the 45% decline in live bryophyte biomass observed after 5 years of goose exclusion at our study site (see Gauthier et al. 2004 for details on this result) may have contributed to the low small-scale species richness in the exclosures. Bryophyte total biomass and species richness seem uncoupled in our system because the difference in species diversity between inside and outside exclosures after 5 years was modest compared to the large difference in bryophyte biomass. This is surprising in light of previous experiments, in which richness generally declines commensurately with biomass (for a recent example see Olofsson and Shams 2007). A possible explanation for the apparent uncoupling between biomass and richness is that the biomass drop inside exclosure may have affected disproportionally bryophyte species with large individuals. Future work including detailed analyses of species composition will be necessary to test this hypothesis. However, the fact that species diversity at higher spatial scales (quadrat and exclosure) does not differ between areas exposed to geese or not suggests that biomass loss, which occurred over whole exclosures, is likely not the sole cause for the lower richness observed inside exclosures and that factors other than goose foraging affect these communities at larger scales.

The coefficient of variation of species richness between quadrats was consistently about 30% higher inside the exclosures both 5 and 11 years after goose exclusion (Fig. 3b), even though richness per quadrat was on average similar inside and outside the exclosures. The fact that this change occurred only at our largest spatial scale (i.e. whole exclosures, 4 × 4 $m^2$) suggests that it was probably driven by increased large-scale heterogeneity of the environment inside the exclosures. This spatially variable response in species richness may result from the uneven increase in vascular plant biomass among species (i.e. *Eriophorum* biomass increased more than *Dupontia*; Gauthier et al. 2004) and the litter accumulation that followed goose exclusion.

We found little difference in the community structure of bryophytes inside the exclosures between 5 and 11 years of goose exclusion (Figs. 1, 2, 3), which was unexpected in light of previous studies. For instance, Virtanen (2000) observed an increase in bryophyte biomass within fenced areas 5 years after lemming exclusion, followed by a decrease in the abundance of almost all lichens and bryophytes species after 11 more years of exclusion (see also Oksanen and Moen 1994). In our system, Gauthier et al. (2004) reported a large decrease in the bryophyte biomass during the second and third year after the erection of the exclosures, with a relative stability during the fourth and fifth year. Taken together these results increase the possibility that the bryophyte community inside the exclosures may have reached equilibrium during the first 4 or 5 years of goose exclusion. In contrast to the situation inside exclosures, it seems that more changes in the bryophyte community took place in areas exposed to geese between our two sampling periods. We suggest that a higher foraging activity of geese at our study site in years preceding our second sampling period may explain this change. We showed that local goose abundance varied from year to year, and was especially high in 2000 and 2001 (Fig. 4). These annual variations depend on many factors, including the annual breeding success of geese (Gauthier et al. 2004). In addition, the intensity of grubbing is highly variable in space and time following the pattern of snow-melt (Gauthier 1993, G. Gauthier, personal observation). It is thus likely that high herbivore pressure a few years before the second sampling was responsible for promoting the fine-scale coexistence of species that we observed outside the exclosures at that period.

In conclusion, our study shows that a herbivore can facilitate the fine-scale coexistence of bryophytes species. This lends support to the idea that herbivores may provide an explanation to the paradox of diversity, namely, the coexistence of species in a common habitat (Pacala and Crawley 1992). It further shows that in this bryophyte community, the average neighbor of an individual bryophyte is likely to be of a different species from its own, thus opening the door to interspecific competition. The experiment that we have reported is ongoing and future data will indicate whether the absence of herbivory for longer time periods (>15 years) can lead to more drastic community changes, such as species extirpation.

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