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Chronic deer browsing leads to biotic homogenization of minerotrophic peatlands

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Abstract: Peatlands could become important foraging habitats, and their plant communities threatened, in areas with an overabundance of large herbivores. Peatland response to herbivore exclusion may vary widely according to abiotic conditions and associated species, due to a strong minerotrophic gradient. We assessed the impact of white-tailed deer (*Odocoileus virginianus* Zimm.) on peatland vegetation using an enclosure experiment. A total of 53 pairs of enclosures and unprotected plots were set up in bogs (13 pairs), sedge fens (20), shrub fens (7) and laggs (13), and surveyed prior to enclosure construction as well as three, five and eight years after. Vascular plant composition of enclosures diverged from that of unprotected plots through time only in shrub fens and laggs. Bryophytes remained constant in all habitats. On average, shrub cover was 30% higher in enclosures in all habitats after five years, while herb cover increased only in laggs, by 43%, after eight years. Reclassification of sites by pH showed deer exclusion promoted alpha diversity in low- and high-moderate rich fens (pH 5.3-6.8) and beta diversity in the latter as well as in rich fens (pH 6.3-7.5). Overall, our results suggest that conservation efforts in areas with overabundant large herbivores should target richer peatland habitats since they showed a higher resilience and fostered alpha and beta diversity.

Key words: bogs, fens, herbivory, laggs, vegetation change, deer exclusion

Résumé : Les tourbières pourraient représenter des habitats importants pour les grands herbivores dans des conditions de surpopulation, ce qui pourrait affecter leur végétation. Caractérisées par un fort gradient de minérotrophie, la réponse des tourbières suivant l'exclusion des herbivores peut varier grandement selon leurs conditions abiotiques et les

espèces associées. Nous avons évalué l'impact du cerf de Virginie (*Odocoileus virginianus* Zimm.) sur la végétation des tourbières à l'aide d'un dispositif d'exclos. Cinquante-trois exclos appariés à des parcelles non-protégées du broutement ont été échantillonnées dans des bogs (13), des fens à *Carex* (20), des fens arbustifs (7) et des laggs (13) avant, ainsi que trois, cinq et huit ans après l'instauration des exclos. Avec le temps, la composition des plantes vasculaires dans les exclos divergeait de celle des parcelles non-protégées seulement pour les fens arbustifs et les laggs. Le couvert des bryophytes est resté stable dans tous les habitats. Le couvert des arbustes était 30% plus important dans les exclos (tout habitat confondu) après cinq ans alors que le couvert des herbacées était de 43% plus élevé après 8 ans. Les sites ont été reclassifiés selon leur pH pour tester l'effet de l'exclusion du cerf le long du gradient minérotrophique. L'exclusion du cerf a engendré une plus grande diversité alpha dans les fens intermédiaires (pH 6.3-6.8) et une plus grande diversité beta dans les fens intermédiaires et riches (pH 6.3-7.5). Globalement, nos résultats suggèrent que les efforts de conservation dans les régions à fortes densités de cerfs devraient cibler les tourbières riches puisqu'elles ont montré une plus grande résilience et une diversité végétale locale et régionale accrue suivant l'arrêt du broutement.

Mots-clés: bogs, fens, herbivorie, laggs, changements floristique, cerf de Virginie

Introduction

In recent decades, many large herbivore populations have increased substantially worldwide, inducing tremendous changes in native ecosystems (Côté et al. 2004). The impacts of overabundant herbivores on forests and grasslands have been studied widely, and include altered plant composition and diversity due to reduced abundance and biomass of preferred species, and increased cover of browsing-tolerant or resistant species (e.g., Rooney and Waller 2003; Tremblay et al. 2007; Mayer et al. 2009; Beguin et al. 2011; Goetsch et al. 2011; Waller 2014). The impacts of large herbivores on peatlands are much less understood. Yet, for wild ungulates, peatlands may represent significant alternative habitats for foraging activities, especially in temperate and boreal regions of North America where populations are overabundant (Massé and Côté 2009) and peatlands widespread.

Most studies on the impacts of large herbivores on peatlands have focused on grazing domestic herbivores (Rawes and Hobbs 1979; Rawes 1983; Ausden et al. 2005). The long-term impacts of grazing and trampling by sheep and cattle in peatlands depend on several factors, such as season of use and management history (Smith et al. 2003), but in general include a reduction in cover and richness of bryophytes (Arnesen 1999; Stammel and Kiehl 2004) and in total vegetation biomass (Ausden et al. 2005), while stoloniferous grasses, sedges and rosette forbs increase in abundance and biomass (Rawes and Hobbs 1979; Rawes 1983; Birnie and Hulme 1990; Ward et al. 2007). Fewer studies have investigated the impact of browsers (but see Johnson and Leopold 1998; Pellerin et al. 2006), a type of herbivore with broad diet niches, specialized in digesting woody plants (Hofmann 1989). In that regard, the specific study by Pellerin et al. (2006) showed that white-tailed deer (*Odocoileus virginianus*), a selective browser, changed plant species composition of

minerotrophic peatlands (fens), but not ombrotrophic ones (bogs), although the latter had a reduced lichen cover and an increased sedge and grass cover when deer were present. Unbrowsed fens also had higher species richness, especially for shrubs and sedges.

Aside from the variation associated with herbivore species, the impact of herbivores on peatlands could vary in relation to local abiotic conditions and plant traits. Peatlands are characterized by a strong minerotrophic gradient, from bogs to extreme-rich fens (Szumigalski and Bayley 1996), along which plant composition and production vary strongly. Herb production or net productivity generally increase along the minerotrophic gradient while decreasing for shrubs (Szumigalski and Bayley 1996; Thormann and Bayley 1997; Moore et al. 2002). The rate of nutrient cycling and N/C ratio in plant tissue increase with minerotrophy, and plants in rich fens should have lower constitutive defences against herbivores since such strategies are fostered in poorer environments (Bryant et al. 1983; Koricheva et al. 1998). These factors combined could promote higher herbivory in fens than in bogs (Mattson 1980). On the other hand, fens could have a higher ability to recover from herbivory than bogs because of higher nutrient availability (Maschinski and Whitham 1989; Wise and Abrahamson 2005). In addition, minerotrophic ecotones between open peatland expanses and adjacent mesic forests, commonly called laggs (Howie and Tromp-van Meerveld 2011), often have a thinner peat deposit than bogs (Paradis et al. 2015). This should facilitate plant recovery after aerial biomass browsing because roots and rhizomes left in place have more direct access to nutrients in the underlying mineral soil. Fens also show a higher abundance of graminoid plants, which are known to have a strong capacity for compensatory growth through basal intercalary meristems (Haukioja and Koricheva 2000). Fens could thus be more resistant or resilient to browsing compared to bogs, but to

our knowledge, no studies have evaluated variation in herbivory or recovery abilities after herbivore control or exclusion along a minerotrophic peatland gradient.

Species richness also varies along the minerotrophic gradient in peatlands and may influence the response of bogs and fens to browser exclusion as ecosystem resilience is thought to be greater within species rich communities (Peterson et al. 1998; Folke et al. 2004; Downing et al. 2012). The few studies that have investigated species diversity over the bog-rich fen gradient point toward either a unimodal response with greater diversity in intermediate to rich fens (Johnson and Leopold 1994; Locky and Bayley 2006), higher diversity in extremely rich fens (Vitt et al. 1995) or, more widely, toward higher diversity in fens compared to bogs (Wheeler 1993; Warner and Asada 2006). Yet, these studies focused mostly on site diversity (alpha-diversity), whereas peatland beta diversity remains basically unexplored. Beta diversity refers to the variation of species composition among sites, and is now recognized as an important component of evaluations of biodiversity loss as well as conservation and management planning (Gering et al. 2003). Overabundant large herbivore populations have been shown to foster biotic homogenization (i.e., an increase in the similarity of communities across space and time) of ground and sapling layers in forests or shrublands (Rooney et al. 2004; Rooney 2009; Schumacher and Carson 2013; Perea et al. 2014), and in meta-communities including grasslands and forests (Ohashi and Hoshino 2014), but their impacts on diversity can vary along abiotic gradients (Austrheim and Eriksson 2001; Bakker et al. 2006; Speed et al. 2013). In grasslands, large herbivores have been shown to increase plant diversity on sites with high productivity, but to decrease diversity on sites with low productivity (Bakker et al. 2006). Because biotic homogenization is considered an important cause of global diversity loss (McKinney and Lockwood 1999) and is associated with decreased ecosystem stability and resilience (Olden

et al. 2004), the impact of herbivores on the homogenization process is of great interest, notably under variable environmental conditions.

The presence of white-tailed deer at high density on Anticosti Island for several decades, the abundance of peatlands and the absence of human disturbance on these wetlands provide a unique opportunity to evaluate the response of peatlands to herbivore exclusion. We set up a deer exclosure experiment in four habitat types (bogs, sedge fens, shrub fens and laggs) and assessed the response of vegetation over eight years. More specifically, we hypothesized that the response of peatlands to deer exclusion would be intimately associated with the minerotrophy of such habitats. Specifically, we predicted that, after deer exclusion, plant communities would diverge from browsed communities in minerotrophic habitats (fens and laggs), but not in nutrient-poor bogs, either because of the greater attractiveness of fens and laggs for deer, compared to bogs, or because of a higher recovery rate in rich habitats. In addition, we expected that herbs and shrubs would be favored by deer exclusion, with the former responding more strongly at high pH and the latter at low pH. Finally, we expected that beta diversity would be greater under deer exclusion than on browsed sites, this difference increasing with peatland minerotrophy, since browsing is likely to intensify on more minerotrophic sites.

Methods

Study area

Our study was carried out on Anticosti Island (7943 km²), located in the Gulf of St. Lawrence in Quebec, Canada (49°28'N; 63°00'W). The climate is maritime and generally humid, with total annual precipitation of 917 ± 130 mm (mean ± standard deviation) and a mean temperature varying from a minimum of about -12°C in February to a maximum of about 16°C in July (Environment Canada 2006). The island's present-day

forests belong to the eastern *Abies balsamea* (L.) Mill.-*Betula papyrifera* Marshall bioclimatic subdomain (Saucier et al. 2009). The original forests were composed of *A. balsamea*, *Picea mariana* (Mill.) B.S.P., *Picea glauca* (Moench) Voss and deciduous species such as *B. papyrifera* (Lavoie and Fillion 2001). Approximately 220 white-tailed deer were introduced on Anticosti Island at the end of the 19th century, and proliferated rapidly in the absence of predators. Today, the deer population reaches a density >20 deer per square kilometre and up to 56 deer per square kilometre locally (Tremblay et al. 2007). Chronic deer browsing has drastically modified forest composition by causing the quasi-disappearance of the shrub layer and most deciduous species, and compromising the regeneration of *Abies balsamea*, which are being gradually replaced by *Picea glauca* (Potvin et al. 2003; Barrette et al. 2010).

Large bogs and fens are common in wet depressions, covering about 25% of the island (Massé and Côté 2009). Since these peatlands have never been exploited or drained, the effects of browsing on them could not be confounded with anthropogenic disturbances. Peatlands selected for the study are located in the western part of the island, where deer density varies between 19 and 24 deer per square kilometre (Rochette and Gingras 2007). We selected four types of habitat that are common on the island: bogs, sedge fens, shrub fens and laggs. Habitats were segregated according to their general vegetation composition. Bogs are dominated by *Sphagnum* mosses and ericaceous shrubs, fens by sedges, herbs and brown mosses. Tall trees were virtually absent from bogs and fens. We further differentiated between sedge and shrub fens according to a threshold of 25% of shrub cover. Laggs are the transition zone between an ombrotrophic bog and the mineral soils of the surrounding landscape. When they are present, they are usually characterized by high water level and nutrient availability, shallow peat of relatively low hydraulic conductivity

and unique ecotonal species (Howie and Tromp-van Meerveld 2011; Paradis et al. 2015). They are recognized as minerotrophic and dominated by fen vegetation, usually with dense shrub and tree covers. On Anticosti Island, laggs are dominated by graminoids, sedges, deciduous shrubs and coniferous trees such as *P. mariana* and *Larix laricina* Du Roi K. Koch. In a previous study, it was found that deer use laggs for movements and foraging activities three times more than bogs and two times more than fens (Massé and Côté 2009).

Experimental design and sampling

In 2007, 4 m² exclosures were established in 13 bogs, 20 sedge fens, 7 shrub fens and 13 laggs. Each exclosure was paired with a similar area in close proximity (ca. 5 m) within the same peatland and used as a control browsed plot (hereafter, unprotected plot) representing in-situ deer density. Overall, there were a total of 106 plots distributed by pairs on 53 sites. When staking out plots, trees and saplings were avoided due to their height compared to the small (2 × 2 m), low (1.22 m) dimensions of exclosures. Deer tracks were also avoided so as not to confuse the effect of browsing with that of trampling. The mesh size of the fences was small enough (1.5 inch) to prevent snowshoe hare (*Lepus americanus*) intrusion.

Vegetation was sampled in July 2007 (prior to exclosure construction), 2010, 2012 and 2015 in a 1 m² plot centered within each exclosure and unprotected plot. The cover of all plant species was estimated to the nearest 1% between 0-10% and 90-100%, otherwise to the nearest 5%. In 2015, the height of the most abundant herbaceous species was measured (3 individuals of each species in each plot). The presence of any flower or fruit was also noted. Surface water pH was also assessed in 2015 using a portable handheld probe (HI98129 pH/Conductivity/TDS Tester, Hannah Instruments, Model #98129) at a single location between paired plots.

Data analyses

Changes in vegetation composition over time

We used Principal Response Curves (PRC) to describe the temporal shifts in vegetation composition in response to browsing cessation (Van den Brink and Ter Braak 1999). PRC is a type of partial redundancy analysis that represent a response (vegetation composition) of a given treatment (exclosures) as a deviation from a comparison benchmark (unprotected plots) along a time axis. An independent PRC was performed for each habitat, with vascular plants and bryophytes analysed separately. To account for the double-absence of species, a Hellinger transformation was applied to species cover data (Legendre and Gallagher 2001). To consider the paired structure of the design, we first conducted an analysis of variance (ANOVA) on the cover of each species using pairs as random factor and then used the residuals to run the PRC. In complement to the PRC, we compared the change in plant composition between exclosures and unprotected plots for each year after the set-up of the experiment using a linear mixed model. For this analysis, site scores along the first axis of the PRC were used as response variables, and treatment and time elapsed since the beginning of deer exclusion as explanatory variables. Normality and homogeneity of variance assumptions were verified and a model with heterogeneous variances for the year was used when necessary (shrub fens and laggs). Spatial (site) and temporal (year) correlation, including time nested within the spatial variables (repeated measures), were used as random factors (Alday and Marrs 2014). A Bonferroni correction was applied to account for multiple year comparisons (four years; $\alpha = 0.0125$; Sokal and Rohlf 1995).

Vegetation structure

Cover of shrubs, herbs and bryophytes was estimated by summing the cover of all species for each stratum for each site. The effects of deer exclusion on cover as well as on

herb height were evaluated by repeated measures ANOVA (Supplementary data, Table S1). When the interaction between deer browsing and type of habitat or time was significant, a Protected Fisher's Least Significant Difference (LSD) test was performed to compare values among the habitats or among years. Cover of all vegetation types was log-transformed to comply with the normality assumption of the parametric tests, and a model with heterogeneous variances for the types of habitats was used when necessary (shrub fens).

Minerotrophic gradient and alpha and beta diversity

Because beta diversity involved comparisons between groups of sites, the exclosures (53) and unprotected plots (53) were reclassified into four groups using a k-means non-hierarchical partitioning analysis of pH values. The pH of the surface water of the first group ranges between 2.8 and 4.2 (bogs: 13 sites), between 5.3 and 6.2 for the second (low moderate rich fens: 6 sites), between 6.3 and 6.8 for the third (high moderate rich fens: 23 sites) and between 6.9 and 7.5 for the fourth group (rich fens: 11 sites; Zoltai and Vitt 1995). These four groups were then used to evaluate whether deer browsing reduced plant alpha and beta diversity in peatlands and whether this process was related to site minerotrophy. Only 2015 data on vascular species was used for this analysis.

For each pH-based site group, we calculated both the species richness (S) and Shannon index (H' ; Shannon and Weaver 1963). Differences in beta diversity along the minerotrophic gradient and between deer browsing levels were analysed using tests of homogeneity for multivariate dispersions (Anderson et al. 2006). A site-by-site distance matrix was first used to compute the centroid of each group of sites (eight groups: four minerotrophic levels and two deer browsing levels). The distance of each site (plot) to its associated group centroid was then calculated. The site-by-site distance matrices required

for this test were computed with the percentage difference dissimilarity measure because it accounts for species abundance, circumvents the double-absence problem (Legendre and Gallagher 2001) and is recommended for testing biotic homogenization (Olden and Rooney 2006). The square root of dissimilarities was calculated to obtain Euclidean matrices. Normality and homogeneity of variance assumptions were reached after transformation. To test the effect of site minerotrophy and deer browsing levels on alpha and beta diversity analyses, we used a linear mixed model with browsing and pH levels as a fixed factor and sites as a random factor.

PRC as well as richness, alpha and beta diversity analyses were performed in R (R Core Team 2016), using respectively *prc*, *specnumber*, *diversity* and *betadisper* in the *vegan* package (Oksanen et al. 2016). Linear mixed model analyses were performed using the *nlme* package (Pinheiro et al. 2016) and k-means cluster analyses using the *kmeans* function of the *stats* package (R Core Team 2016). Statistical analyses of structure (strata cover and herb height) were performed using the MIXED procedure in SAS software (SAS Institute Inc. 2012).

Results

Changes in vegetation composition over time

Vascular species composition of exclosures diverged from that of unprotected plots through time, but only in shrub fens and lags (Fig. 1). Changes in composition of exclosures in these two habitats were pronounced soon after deer exclusion, slowed down for two years and then intensified again during the last three years of the survey. Yet, only after eight years of deer exclusion did composition differ significantly between unprotected plots and exclosures (Fig. 1). The exclusion of deer did not change bryophyte composition of peatlands, as no significant difference between exclosures and unprotected plots was

found at any time in any habitat (Table S2; Fig. S1). The succession in exclosures of shrub fens and laggs was attributed to seven species that benefitted from deer exclusion (positive scores on the right vertical axis), among them *Sanguisorba canadensis* L. and *Betula pumila* L. On the other hand, five to seven species including *Dasiphora fruticosa* (L.) Rydberg, *Trichophorum cespitosum* (L.) Hartman, *Carex flava* L. and *C. aquatilis* Wahlenberg were associated with browsing in shrub fens and laggs.

Vegetation structure

The exclusion of deer promoted shrub expansion equally in all habitats (habitat-deer interaction: $F_{[3,49]} = 0.08$, $p = 0.97$) and the effect intensified with time (deer-year interaction: $F_{[3,286]} = 3.22$, $p = 0.02$) (Fig. 2; see complete results in Table S3). Mean shrub cover was about 30% higher in exclosures than in unprotected plots after both five ($F_{[1,286]} = 8.4$, $p = 0.004$) and eight years ($F_{[1,286]} = 12.1$, $p = 0.0006$). Herbaceous cover responded to deer exclusion only in laggs, where their cover was 43% greater in exclosures than in unprotected plots (Fig. 3; $F_{[1,49]} = 34.65$, $p = < 0.0001$), and the impact of deer exclusion seemed to increase with time, although this trend was not significant (deer-time interaction $F_{[3,294]} = 2.15$, $p = 0.09$; Table S4). Regarding height, the 12 herbaceous species measured in 2015 were 70% taller in exclosures (mean 32 cm) than in unprotected plots (mean 19 cm) of laggs (Fig. 4; $F_{[1,39]} = 37.5$, $p < 0.0001$), and there was a similar tendency in shrub fens ($F_{[1,39]} = 3.2$, $p = 0.08$; Fig. 4; Table S5). Furthermore, we observed that two of the herbaceous species flowered only in exclosures: *Sanguisorba canadensis* (2 flowers) and *Thalictrum pubescens* Pursh (16 flowers).

Alpha and beta diversity

Although species richness increased with site minerotrophy ($F_{[3,49]} = 24.81$, $p < 0.0001$), there was no effect of deer browsing ($F_{[1,49]} = 1.15$, $p = 0.11$; Table S6). On the other hand,

deer impacted alpha diversity (Shannon index), but this varied according to site minerotrophy (pH-deer interaction; $F_{[3,49]} = 3.00$, $p = 0.04$; Table S7). More precisely, there was a significant increase in alpha diversity following deer exclusion in low moderate rich sites (pH of 5.3 to 6.3; $F = 5.43$, $p = 0.02$; Fig. 5) and high moderate rich sites (pH of 6.3 to 6.8; $F = 9.24$, $p = 0.004$). Beta diversity followed a unimodal hump-shaped relationship with minerotrophy for both exclosures (quadratic contrast, $p = 0.0004$) and unprotected plots ($p = 0.002$) and was highest at high moderate rich sites (pH of 6.3 to 6.8; Fig. 5). Beta diversity was higher in exclosures than in unprotected plots on more minerotrophic sites (pH > 6.3), eight years after initiation of deer exclusion ($F = 7.29$, $p = 0.01$; $F = 15.37$, $p = 0.0003$; Fig. 5, Table S8).

Discussion

Changes in vegetation composition over time

As predicted, the response of peatlands to deer exclusion was strongly linked to site minerotrophy: only shrub fens and lags showed divergent plant communities between exclosures and unprotected plots, after eight years of deer exclusion. The lack of response of sedge fens is likely due to the abundance of graminoid plants. Although graminoids can compose more than 50% of white-tailed deer diet in early spring (Huot 1982), they are particularly tolerant to herbivory because of their capacity for compensatory growth through basal intercalary meristems (Haukioja and Koricheva 2000). Under high herbivory pressure, graminoids can, however, prevent plant community recovery after deer exclusion and even be associated with alternative successional trajectories (Hidding et al. 2013). In bogs, the absence of vegetation change through time could be related to less herbivory pressure, because plants in nutrient-poor environments usually contain more defence compounds than those in nutrient-rich environments (Bryant et al. 1983; Koricheva et al.

1998). In the context of high deer density, however, deer have been shown to browse even species they usually avoid (Pellerin et al. 2006; Lefort et al. 2007): high rates of browsing have been measured on ericaceous species of Anticosti (78% for *Chamaedaphne calyculata* (L.) Moench, 48% for *Kalmia angustifolia* L., 47% for *Kalmia polifolia* Wangenheim, 43% for *Andromeda glaucophylla* Link, 35% for *Rhododendron groenlandicum* (Oeder) Kron and Judd; Pellerin et al. 2006). On the other hand, plants in bogs could be less tolerant to herbivory than plants in fens due to lower nutrient availability and associated reduced recovery abilities (Maschinski and Whitham 1989; Wise and Abrahamson 2005); as well, more than eight years may be necessary to detect any recovery from herbivory in bogs. Direct browsing measurements in bogs and sedge fens would nevertheless make it possible to clarify whether the lack of response after deer exclusion is rather associated with a low initial rate of plant consumption or slow recovery after browsing.

No response was observed in bryophytes after deer exclusion. Trampling by large herbivores in peatlands has previously been shown to induce changes in bryophyte diversity and cover, especially in the wettest portions of peatlands, due to the destruction of plants and compaction or sinking of living mosses in the peat deposit (e.g., Pellerin et al. 2006; Groome and Shaw 2015), *Sphagnum* mosses being particularly sensitive to trampling (e.g., Studlar 1980; Arnesen 1999). However, the impacts of herbivores on bryophytes are usually limited to tracks, whereas these were avoided when setting up exclosures and paired unprotected plots.

Although the use of PRC for assessing changes in plant communities following restoration is only emerging (Poulin et al. 2013), this technique made it possible to identify the main species responsible for the observed changes in shrub fens and lags with a clear

statistical evaluation of each species' contribution. In shrub fens, the changes in plant communities after deer exclusion were driven by palatable species such as *Sanguisorba canadensis* L. and *Betula pumila* L. The former is a highly palatable forb found in calcareous fens (Bergerud 1972). Its flowers were observed in two exclosures, in 2012 and 2015. Similar observations were reported in Shenandoah National Park (USA), where this species was found to have a greater cover and 33% more flowering plants in deer exclosures than in controls in a fen after two years (National Park Service 2010). As for *Betula pumila*, a deciduous shrub highly palatable for large herbivores (Bergerud 1972), its total leaf area has been previously shown to be six times smaller on Anticosti Island than on the nearby deer-free Mingan Archipelago (Pellerin et al. 2006). Among the species characterizing unprotected plots of shrub fens and laggs, *Dasiphora fruticosa* is a shrub resistant to herbivores (Lovaas 1958; Elkington and Woodell 1963) but known to be highly browsed on Anticosti Island (Pellerin et al. 2006), likely due to the scarcity of other resources, as suggested by Elkington and Woodell (1963). Five graminoid species remained associated with browsing in both shrub fens and laggs, reinforcing comments above concerning the high ability of these plants to persist in browsed environments (Stockton et al. 2005; Rooney 2009; Bachand et al. 2015).

Vegetation structure

Shrub cover responded positively to deer exclusion, regardless of habitat type. Contrary to our prediction, this reveals that browsing on shrubs occurred in all habitats and that minerotrophy did not influence the capacity of shrubs to respond after deer exclusion. Similarly, shrub cover expansion (Middleton 2002; Middleton et al. 2006) and densification (McShea et al. 2000) or shoot elongation (Johnson and Leopold 1998) following deer exclusion have been previously observed in some peatlands, while other studies found no

change when comparing regions with or without deer browsing history (Pellerin et al. 2006). On the other hand, we found that herbs benefitted only in lags where there was an increase in both their cover and height after deer exclusion. Prior to exclusion, lags not only showed the highest cover of herbs compared to other habitats; but also higher mineral and nutrient contents, due in part to runoff from adjacent mineral soils, which could have fostered herb recovery (Paradis et al. 2015). The peat deposit was also thinner in lags (mean 75 cm) than in other peatland types (mean 174 cm), which could have favored root access to the underlying mineral soil layer (Glaser et al. 1990) and thus herbaceous growth when deer browsing was suppressed. Alternatively, deer browsing could be more important in lags because the high nutrient availability usually generates high nutritional quality, as suggested by the carbon-nutrient balance hypothesis (Bryant et al. 1983; Koricheva et al. 1998). Again, direct measurements of browsed vegetation and direct analyses of plant quality would be required to validate either hypothesis. The lack of response of bryophytes in all habitats could be attributed to low recovery ability or to low browsing, as for herbs in bogs and fens, but could also be attributed to the fact that their cover was difficult to evaluate. We suspect that the main effect of year ($F_{[3,290]} = 3.78$, $p = 0.01$) was intimately linked with the capacity of observers to distinguish moss carpets from bare peat, especially under standing water.

Alpha and beta diversity

Although species richness was not influenced by deer exclusion, we showed that both alpha and beta diversity increased after deer exclusion, but only on more minerotrophic sites. Studies investigating the impact of herbivores on species diversity of peatlands have mostly considered grazing livestock on managed sites. Grazing suppression in calcareous fens of Wisconsin (USA) raised species richness for four years, after which richness

converged toward that found on heavily and lightly browsed sites (Middleton 2002); fens that had never been grazed were even poorer in species. In contrast, species richness was reduced by grazing in managed calcareous fens in Germany (Stammel et al. 2003).

In regard to beta diversity, many studies have revealed that large herbivores can induce biotic homogenization in forests (Rooney 2009; Holmes and Webster 2011) and in shrublands (Perea et al. 2014), but to our knowledge, no study has assessed their impact on plant diversity in relation to site minerotrophy. The increase in herbaceous production along this gradient may have contributed to the increase in beta diversity after deer exclusion on our study sites (Maschinski and Whitham 1989; Wise and Abrahamson 2005). Yet, in other ecosystems such as prairies and rangelands, large herbivores have been shown to have a positive impact on plant diversity at high plant productivity (Osem et al. 2002; Frank 2005; Bakker et al. 2006), potentially by limiting competition for light through biomass removal. This is less likely to occur in stressful environments, such as waterlogged peatlands, for which facilitation interactions have been shown to be more important than competition (Bertness and Callaway 1994; Calaway 2007; Maestre et al. 2009). The increase in beta diversity after deer exclusion on more minerotrophic sites in our study may therefore rather be associated with the variability of site conditions. Indeed, rich fens and laggs are highly influenced by water seepage from surrounding landscapes, whereas bogs are fed by atmospheric water supply alone (Wieder and Vitt 2006). Deer exclusion can therefore allow the establishment of a more diverse herbaceous flora in richer peatlands than in bogs, simply because recolonizing species will be adapted to local conditions, which vary among sites. Under browsing pressure, these species could indeed persist in the seed bank and help regenerate plant communities after deer exclusion, as a high proportion

of herb species of standing vegetation has been associated with the seed bank in fens in particular (Valkó et al. 2011).

Conclusion

Our study showed that herbivores can impoverish the flora of peatlands both locally and regionally, but that richer sites are resilient to browsing. Discrepancies between exclosures and unprotected plots were indeed more important in shrub fens and lags than in bogs and sedge fens. Bogs may be resistant to browsing because they harbor few palatable species, while sedge fens may be resilient to browsing due to high compensatory growth of graminoids under the continuous presence of herbivores. These peatland habitats may also have a lower resilience when deer are excluded due to a slow response of plant communities, but studies with a longer time-frame will be needed to evaluate this aspect. Richness and diversity results also suggest that conservation efforts in regions with overabundant large herbivores should focus on richer peatland habitats to promote alpha and beta diversity. Although our study was conducted in a boreal region where white-tailed deer are usually not overabundant, we believe our results could also apply to temperate regions where peatlands are abundant and situated close to forests exposed to high deer densities. For example, deer populations are high in the St. Lawrence lowlands (Huot and Lebel 2012) where peatlands still cover as much as 10% of the area (Poulin et al. 2016) and are surrounded by mixed or deciduous forests. Newfoundland (Canada), also hosts similar contexts where forests and peatlands co-occur and cervid densities are high (Gosse et al. 2011). Finally, our study improves our understanding of the influence of minerotrophy on the capacity of ecosystems to respond to disturbances. Peatlands are indeed valuable model

ecosystems in this regard, as their pH can vary from 3.6 to 7 within a single region and allow comparison of browsing treatments over a range of minerotrophy.

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Figure captions

Fig. 1. Principal response curves representing changes in vascular plant composition between exclosures and unprotected plots by white-tailed deer over time for all types of peatland habitats (Anticosti Island). The proportion of variance explained by the first axis of the PRC is indicated in parentheses. Species on the right-side vertical axis are listed according to their respective score in the PRC, which indicates how each species is correlated with the curves. Only species with a score >0.2 are shown. Asterisks indicate significant differences of plant composition between exclosures and unprotected plots (shrub fen: $t = 2.8$, $p = 0.01$; lagg: $t = 3.6$, $p = 0.001$). For a complete list of species for each habitat, see Table S9 to S12.

Fig. 2. Shrub cover in peatlands (Anticosti Island), all habitats combined. Least squares means $\pm$ SE of the original data of the interaction between deer and habitats are presented. Significant differences were determined with Fisher's Least mean differences test (* = $p < 0.05$; ** = $p < 0.01$).

Fig. 3. Herbaceous and bryophyte covers in the four types of peatland habitat (Anticosti Island), all years combined. Least squares means $\pm$ SE of the original data of the interaction between deer and habitats are presented. Significant differences were determined with Fisher's Least mean differences test (* = $p < 0.05$; ** = $p < 0.01$).

725

726 **Fig. 4.** Herbaceous plant height in the four types of peatland habitat (Anticosti Island), all
727 years combined. Least squares means $\pm$ SE of the original data of the interaction between
728 deer and habitats are presented. Significant differences were determined with Fisher's
729 Least mean differences test (* = $p < 0.05$; ** = $p < 0.01$). See Table S4 for a list of the 12
730 species for which height was measured.

731

732 **Fig. 5.** Influence of browsing and minerotrophy (determined using water pH) on alpha
733 diversity (Shannon index) and beta diversity in peatlands of Anticosti Island. Beta
734 diversity was measured as the average distance between sites and their group (water pH)
735 centroid in exclosures and unprotected plots eight years after deer control. Least squares
736 means $\pm$ SE of the original data of the interaction between deer and group of pH are
737 presented; comparisons of exclosures and unprotected plots were performed for the four
738 groups of pH. Significant differences were determined by Fisher's Least mean
739 differences test (** for $P < 0.01$).

Fig. 1

Fig. 2

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Fig. 3

Fig. 4

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