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# Long term effects of deer browsing and trampling on the vegetation of peatlands

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## ARTICLE INFO

### Article history:

Received 4 February 2005

Received in revised form

14 September 2005

Accepted 28 September 2005

Available online 15 November 2005

### Keywords:

Anticosti Island

Plant diversity

Herbivory

Vegetation change

White-tailed deer

## ABSTRACT

Overabundance of wild ungulates, especially exotic species, is a major threat to several ecosystems worldwide. While the response of forest vegetation to high density of herbivores has been well studied, far less is known about peatland vegetation. In this paper, we assessed the long term impact of white-tailed deer (*Odocoileus virginianus*) on plant communities of ombrotrophic (bog) and minerotrophic (fen) peatlands in eastern North America. Vegetation of five peatlands that have experienced high deer densities for at least 75 years was compared with that of five peatlands situated at proximity but on deer-free islands. We investigated deer impacts on plant species composition and cover, shrub height and cloudberry (*Rubus chamaemorus*) fruit/flower production and morphology. In bogs, white-tailed deer had no long term impact on plant species assemblages, but reduced lichen cover and increased sedges and grasses cover as well as the surface area of bare peat. On the other hand, the floristic composition of fens differed significantly between sites where deer were present or absent. Plant diversity was greater in undisturbed fens than in disturbed fens, especially for shrubs, sedges and liverworts. No detrimental effects of browsing on shrub height were observed. Conversely, deer browsing seemed to have deleterious impacts on cloudberry fruit/flower production as well as on the number of leaves per individual. Overall, our results suggest that white-tailed deer had some important impacts on the vegetation of peatlands that could be harmful for the long term conservation of peatland plant diversity.

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## 1. Introduction

During the last 50 years, several cervid populations have dramatically increased worldwide due to hunting regulations and land management practices that have augmented forage availability and reduced the number of predators (Côté et al., 2004). In many regions, overbrowsing by cervids has induced tremendous changes on forest composition and structure (Russell et al., 2001; Husheer et al., 2003; Côté

et al., 2004; Webster et al., 2005). In temperate forests of northeastern North America, heavy browsing pressure by white-tailed deer (*Odocoileus virginianus*) has limited the regeneration of many sensitive tree species and has disturbed the composition of understory communities (Cornett et al., 2000; Russell et al., 2001). For instance, the abundance of more palatable species such as *Trillium grandiflorum* is decreasing (Augustine and Frelich, 1998) while the abundance of less palatable or browse-tolerant species such

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doi:10.1016/j.biocon.2005.09.039

as ferns, grasses and sedges is increasing (Horsley et al., 2003).

Compared to other ecosystems, such as forests or grasslands, our understanding of the impacts of large herbivores on peatlands is limited. In European countries, their use by livestock is known to affect plant communities through browsing, grazing and trampling. Under grazing pressure, ericaceous shrubs cover decreases while the cover of grass and sedge species increases (Rawes and Hobbs, 1979; Rawes, 1983; Welch and Scott, 1995; Hulme et al., 2002). Browsing and grazing also reduced the growth of heathers and shrubs (Johnson and Leopold, 1998; Alonso et al., 2001) and the total vegetation biomass (Ausden et al., 2005). Plants growing on waterlogged peaty soil are easily damaged by trampling, even when subjected to low trampling intensity. Trampling reduces *Sphagnum*, lichen and liverwort cover and richness (Rawes and Hobbs, 1979; Arnesen, 1999) and increases the surface cover of bare peat (Grant et al., 1985; Arnesen, 1999). Although bare peat surfaces are sensitive to water erosion (MacGowan and Doyle, 1998), some species including *Drosera rotundifolia*, *Galium uliginosum* and *Parnassia palustris* appear favoured by trampling (Gibbons, 1992; Arnesen, 1999; Stammel and Kiehl, 2004).

The floristic and environmental changes caused by livestock management practices on peatlands have been relatively well described (Grant et al., 1985; Welch and Scott, 1995; Bullock and Pakeman, 1997; Smith et al., 2003; Ausden et al., 2005), but impacts of wild large ungulates on peatlands remain unknown. Wild herbivores are not confined to peatlands. At high densities, however, they might have detrimental effects on peatland vegetation. Anticosti Island provides an excellent opportunity to assess their long term impact on peatland vegetation due to its long history of white-tailed deer overabundance. Furthermore, peatlands on Anticosti are not subjected to artificial drainage which could mask deer effects. Since no peatland is free of deer on Anticosti, we used peatlands on Mingan Archipelago, located nearby, as control sites. Anticosti and Mingan have similar environmental conditions, but deer have never been present on the Mingan islands. We hypothesized that the overabundance of wild large herbivores has detrimental effects on peatland vegetation by decreasing: (1) its floristic diversity; (2) the ground cover of sensitive species such as lichens; (3) the height and leaf area of shrubs; and (4) the fruit/flower production as well as the number of leaves of cloudberry, a common species in North American bogs.

## 2. Methods

### 2.1. Study areas

Anticosti is a 7943 km<sup>2</sup> island located in the northern half of the Gulf of St. Lawrence (Fig. 1). The Mingan Archipelago (total area: 110 km<sup>2</sup>) includes a string of 30 islands stretching some 85 km along the North Shore of the St. Lawrence River, and is part of the Canadian National Parks network. Anticosti Island and Mingan Archipelago form a unique biological and geological unit contrasting strongly with nearest mainlands (Marie-Victorin and Rolland-Germain, 1969). Vegetation belongs to

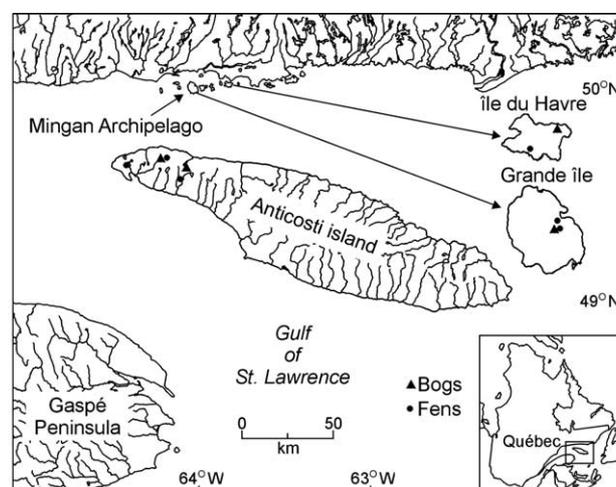


Fig. 1 – Location of study sites on Anticosti (deer) and Mingan Archipelago (no deer), eastern Québec, Canada.

the boreal zone. On mesic and xeric sites, forests are characterized by *Abies balsamea*, *Picea glauca*, *P. mariana* and *Betula papyrifera*. Large ombrotrophic peatlands (bogs), dominated by *Sphagnum* mosses and ericaceous shrubs, and minerotrophic peatlands (fens), dominated by sedges, herbs and brown mosses, are common in wet depressions. The climate is maritime with cool summers and mild and long winters. Mean annual temperatures are slightly above 0 °C (Environment Canada, 1982).

In 1896 and 1897, approximately 220 white-tailed deer were introduced to Anticosti Island and, in the absence of predation, the population irrupted in such a way that the island was considered among the over-populated deer ranges in North America in the mid-1940's (Leopold et al., 1947). Today, the population is estimated at approximately 125,000 individuals or 15–20 deer/km<sup>2</sup> (Rochette et al., 2003), which is a density typical of several regions where deer populations are increasing in North America (Boucher et al., 2004). The impacts of deer browsing on forest ecosystems of Anticosti are overwhelming. For instance, the shrub layer is practically absent and the most palatable woody browse have almost been extirpated (Pimlott, 1963; Potvin et al., 2000). Deer browsing also lead to the progressive conversion of *A. balsamea* stands into almost pure stands of *P. glauca* (Potvin et al., 2003). The only other two mammalian browsers on Anticosti are the moose (*Alces alces*) and the snowshoe hare (*Lepus americanus*). The density of moose is very low (0.04 moose/km<sup>2</sup>: Beaupré et al., 2004) and their impact on the vegetation is minimal (Potvin et al., 2003). Hare density on Anticosti is unknown. Deer have never been present on the islands of the Mingan Archipelago while moose are sporadically present. Hare density is moderate in most of the islands (Mingan Archipelago National Park Reserve of Canada, unpublished data). Climate is the main factor controlling peatland dynamics on Mingan and Anticosti because no human activities or major fires have affected them during the Holocene (Lavoie and Filion, 2001).

## 2.2. Field sampling

We surveyed three fens (7, 32 and 3 ha) and two bogs (34 and 32 ha) located in the western part of Anticosti Island and three fens (4, 3 and 8 ha) and two bogs (14 and 35 ha) on two islands of the Mingan Archipelago (Grande île: 28 km<sup>2</sup> and île du Havre: 9 km<sup>2</sup>) during July and August 2003 (Fig. 1). We selected peatlands among all open string fens and raised bogs (forest cover not exceeding 50%) that were easily accessible and surrounded by coniferous forest with no recent logging or evidence of other disturbances (wind-fall, fire). According to aerial surveys of deer conducted in summer 2001, all peatlands sampled on Anticosti had deer densities between 7.5 and 15 deer/km<sup>2</sup> (Rochette et al., 2003).

We sampled each peatland using a systematic sampling grid design. The distance between each sampling station was set at 25–50 m to obtain at least 20 stations per peatland. A total of 114 (59 and 55) and 108 (64 and 44) stations were established in bogs whereas 120 (26, 54 and 40) and 111 (46, 34 and 31) stations were established in fens of Anticosti and Mingan, respectively. Only plots located at more than 20 m from the forest edge were sampled in order to avoid the lag ecotone.

At each sampling station, we identified all plant species present in a 50 by 50 cm plot laid on the ground. We visually estimated the percent cover of lichens, bryophytes, sedges and grasses, bare peat and deer tracks according to five classes: 0; 1–25; 26–50; 51–75; and 76–100%. We used such large classes to minimize differences between observers and to ensure that the precision of our cover estimates was secondary to accuracy. We measured the height of all shrubs rooted within the plot and noted any sign of deer browsing. We did not measure the height of trees because they were scarce in all sampled peatlands. To evaluate whether the leaf area of shrubs is smaller on Anticosti than on Mingan because of deer browsing, we collected all leaves from ten *Betula pumila* individuals (randomly selected within a particular peatland) in each fen. We measured the total leaf area with an Area Meter Planimeter. We selected *B. pumila* for evaluating browsing impact on leaf area because it is a preferred browse of large herbivores (Bergerud, 1972).

At the end of the 1920s, cloudberry was the only species still producing large quantities of berries on Anticosti (Marie-Victorin and Rolland-Germain, 1969). It no longer seems to be the case because we have consistently found very few fruits and flowers of cloudberry during repeated visits to several bogs of Anticosti during the last four summers. Cloudberry is a small perennial bearing one to three leaves and a single flower. To evaluate whether the fruit production and morphology of cloudberry were affected by deer browsing, we counted the number of individuals bearing one, two or three leaves in each plot. We also separated individuals bearing a flower (or a bud) or a fruit (mature, immature and aborted) and those with no signs of flowering or fruit production.

Since the composition and structure of peatland vegetation are influenced by many local abiotic variables, we investigated some of the main parameters known to regulate peatland vegetation to ensure that the differences found between peatlands of the two regions were more likely to be

related to deer presence or absence than to environmental differences. Thus, we measured the thickness of the peat deposit, using an iron rod driven into the soil, every 50 or 100 m to obtain at least ten measures per peatland. We determined the water table depth from at least six wells located on two central transects (North/South and East/West). Wells were also separated by 50 or 100 m. A water sample (150 ml) was taken in each well for pH, conductivity and nutrient component analyses. Water samples were taken in sterilized polyethylene bottles and stored at 4 °C until analyses. The water pH was measured with an Acumet pH Meter and we determined conductivity with a Conductivity and Temperature Meter. Conductivity values were adjusted to 20 °C and corrected for the concentrations of hydrogen ions (Sjörs, 1950). We measured PO<sub>4</sub><sup>3-</sup>, NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup> contents with a flow injection ion analyser.

## 2.3. Data analyses

To evaluate if the peatlands of Anticosti and Mingan had comparable environmental conditions, we compared each abiotic variable (water table depth, water pH and conductivity, peat thickness and nutrient components) using nested analysis of variance (ANOVA). The independent variables were the peatland origin (Anticosti or Mingan) and sampling site, which had two values for bogs and three for fens, and which were nested within peatland origin. We also used nested ANOVAs to test for differences in shrub height and total leaf area of *B. pumila*. We performed ANOVAs with SAS 8.2 (SAS Institute Inc., NC, USA).

We used Mantel tests to determine if there were differences between plant species assemblages of the fens and bogs of Anticosti and those of Mingan. Mantel tests measure the association between elements of two similarity matrices (Sokal and Rohlf, 1995). The observed similarity matrix was compared to a model similarity matrix that was constructed with zeros for comparisons between geographic regions and with ones for comparisons within regions. We used the Steinhaus similarity index, which takes into account occurrence and does not include species that are absent in pairwise comparisons, to calculate similarities in the observed matrix (Legendre and Legendre, 1984). We calculated occurrence as the percentage of sampling stations where a species was present; all species were included in our calculations. A positive and significant association between the two matrices indicates that species similarity is greater within regions than between regions. Mantel tests were performed with 5000 permutations using XLStat 7.5 (Addinsoft, NY, USA).

To determine whether lichens, bryophytes, sedges and grasses as well as bare peat cover are affected by deer, comparisons of the frequency distribution of their cover classes between Anticosti and Mingan were made using Chi-square goodness-of-fit tests ( $\chi^2$ ). Similar analyses were used to compare between the two regions the frequency of cloudberry bearing one, two or three leaves, and a fruit or a flower. Analyses were performed with Statgraphics 3.0 (STSC Inc., MD, USA). ANOVAs and Mantel tests were considered to indicate significant differences when *p* values were less than 0.05 whereas the results of Chi-square tests were considered

significant when  $p < 0.01$  to account for the non-independence of the plots.

### 3. Results

#### 3.1. Environmental characteristics

The peat deposit thickness and the water table depth did not differ between bogs of Anticosti and Mingan (Table 1). Water chemistry values of bogs on Anticosti were also similar to those of Mingan, with the exception of some  $\text{NH}_4^+$  enrichment and higher water conductivity on Anticosti compared to Mingan. All environmental variables were similar for the fens of the two regions (Table 1).

#### 3.2. Plant species assemblages

We recorded a total of 59 species in bogs of Anticosti and Mingan, but most of them were only scarcely present (Appendix 1). The most common species on Anticosti in terms of occurrence in plots were *Chamaedaphne calyculata*, *D. rotundifolia*, *Kalmia angustifolia*, *Kalmia polifolia*, *Rhododendron groenlandicum*, *Rubus chamaemorus* and *Vaccinium oxycoccos*. On Mingan, the most common species were *C. calyculata*, *K. angustifolia*, *R. groenlandicum* and *R. chamaemorus*. Twelve and 15 species were restricted to bogs on Anticosti and Mingan, respectively. On Anticosti, however, none of those was present in more than 10% of the sampling plots. On Mingan, four species, *Cetraria islandica*, *Cephalozia lunulifolia*, *Geocaulon lividum* and *Myrica gale*, occurred in more than 10% of the sampling plots.

Bog species assemblages did not differ between Anticosti and Mingan ( $r = 0.37$ ,  $p = 0.34$ ). Lichens, however, were more frequently found on Mingan (all species occurrence: 86%) than on Anticosti (all species occurrence: 58%;  $\chi^2 = 29.6$ ,  $p < 0.001$ ). Furthermore, *D. rotundifolia*, that is known to be favoured by trampling was more common in bogs on Anticosti (occurrence: 94%) than on Mingan (occurrence: 53%;  $\chi^2 = 40.2$ ,  $p < 0.001$ ). Finally, *K. polifolia*, an unpalatable species (Kings-

bury, 1964), was also more common on Anticosti (occurrence: 93%) than on Mingan (occurrence: 68%;  $\chi^2 = 11.5$ ,  $p < 0.01$ ).

We recorded a total of 131 species in fens, but few had a widespread occurrence (Appendix 1). The most common species on Anticosti were *Andromeda polifolia*, *Campylyum stellatum*, *Dasiphora floribunda*, *M. gale*, *Trichophorum caespitosum* and *V. oxycoccos*. On Mingan islands, the most common species were *A. polifolia*, *C. stellatum*, *D. floribunda* and *M. gale*. Nineteen species were found only in fens on Anticosti, whereas 39 species were restricted to fens on Mingan. Only *Warnstorfia fluitans* occurred in more than 10% of sampling plots on Anticosti, whereas *Carex sterilis*, *Empetrum nigrum*, *Eriophorum angustifolium*, *K. polifolia* and *Mitella nuda* were present in more than 10% of the plots on Mingan.

The assemblages of plant species in fens on Anticosti differed significantly from species assemblages in fens of Mingan ( $r = 0.56$ ,  $p = 0.03$ ). The main difference was the higher species richness in fens of Mingan compared to Anticosti, especially for shrubs (12 Anticosti, 20 Mingan), sedges (13 Anticosti, 19 Mingan) and liverworts (1 Anticosti, 5 Mingan). Furthermore, most palatable species including *Maianthemum trifolium* and *Rhamnus alnifolia* (Bergerud, 1972; Kasworm et al., 1984) were found more often on Mingan than on Anticosti ( $\chi^2 = 12.9$ ,  $p < 0.001$  and  $\chi^2 = 12.1$ ,  $p < 0.001$ , respectively) (Appendix 1). On the other hand, genus known to be favoured by trampling, such as *Parnassia*, were found more frequently on Anticosti (occurrence: 54%) than on Mingan (occurrence: 25%;  $\chi^2 = 20.1$ ,  $p < 0.001$ ).

#### 3.3. Strata cover

On Anticosti, we found deer tracks in approximately 38% and 16% of the sampling plots in bogs and fens, respectively. In fens, track cover never exceeded 25% while 11% of the sampling plots in bogs had a track cover exceeding 25%, suggesting that deer used bogs more often than fens (Fig. 2).

Lichen, bryophyte, sedge and grass, and bare peat cover differed significantly between bogs on Anticosti and Mingan

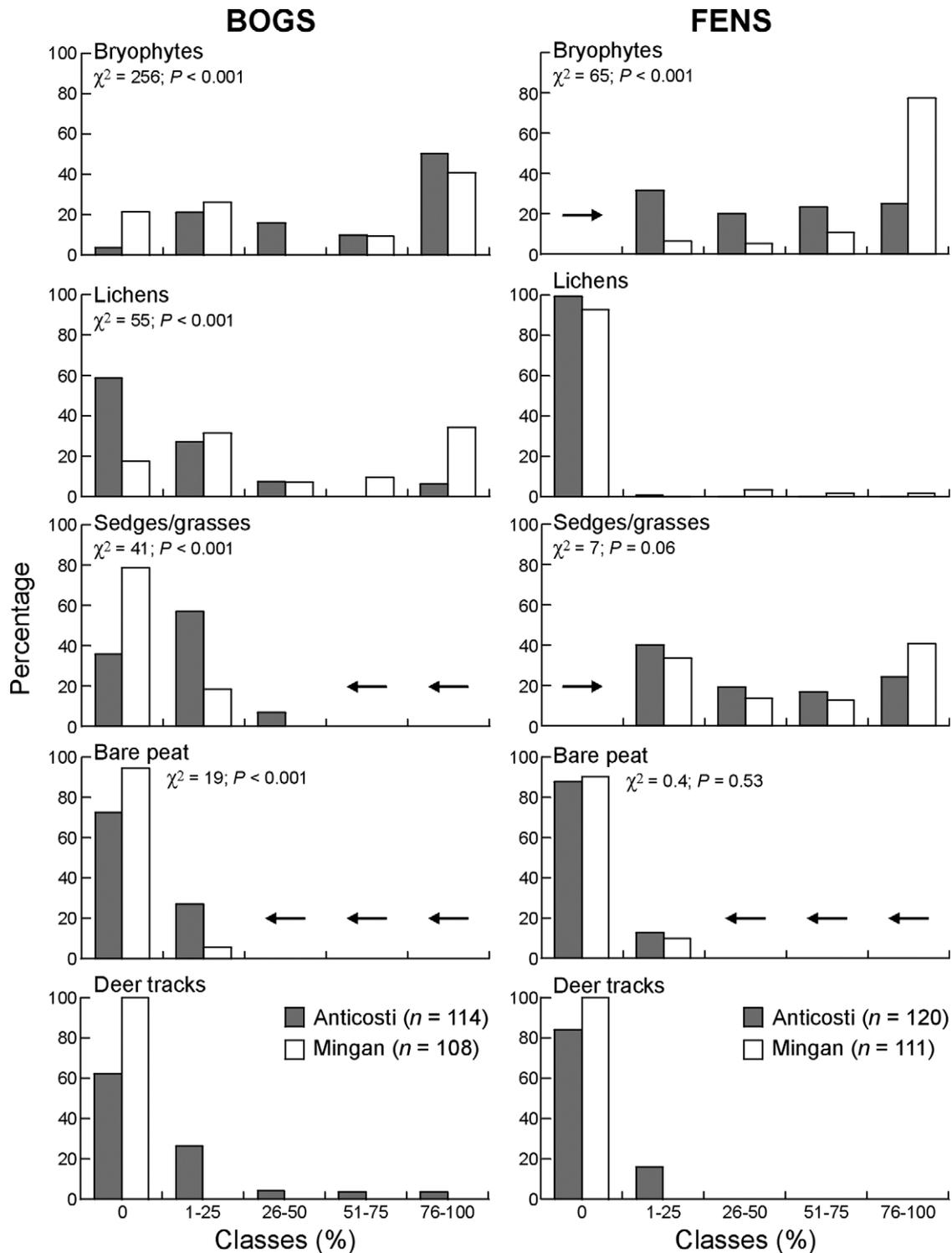
**Table 1 – Differences in mean ( $\pm$ SD) environmental variables between bogs and fens of Anticosti (deer) and Mingan Archipelago (no deer). Values of F and p are from nested analyses of variance comparing Anticosti and Mingan**

	Peat thickness <sup>a</sup> (cm)	Water table depth <sup>b</sup> (cm)	Conductivity <sup>b</sup> ( $\mu$ S)	Water chemistry <sup>b</sup>			
				pH	$\text{PO}_4^{3-}$ (mg/L)	$\text{NH}_4^+$ (mg/L)	$\text{NO}_3^-$ (mg/L)
<b>Bogs</b>							
Anticosti	280 $\pm$ 95	16 $\pm$ 3	23 $\pm$ 2	4.3 $\pm$ 0.1	0.06 $\pm$ 0.03	0.36 $\pm$ 0.17	0.01 $\pm$ 0.00
Mingan	280 $\pm$ 180	19 $\pm$ 9	19 $\pm$ 3	4.3 $\pm$ 0.1	0.05 $\pm$ 0.01	0.18 $\pm$ 0.08	0.01 $\pm$ 0.01
F	0.22	5.24	27.23	0.97	0.31	80.9	0.09
p	0.68	0.15	0.03	0.43	0.63	0.01	0.79
<b>Fens</b>							
Anticosti	190 $\pm$ 70	4 $\pm$ 4	225 $\pm$ 129	6.6 $\pm$ 0.3	0.03 $\pm$ 0.03	0.18 $\pm$ 0.22	0.07 $\pm$ 0.10
Mingan	100 $\pm$ 50	6 $\pm$ 6	319 $\pm$ 64	6.9 $\pm$ 0.2	0.04 $\pm$ 0.03 <sup>c</sup>	0.19 $\pm$ 0.18	0.04 $\pm$ 0.05
F	7.49	0.53	1.02	1.50	0.99	0.14	0.24
p	0.05	0.51	0.37	0.29	0.52	0.73	0.65

a Bogs: Anticosti, n = 60; Mingan, n = 59. Fens: Anticosti, n = 40; Mingan, n = 30.

b Bogs: Anticosti, n = 22; Mingan, n = 18. Fens: Anticosti, n = 21; Mingan, n = 23.

c One outlier was removed for the analysis.



**Fig. 2** – Percentage distribution of bryophytes, lichens, sedges and grasses, bare peat and deer tracks in bogs and fens of Anticosti (deer) and Mingan Archipelago (no deer). Differences between sites were tested with chi-square tests. Arrows indicate that data were grouped in the previous or the following classes. Lichens in fens were too rare to allow statistical analysis.

(Fig. 2). Lichen cover was greater in bogs on Mingan than on Anticosti. On the other hand, sedge and grass cover as well as bare peat cover were greater in bogs of Anticosti than in bogs of Mingan. Ground cover of sedges and grasses as well

as bare peat cover did not differ between fens on Anticosti and Mingan (Fig. 2). In contrast, bryophyte cover was greater in fens on Mingan than in fens on Anticosti. Lichens were almost absent in the fens of both areas.

3.4. Shrub height and leaf area

We measured a total of 1406 (640 Anticosti, 766 Mingan) and 1464 (666 Anticosti, 798 Mingan) shrubs in the plots of bogs and fens, respectively (Fig. 3). All shrub species were browsed by deer on Anticosti, even species reported to be unpalatable to deer such as *K. polifolia*. However, we did not find any significant difference between Anticosti and Mingan in the height of shrubs growing in bogs and in fens (Fig. 3). Finally, the total leaf area of *B. pumila* was much smaller on Anticosti ( $46 \text{ cm}^2 \pm 31 \text{ SD}$ ,  $n = 30$ ) than on Mingan ( $290 \text{ cm}^2 \pm 230$ ,  $n = 30$ ;  $F = 16.5$ ,  $p < 0.01$ ).

3.5. Cloudberry

Cloudberry occurred in 85% of the sampling plots in bogs of both study areas. We counted a total of 2675 ( $23 \pm 21 \text{ SD}$  per plot) and 2188 ( $20 \pm 18$  per plot) individuals in bogs on Anticosti and Mingan, respectively. The frequency of individuals bearing one, two or three leaves differed between regions ( $\chi^2 = 337$ ,  $p < 0.001$ ,  $n = 4863$ ). We found a higher proportion of cloudberry bearing one leaf on Anticosti (80%) than on Mingan (58%). Moreover, the proportion of individuals bearing three leaves was 18 times smaller on Anticosti (0.3%) than on Mingan (5.8%). Few individuals bore a fruit or a flower in

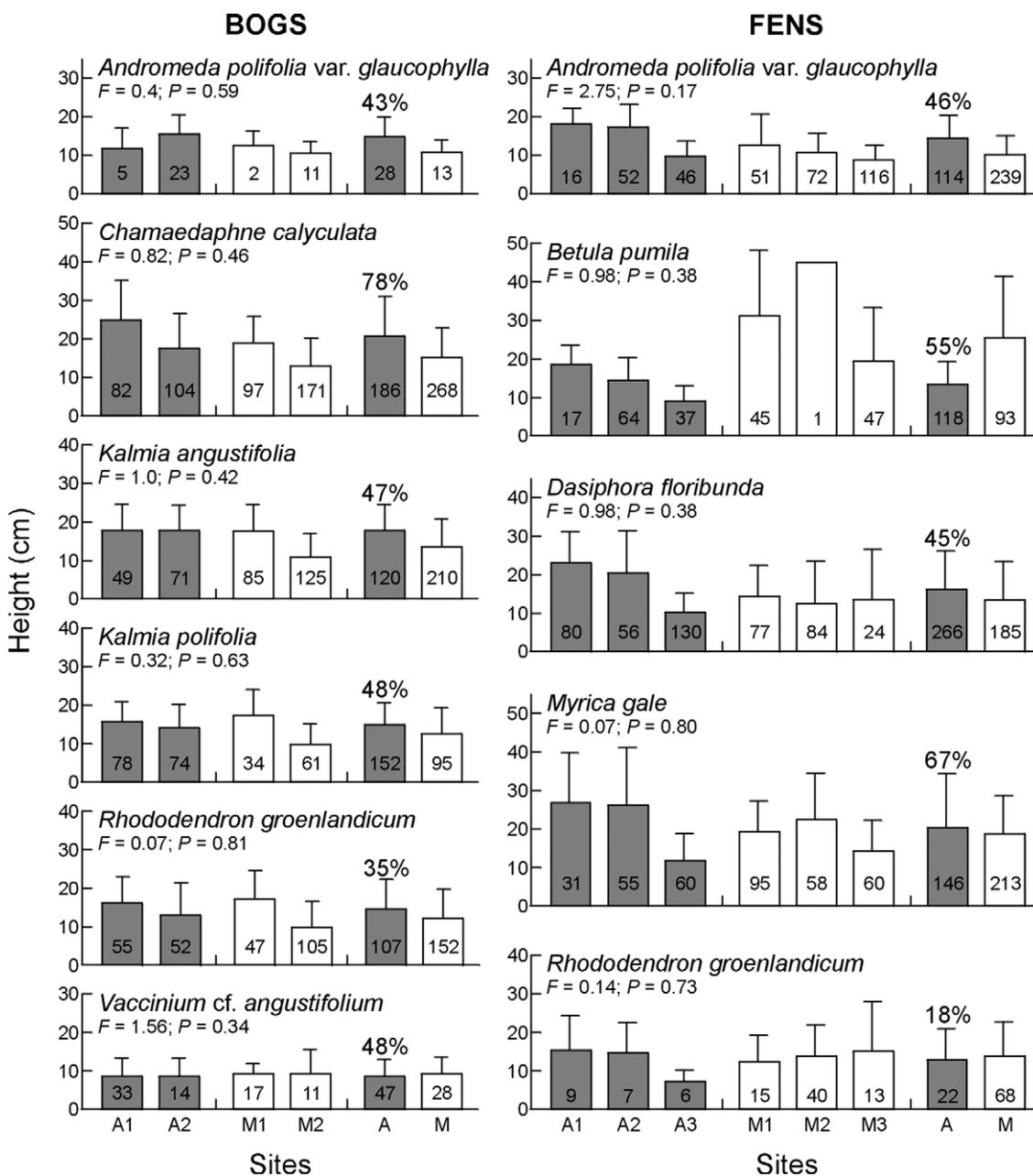


Fig. 3 – Mean shrub height ( $\pm \text{SD}$ ) of the most abundant shrub species in bogs and fens of Anticosti (A and grey; deer) and Mingan Archipelago (M and white; no deer). The number of shrub individuals measured, and used for statistical analyses, is indicated for each studied peatland. Differences between sites were tested with nested ANOVAs. For Anticosti, the percentage of individuals with at least one evidence of deer browsing is also indicated.

both areas, but there were 5 times less individuals bearing a fruit or a flower on *Anticosti* (4%) than on *Mingan* (18%;  $\chi^2 = 275$ ,  $p < 0.001$ ,  $n = 493$ ).

## 4. Discussion

In non-experimental studies such as this one, the presence of association does not necessarily imply a causal relationship. Factors other than the one hypothesized (here the difference in deer browsing and trampling pressure) may be responsible for the observed differences. In this study, we examined some of the most important physical parameters known to influence vegetation in North American peatlands (Vitt and Chee, 1990; Payette and Rochefort, 2001) and we indeed found significant differences in  $\text{NH}_4^+$  concentration and water conductivity in bogs. Deer might have induced this nutrient enrichment through dung and urine deposition (Bullock and Pakeman, 1997; Welch, 1997; but see Van Hoewyk et al., 2000). However, if that was the case we would have expected to observe the same pattern in fens, which was not the case. Thus, we conclude that the observed differences in bogs were probably due to another factor than deer. Although the results for  $\text{NH}_4^+$  concentration and water conductivity were statistically significant, they were within the natural range of variability found within homogeneous peatlands in North America (Vitt and Chee, 1990; Wind-Mulder and Vitt, 2000), and thus they are probably not important enough to induce major differences in plant communities. The main difference between the peatlands of the two regions appears therefore to be the presence or absence of deer. Consequently, we argue that the dissimilarity observed in peatland vegetation is likely the result of the deer introduction on *Anticosti*, although we do not exclude the possibility that some differences could also be attributed to natural variability.

### 4.1. Deer effects on bog vegetation

In bogs, white-tailed deer browsing and trampling had no detectable long term impacts on plant species assemblages. Most of the species in bogs are unpalatable to vertebrate herbivores (Mason and Standen, 1983), and this may perhaps explain the absence of any significant impact. Although the floristic composition of bogs did not differ between regions with and without deer, our results did show differences in the relative occurrence and cover of some species. The most important discrepancy between the two regions was the reduced cover of lichen mats in peatlands disturbed by deer. This result is consistent with a previous study conducted in four other peatlands of the same study areas which demonstrated that lichen cover was two times greater in bogs of *Mingan* than in bogs of *Anticosti* (Viera, 2003). Several studies, especially in arctic and subarctic ecosystems, have also shown a decrease in lichen cover and diversity following trampling by large herbivores (e.g. Bayfield et al., 1981; Manseau et al., 1996). In *Anticosti*, most of the lichen mats surveyed showed signs of trampling disturbance (Pellerin, unpublished data). Although lichens have the ability to regrow from broken thalli, this growth is slower than that of intact thalli (Cooper et al., 2001). In bogs, growth rates of lichens are much lower than those of *Sphagnum* mosses

(Vasander, 1981). Thus, it is likely that *Sphagnum* colonies are overgrowing the lichen mats disturbed by deer and accelerating the decline of most of the lichens in bogs of *Anticosti*.

Deer trampling also negatively impacted bogs by destroying surface vegetation and increasing bare peat cover. The presence of bare peat in bogs usually increases surface run-off, initiates water erosion and further prevents plant re-establishment (MacGowan and Doyle, 1998). On *Anticosti*, no indices of surface run-off or erosion channels were observed, indicating that bogs were probably only subjected to low levels of trampling. Low trampling may be favourable to various plants in bogs. For instance, in Europe, the density of *D. rotundifolia*, was greater in areas subjected to sporadic trampling than in untrampled or severely trampled areas (Gibbons, 1992; Dupieux, 1998). In our study, the occurrence of *D. rotundifolia* was also greater in trampled (94%) than in untrampled (53%) bogs. *Drosera* occurrence in trampled bogs was probably favoured by the formation of small wet furrows created by deer hoof pressure because this plant species is usually confined to very humid habitats (Crowder et al., 1990).

### 4.2. Deer effects on fen vegetation

Plant species assemblages of fens differed between *Anticosti* and *Mingan* Archipelago. Species richness was greater in fens not subjected to deer browsing and trampling than in fens used by deer. These results suggest that white-tailed deer have deleterious effects on the floristic composition of fens. However, the natural diversity of plant species between fens is high, much more so than between bogs (Poulin et al., 2002). Thus, we cannot fully rule out the possibility that some of the observed differences between fens of the two study areas are due to natural variability, although deer browsing and trampling probably accounted for most of the discrepancies. Indeed, most of the differences we found, such as the greater occurrence of more palatable species on *Mingan* where deer are absent, are usually ascribed to a direct effect of herbivory (Hulme et al., 2002; Horsley et al., 2003). Furthermore, lower bryophyte cover as well as liverworts diversity, are usually attributed to trampling (Arnesen, 1999; Stammel and Kiehl, 2004). Overall, the long term impacts of deer on vegetation appear more important in fens than in bogs, although we observed fewer deer tracks in the former. However, the dominant species in fens, especially sedges and grasses, are much more tolerant to trampling than those on bogs, particularly *Sphagnum* mosses (Sun and Liddle, 1993). Deer are therefore more likely to leave tracks in bogs than in fens, and so deer feeding activity is probably more intense on fens than deer tracks indicate.

### 4.3. Deer effects on shrub height

All shrub species, even those unpalatable or considered to be poisonous such as *K. angustifolia*, were browsed by deer on *Anticosti* Island. Such browsing probably reflects the high abundance of deer on the island and/or the critical reduction or extirpation of more palatable species in forest habitat. Although nearly half of the shrub individuals of peatlands on *Anticosti* were browsed, we did not observe detrimental effects of browsing on their growth. This phenomenon might

be linked to some extent to overcompensatory growth following browsing (Paige and Whitham, 1987). In browsed bogs, some  $\text{NH}_4^+$  enrichment may also have favoured shrub growth. Finally, although deer browsing did not significantly reduce shrub height, the total leaf area of *B. pumila* was considerably lower on Anticosti than on Mingan islands.

#### 4.4. Deer effects on cloudberry plants

The occurrence of cloudberry did not differ between browsed and unbrowsed bogs. This probably reflects the adaptation of this species that reproduces mainly by rhizomes (Taylor, 1971). Conversely, the morphology of cloudberry plants appeared greatly influenced by deer because individuals growing in regions subjected to browsing had fewer leaves than those on deer-free islands. Such an effect may reflect the extirpation of more palatable species in Anticosti since cloudberry leaves are usually grazed only when alternative and more palatable forage is deficient (Taylor, 1971). Deer browsing also appeared to be detrimental to flowering and fruit production since there were fewer individuals bearing a flower or a fruit in browsed peatlands than on unbrowsed peatlands. Similar results were reported by Taylor and Marks (1971) for a bog that had been subjected to grazing by sheep in the British Isles. However, cloudberry flower and fruit production, and especially fruit abortion, are known to vary greatly from year to year (Jean and Lapointe, 2001). High levels of fruit abortion in cloudberries are usually the result of frost and insufficient pollination (Ågren, 1988, 1989). In our study, we took into account aborted fruits in our calculations, which should reduce to some extent the inter-annual variations. Differences observed between browsed and unbrowsed peatlands are therefore likely to be due to deer browsing. Moreover, on Mingan the percentage of floral ramets (18%) was near the average percentage of floral ramets (20–30%) for cloudberry growing in northern Quebec (Dumas and Maillette, 1987; Jean and Lapointe, 2001). Finally, the effect of deer on the total number of flowers and fruits is probably a direct impact of cropping instead of a consequence of defoliation. Indeed, it has been shown that defoliation has no influence on fruit production in cloudberry (Ågren, 1989).

#### 4.5. Implications for conservation

The results of our study suggest that high densities of free ranging wild ungulates could have negative impacts on the vegetation of peatlands. However, the impacts we found were less important than those observed with domestic ungulates on European peatlands, likely because peatlands on Anticosti are protected from deer browsing and trampling by snow cover between mid December and late April which is not always the case for European peatlands, especially in British Islands.

Anticosti island is a significant component in Quebec's provincial conservation strategy. Two Biodiversity Reserves (UICN category Ia) and one National Park (UICN category II), extending over 61,400 ha, have been established on the island. Peatlands represent about 35% of their area, and more than 65% of the area of all protected peatlands in Quebec (Poulin and Pellerin, 2001). To achieve the conservation objectives of these protected areas, we recommend: (1) a regular monitoring of the composition of their plant community because no moni-

toring has been conducted since their establishment; and (2) if major changes are observed, management actions such as fencing and perhaps subsequent reductions in deer density. Such actions are presently experimented in forested habitats on the island (Côté et al., in press). Outside those protected areas, we also recommend to include peatlands in fenced deer exclosures that are presently established to protect regeneration of forests. To reduce the cost of fencing, peatlands are currently avoided when exclosures are built.

#### Acknowledgements

Our research was financed by The Natural Sciences and Engineering Research Council of Canada and Produits forestiers Anticosti. We are grateful to Parks Canada for providing numeric maps and field logistics while we worked at The Mingan Archipelago National Park Reserve. We thank M. Renière, S. De Bellefeuille, and V. Viera for field assistance and M. Garneau and C. Roy of the Louis-Marie Herbarium, as well as D. Morin of the Ministère des Ressources Naturelles et de la faune du Québec, for their help with plant identification. S. Daigle and P. Legendre of the Université of Montréal helped with statistical analyses, and A. Buttler, F. Fournier, P. Hulme, M. Lavoie, M. Poulin and two anonymous reviewers made helpful comments on earlier drafts of the manuscript.

#### Appendix 1

**Occurrence (% of all plots) of all species recorded on bogs and fens of Anticosti (A = deer) and Mingan Archipelago (M = no deer)**

	Bogs <sup>a</sup>		Fens <sup>b</sup>	
	A	M	A	M
<b>Trees</b>				
<i>Abies balsamea</i>				1
<i>Betula papyrifera</i>		2		
<i>Larix laricina</i>	17	3	38	25
<i>Picea mariana</i>	19	24	9	1
<b>Shrubs</b>				
<i>Andromeda polifolia</i> var. <i>glaucophylla</i>	33	9	77	68
<i>Betula pumila</i>		2	35	41
<i>Chamaedaphne calyculata</i>	98	98	14	8
<i>Dasiphora floribunda</i>			73	65
<i>Empetrum nigrum</i>	54	76		12
<i>Gaultheria hispidula</i>				1
<i>Juniperus communis</i>				3
<i>Juniperus horizontalis</i>			6	22
<i>Kalmia angustifolia</i>	83	90	6	6
<i>Kalmia polifolia</i>	93	68		15
<i>Myrica gale</i>		14	61	72
<i>Nemopanthus mucronatus</i>				2
<i>Rhamnus alnifolia</i>			13	32
<i>Rhododendron groenlandicum</i>	83	86	13	28
<i>Salix candida</i>				1

(continued on next page)

Appendix 1—continued				
	Bogs <sup>a</sup>		Fens <sup>b</sup>	
	A	M	A	M
<i>Salix vestita</i>				3
<i>Vaccinium angustifolium</i>	37	29		3
<i>Vaccinium macrocarpon</i>		2	3	3
<i>Vaccinium oxycoccus</i>	85	63	70	32
<i>Vaccinium uliginosum</i>	2		3	1
Cyperaceae				
<i>Carex aquatilis</i>			15	5
<i>Carex buxbaumii</i>				1
<i>Carex capillaris</i>	4		6	2
<i>Carex echinata</i>				1
<i>Carex exilis</i>			26	23
<i>Carex flava</i>			12	1
<i>Carex gynocrates</i>				7
<i>Carex interior</i>				2
<i>Carex lasiocarpa</i>			19	6
<i>Carex leptalea</i>				1
<i>Carex limosa</i>				3
<i>Carex livida</i>		2	48	37
<i>Carex rariflora</i>		3		
<i>Carex rostrata</i>				4
<i>Carex stricta</i>				9
<i>Carex sterilis</i>				23
<i>Carex viridula</i>			7	7
<i>Eriophorum angustifolium</i>				18
<i>Eriophorum vaginatum</i> var. <i>spissum</i>	4	7		
<i>Eriophorum viridicarinatum</i>				1
<i>Rhynchospora alba</i>				1
<i>Trichophorum alpinum</i>			5	23
<i>Trichophorum caespitosum</i>	56	20	63	59
Herbs/forbs				
<i>Arethusa bulbosa</i>			4	
<i>Calamagrostis canadensis</i>				1
<i>Campanula rotundifolia</i>				5
<i>Cirsium muticum</i>				1
<i>Comandra umbellata</i>			3	8
<i>Conioselinum chinense</i>				3
<i>Coptis trifolia</i>	2		2	3
<i>Cornus canadensis</i>	2		10	8
<i>Drosera anglica</i>			2	
<i>Drosera intermedia</i>			6	8
<i>Drosera rotundifolia</i>	94	53	25	24
<i>Dryopteris carthusiana</i>				1
<i>Elymus repens</i>				1
<i>Epilobium palustre</i>				1
<i>Equisetum arvense</i>			10	7
<i>Equisetum fluviatile</i>			8	
<i>Eurybia radula</i>			10	9
<i>Galium labradoricum</i>			21	3
<i>Galium palustre</i>				7
<i>Geocaldon lividum</i>		12	7	7
<i>Iris versicolor</i>				9
<i>Juncus arcticus</i>				10
<i>Linnaea borealis</i>			18	23
<i>Lobelia kalmii</i>			8	5

Appendix 1—continued				
	Bogs <sup>a</sup>		Fens <sup>b</sup>	
	A	M	A	M
<i>Maianthemum trifolium</i>	6	5	18	39
<i>Malaxis unifolia</i>			1	1
<i>Melampyrum lineare</i>			3	3
<i>Menyanthes trifoliata</i>			20	21
<i>Mitella nuda</i>				13
<i>Muhlenbergia glomerata</i>			16	18
<i>Packera paupercula</i>			16	24
<i>Parnassia glauca</i>			54	25
<i>Pinguicula vulgaris</i>			25	17
<i>Platanthera dilatata</i> var. <i>dilatata</i>			1	5
<i>Platanthera hookeri</i>				1
<i>Primula mistassinica</i>			3	9
<i>Pyrola minor</i>				2
<i>Rorippa islandica</i>			2	
<i>Rubus arcticus</i> ssp. <i>acaulis</i>			43	13
<i>Rubus chamaemorus</i>	85	85		
<i>Rubus pubescens</i>			1	1
<i>Sanguisorba canadensis</i>			33	24
<i>Sarracenia purpurea</i>	20	22	22	32
<i>Scheuchzeria palustris</i>			3	3
<i>Selaginella selaginoides</i>			44	34
<i>Solidago uliginosa</i>			19	9
<i>Taraxacum officinale</i>			3	
<i>Thalictrum alpinum</i>			33	23
<i>Thalictrum pubescens</i>			3	2
<i>Tofieldia glutinosa</i>	2		31	33
<i>Trientalis borealis</i>			1	2
<i>Triglochin maritimum</i>			3	10
<i>Viola cucullata</i>			4	
<i>Viola nephrophylla</i>			8	5
<i>Zigadenus elegans</i> ssp. <i>glaucus</i>				5
Mosses				
<i>Aulacomnium palustre</i>				2
<i>Campylium stellatum</i>			73	76
<i>Dicranum bonjeanii</i>			2	
<i>Dicranum fuscescens</i>				3
<i>Dicranum leioneuron</i>	9	22	3	
<i>Dicranum polysetum</i>				4
<i>Dicranum undulatum</i>	28	7	3	3
<i>Drepanocladus aduncus</i>			16	27
<i>Fissidens osmundioides</i>			3	2
<i>Helodium blandowii</i>			3	2
<i>Limprichtia revolvens</i>			12	25
<i>Paludella squarrosa</i>				7
<i>Pleurozium schreberi</i>	4	12		3
<i>Pohlia nutans</i>	9	29		
<i>Polytrichum strictum</i>	2	15	2	2
<i>Rhizomnium punctatum</i>				2
<i>Rhytidiadelphus triquetrus</i>			2	
<i>Sphagnum angustifolium</i>	2			
<i>Sphagnum capillifolium</i>	6			1
<i>Sphagnum fuscum</i>	76	53	1	4
<i>Sphagnum girgensohnii</i>		3		
<i>Sphagnum magellanicum</i>	6	7	2	

**Appendix 1–continued**

	Bogs <sup>a</sup>		Fens <sup>b</sup>	
	A	M	A	M
<i>Sphagnum rubellum</i>	39	27	3	1
<i>Sphagnum russowii</i>		3	13	2
<i>Sphagnum subsecundum</i>			4	
<i>Sphagnum teres</i>			3	
<i>Sphagnum warnstorffii</i>			8	15
<i>Scorpidium scorpioides</i>			16	1
<i>Tomenthypnum nitens</i>			3	20
<i>Warnstorffia fluitans</i>			13	
<b>Liverworts</b>				
<i>Aneura pinguis</i>				3
<i>Calypogeia muelleriana</i>	2			1
<i>Cephalozia lunulifolia</i>		14		
<i>Cladopodiella fluitans</i>	11	5		
<i>Kurzia pauciflora</i>	6	7		
<i>Lophocolea heterophylla</i>	2			2
<i>Lophozia rutheana</i>	2			2
<i>Mylia anomala</i>	72	54	1	3
<i>Ptilidium ciliare</i>	4	4		
<b>Lichens</b>				
<i>Cetrariella delisei</i>		2		
<i>Cetraria islandica</i>		25		
<i>Cladina arbuscula</i>	4			
<i>Cladina mitis</i>	2	15		
<i>Cladina rangiferina</i>	20	46		5
<i>Cladina stellaris</i>	20	53		2
<i>Cladonia crispata</i>	2			
<i>Cladonia wainioi</i>		2		
a Number of plots in bogs: Anticosti, n = 114; Mingan, n = 108.				
b Number of plots in fens: Anticosti, n = 120; Mingan, n = 111.				

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