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NOTE

Compositional and functional trajectories of herbaceous communities after deer density control in clear-cut boreal forests

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Abstract: Overabundant populations of large herbivores have strong persistent effects on forest composition, structure, and function. However, the mechanism through which plant communities recover their original composition and function after herbivore management remains poorly understood. We assessed the temporal trajectories of the herbaceous communities in *Abies balsamea* (L.) Mill. and *Picea glauca* (Moench) Voss stands on Anticosti Island (Quebec, Canada) over 8 years following clear-cutting and deer management. The impact of deer exclusion or reduction to 7.5 and 15 deer·km^{-2} was compared with benchmark in situ deer densities (27 and 56 deer·km^{-2}). Effects of deer management treatments on plant species and functional trait assemblages over time were assessed using principal response curves. Although complete deer exclusion seemed necessary to modify species composition from that occurring under intense browsing, a reduced density of 7.5 deer·km^{-2} was sufficient to induce significant changes in functional trait assemblages of regenerating stands. For instance, reduced deer densities favored plants with brightly colored flowers and compound inflorescences pollinated by animals and producing large seeds and fleshy fruits dispersed by animals. We conclude that the boreal forest's herbaceous communities are resilient to chronic browsing when deer population reduction and forest clearcutting are applied in synergy.

Key words: resilience, species composition, functional traits, plant–herbivore interactions, deer.

Résumé : Les populations surabondantes de grands herbivores ont des effets majeurs et persistants sur la composition, la structure et le fonctionnement de la forêt. Toutefois, le mécanisme par lequel les communautés végétales retrouvent leur composition et leur fonctionnement originels en réponse au contrôle des herbivores demeure mal compris. Nous avons évalué les trajectoires temporelles des communautés herbacées dans des peuplements d'*Abies balsamea* (L.) Mill. et de *Picea glauca* (Moench) Voss à l'île d'Anticosti (Québec, Canada) pendant 8 années après avoir effectué une coupe à blanc et contrôlé les populations de cerfs. L'impact de l'exclusion du cerf ou d'une réduction de la densité à 7,5 ou 15 cerfs·km^{-2} a été comparé à des densités témoins in situ (27 et 56 cerfs·km^{-2}). Les effets des traitements de gestion du cerf sur les espèces végétales et les assemblages de traits fonctionnels ont été évalués en fonction du temps au moyen de la méthode des courbes de réponses principales. Bien que l'exclusion complète du cerf ait semblé nécessaire pour modifier la composition spécifique par rapport à celle observée en conditions de broutage intense, une densité réduite à 7,5 cerfs·km^{-2} était suffisante pour induire des changements significatifs dans les assemblages de traits fonctionnels des peuplements en régénération. À titre d'exemple, des densités réduites de cerfs ont favorisé les plantes à fleurs de couleur vive et les plantes à fleurs composées pollinisées par les animaux et produisant de grosses graines et des fruits charnus dispersés par les animaux. Nous concluons que les communautés herbacées de la forêt boréale sont résilientes au broutage chronique quand une réduction des populations de cerfs et une coupe forestière à blanc sont appliquées en synergie. [Traduit par la Rédaction]

Mots-clés : résilience, composition spécifique, traits fonctionnels, interactions plantes–herbivores, cerf.

Introduction

Overabundant populations of large herbivores represent a threat to forest ecosystems around the world, overexploiting their habitat to the point of compromising forest regeneration and composition (Côté et al. 2004), the dynamics of associated animal communities (Bush et al. 2012), and ecosystem functioning (Rooney and Waller 2003). The selective browsing of preferred species, the apparent competitive advantage for plants tolerant or resistant to browsing (Tremblay et al. 2007), and the potential impoverishment of seed banks (Maron and Crone 2006) may even push the forest toward an alternative successional trajectory (sensu Suding

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et al. 2004), with the development of recalcitrant understory layers (Royo and Carson 2006) impeding the system's recovery after density control (Hidding et al. 2013).

Exclusion experiments have been widely used to study vegetation recovery following large herbivore management, but the scope of these studies is rather limited, as a single level of browsing (i.e., natural deer density) is usually compared with plots from which herbivores have been excluded (e.g., Newman et al. 2014). Very few studies have used a complete experimental design with multiple herbivore densities (but see Horsley et al. (2003)). Furthermore, studies have typically used a classic botanical approach (plant composition and structure), and considering plants in terms of functional traits may facilitate the identification of processes controlling the succession of plant assemblages (Pywell et al. 2003). Although the trait-based approach is gaining popularity for evaluating plant regeneration after restoration or management practices, few studies on herbivore density control have analyzed the response of an entire plant group from a functional-trait perspective (but see Bachand et al. (2014a)). The development of a large database of functional traits and the refinement of multivariate statistical tools now favor detailed examination of plant community succession following herbivore control to gain a mechanistic understanding of ecosystem resilience.

In this study, we used Anticosti Island as a laboratory to investigate the capacity of forest herbaceous communities to re-establish after long-term intense browsing pressure. Anticosti is a predator-free island, supporting a white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) population that became overabundant (>20 deer·km⁻²) about 30 years after the introduction of 220 deer in 1896–1897. Since then, most of the disturbed *Abies balsamea* (L.) Mill. stands have been replaced by *Picea glauca* (Moench) Voss stands, and several shrub and herb species have become locally extinct (Potvin et al. 2003). Since 1995, large fenced areas have been clear-cut, preserving soils and advancing regeneration, to increase light and stimulate young *A. balsamea* growth, because this species represents a critical food resource on the island for deer survival in the winter (Beaupré et al. 2004). In 2001, an extensive experiment was established in a mosaic of forests and clear-cut areas to evaluate the impact of four different deer densities (0, 7.5, and 15 deer·km⁻² and in situ density of 27–56 deer·km⁻²) on plant succession. Using principal response curves (PRC) analyses (Van den Brink and Ter Braak 1999), we compared the temporal trajectory of the herbaceous plant community on clear-cut areas under different deer densities from both compositional (species) and functional (traits) perspectives.

Materials and methods

Study area

Anticosti Island (7943 km²) is located in the Gulf of St. Lawrence in Quebec, Canada (49°28′N, 63°00′W). The climate is classified as cold maritime, with a total annual precipitation of 917 ± 130 mm (mean ± standard deviation), one-third of which falls as snow, and mean temperatures varying from a minimum of –11.5 ± 1.9 °C in February to a maximum of 16.1 ± 1.1 °C in July (Environment Canada 2006). The forests of Anticosti Island belong to the boreal zone and are part of the eastern *A. balsamea* – *Betula papyrifera* bioclimatic region (Saucier et al. 2009). These forests were originally dominated by *A. balsamea*, *Picea mariana* (Mill.) Britton, Sterns & Poggenb., and *P. glauca*, with deciduous tree species such as *B. papyrifera* Marshall, *Populus tremuloides* Michx., and *Populus balsamifera* L. occurring sporadically. Stands that regenerated after the 1930s are now dominated by *P. glauca*, whereas in clear-cut stands under chronic deer browsing, white-tailed deer have eliminated the competing species, resulting in *P. glauca* barrens (Barrette

et al. 2014). Moose (*Alces alces* (Linnaeus, 1758)) is the only other introduced large browser that has survived on Anticosti Island, but its density is very low (0.04 moose·km⁻²; Beaupré et al. 2004), and its impact on the vegetation is minimal (Potvin et al. 2003). The indigenous black bear (*Ursus americanus* Pallas, 1780) was abundant on the island at the time of deer introduction but became extinct around the year 2000 (Côté 2005).

Experimental design

Our study used the infrastructure of an experiment on deer density control established in 2001 on sites with both intact and clear-cut forested areas (Tremblay et al. 2006). As plant responses in the forests were slow (Hidding et al. 2012), we chose to focus on clear-cut areas in the current study. We tested four deer densities replicated in three blocks located 4–71 km apart. Each block consisted of three large fenced areas in which deer densities were controlled; all deer were removed from 10 ha exclosures, whereas three deer were stocked in both 40 ha (7.5 deer·km⁻²) and 20 ha (15 deer·km⁻²) enclosures. An unfenced experimental unit at the in situ deer density (27–56 deer·km⁻², estimated from pellets counts; for details, see Tremblay et al. (2006)) was associated with each block. To maintain experimental deer density, we culled all deer from fenced areas in late autumn each year and monitored tracks in winter. New individuals (mainly yearlings) were stocked in enclosures each spring from 2002 to 2009. At the time that the experiment was established (2001), all trees >9 cm in diameter at breast height (1.3 m) were removed from about 70% of the surface of each experimental unit, leaving about 30% mature *A. balsamea* forest fragments.

Sampling procedures

We surveyed herbaceous plant communities in 20 permanent quadrats (10 m × 10 m) that had been randomly positioned in clear-cut areas of each of the 12 experimental units (four deer densities × three blocks). We estimated the cover of each herbaceous species (including ferns) in two 1 m × 1 m subquadrats randomly located in each permanent quadrat 2, 6, and 8 years after the beginning of deer control. The cover of each species was evaluated according to 12 classes (<1%, 1%–5%, 6%–15%, 16%–25%, 26%–35%, 36%–45%, 46%–55%, 56%–65%, 66%–75%, 76%–85%, 86%–95%, 96%–100%). We removed rare species (found in only one subquadrat) from the database for subsequent analyses.

Plant traits

We described each species in terms of its functional traits, including biological traits related to morphology, reproduction, and dispersal, as well as traits related to resources used by plants (Violle et al. 2007) and plant origin (indigenous or exotic). We selected 14 traits (Table 1) that have been previously associated with herbivore density (Bachand et al. 2014a). Trait values (Supplementary Table S1[1]) were gathered from the TOPIC database (http://topic.rncan.gc.ca) and from a literature review.

Statistical analyses

We used PRC analysis (Van den Brink and Ter Braak 1999) to compare the trajectory of plant species assemblages after clear-cutting in stands with deer excluded or at a reduced density with that in stands with the in situ deer density. This type of redundancy analysis (RDA) expresses attributes (species or traits composition) of a given treatment (deer density) as a deviation from a comparison benchmark along a time axis (Lepš and Šmilauer 2003). Our PRC analysis displays three curves, each representing the trajectory of the species or trait community over time at a specific deer density, using the in situ deer density as the point of refer-

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Table 1. Functional traits of herbaceous plants on Anticosti Island, extracted from the TOPIC database (http://topic.rncan.gc.ca) and from a literature review.

Functional trait	State
Morphology	
Foliage structure	0, no leaf; 1, rosette; 2, graminoid; 3, erect leaves; 4, decumbent; 5, erect leafy stem
Raunkiaer life form	1, therophyte; 2, geophyte; 3, hemicryptophyte; 4, chamaephyte
Rhizome	0, absence; 1, presence
Storage organ	0, absence; 1, presence
Reproduction and dispersal	
Principal means of reproduction	1, seeds only; 2, vegetative propagation possible but mostly by seeds; 3, mostly by vegetative propagation
Inflorescence type	1, no flower; 2, single flower; 3, spike or cluster; 4, compound inflorescence
Inflorescence color	1, no flower; 2, green, brown, and black; 3, white; 4, other colors
Flowering phenology	
Spring	0, absence; 1, presence
Summer	0, absence; 1, presence
Fall	0, absence; 1, presence
Pollinator vector	
Abiotic	0, absence; 1, presence
Biotic	0, absence; 1, presence
Self-pollination	0, absence; 1, presence
Seed size (mm)	
Seed dispersal vector	
Wind	0, absence; 1, presence
Endozoochore	0, absence; 1, presence
Epizoochore	0, absence; 1, presence
Bird	0, absence; 1, presence
Gravity	0, absence; 1, presence
Dispersal type	1, spore; 2, dried fruit; 3, fleshy fruit
Resource use	
Shade tolerance	1, shade tolerant; 2, mid tolerant; 3, intolerant
Status	
Status	0, indigenous; 1, exotic

Note: Seed size was measured in millimetres.

ence. We tested the significance of the RDA axes using 999 Monte Carlo permutation tests ($\alpha = 0.05$).

We conducted a second PRC analysis using functional traits rather than species identity. For this, we first calculated the community weighted mean value for each trait as the mean of trait values in the community weighted by the relative abundance of the species for each site (Garnier et al. 2004). Both PRCs were followed by post-hoc comparisons of curves at year 8 after treatment establishment, using Monte Carlo permutations ($n = 999$). To respect the comparisonwise error of 0.05, a Šidák correction was applied to each pairwise comparison (Šidák 1967). As we had four treatments, the p value for each pair was determined to be 0.0085. For the above analyses, we applied a Hellinger transformation to control for double absence of species between two sites (Legendre and Gallagher 2001). We performed all statistical analyses using R version 2.15.2 (R Development Core Team, Vienna, Austria; available from http://www.r-project.org/).

Results and discussion
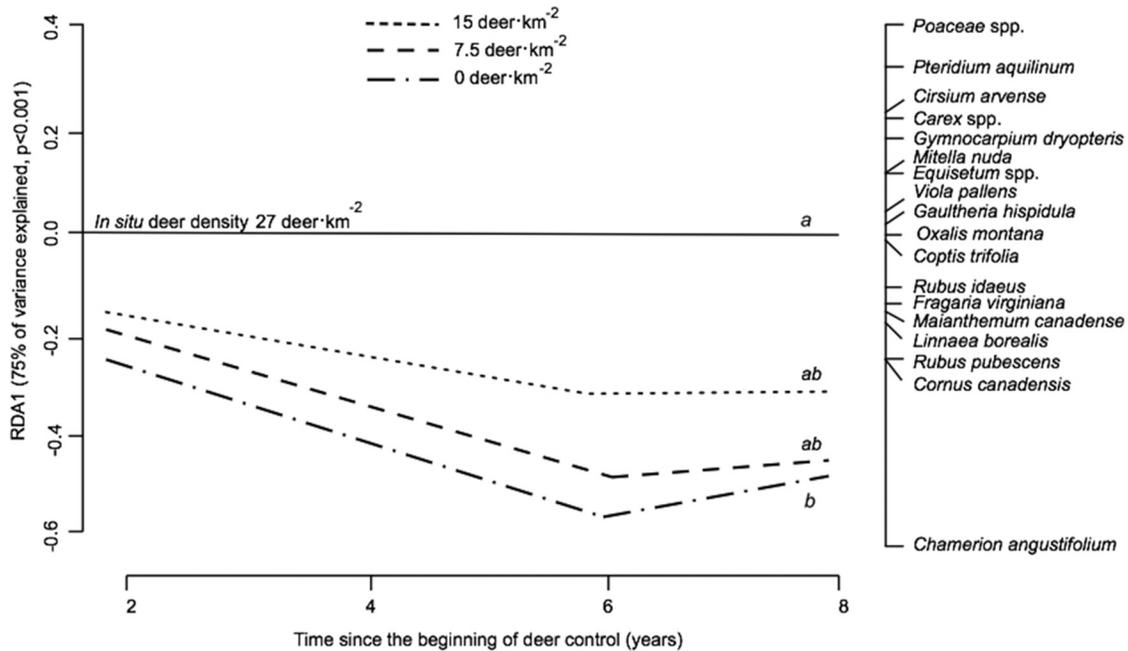
Species composition

Deer density management led to rapid changes in the composition of the herbaceous community in clear-cut areas, as the three curves corresponding to density exclusion and reduction were already lower than the in situ density 2 years after treatment establishment (Fig. 1). However, changes slowed after 6 years, and

only plots in deer exclosures had significantly different species composition than plots under intensive browsing (in situ density) during the final year of the experiment (Table 2; Fig. 1). Indeed, a small density reduction to 15 deer·km⁻² led to a distinct plant temporal pathway from that observed under intensive browsing, but further reduction, even to 7.5 deer·km⁻², was insufficient to significantly alter plant communities over a period of 8 years after clear-cutting. More time would be required to determine whether plant communities under the intermediate deer densities tested could eventually emerge from the apparent stable state achieved at year 6 and further diverge from those affected by intensive browsing.

The positive score of Poaceae spp., *Pteridium aquilinum* (L.) Kuhn, *Cirsium arvense* (L.) Scop., *Carex* spp., *Gymnocarpium dryopteris* (L.) Newman, *Mitella nuda* L., and *Equisetum* spp. along the right vertical axis of the PRC indicates that these species benefited from the conditions generated by heavy browsing at the in situ deer density, notably via the suppression of competitive species (Fig. 1). Graminoid plants (including *Carex* spp.) usually thrive under high deer densities (Fisichelli et al. 2013), likely due to their basal meristems, high shoot densities, and capacity for compensatory growth (Ferraro and Oesterheld 2002). Although pteridophytes could constitute an alternative foraging choice at very high deer browsing intensities (Rooney 2009), their palatability is usually considered low due to the presence of defense metabolites such as a high concentration of tannins (Jones and Firn 1979). This could explain the association of *P. aquilinum*, *G. dryopteris*, and *Equisetum* spp. with the in situ deer density on Anticosti Island. Furthermore, decline (Perrin et al. 2011) and even elimination (Kelly 2000) of ferns has often occurred following deer exclusion, a trend that has been associated with increased competition from recovering species sensitive to browsing. *Cirsium arvense* has the advantage of possessing physical defenses, which are generally recognized to be efficient protection against herbivores, although its greater abundance under high herbivore density has been mainly associated with competitive release (Edwards et al. 2000). Despite the presence of physical defenses, *Cirsium* species could contribute to the diet of the deer (Austin and Urness 1983), especially after the first frosts of the fall, and its seeds can be hooked to herbivore fur and dispersed around, which may contribute to its occurrence under high herbivore densities.

Under reduced browsing pressure, palatable species with lower tolerance to browsing such as *Chamerion angustifolium* (L.) Holub., *Rubus pubescens* Raf., and *Cornus canadensis* L. were the main species responsible for the temporal trajectories of communities (Fig. 1). *Chamerion angustifolium* is a highly palatable species that has been recently identified as a biological indicator of low deer densities in clear-cut boreal forests (≤7.5 deer·km⁻²; Bachand et al. 2014b). Although *C. angustifolium* is not known to create a long-term seed bank (Thompson et al. 1993), its seeds can be dispersed over hundreds of kilometres (Solbreck and Andersson 1987), which could explain how it can establish in Anticosti Island deer exclosures despite its quasi-absence from unmanaged areas of the island. *Rubus* spp. are known to thrive after clear-cutting (Horsley et al. 2003), and their positive response to the reduced deer density might reflect their sensitivity to competition with graminoids and other spiny plants such as *C. arvense* at high deer densities. Spines of *R. pubescens* are also rather soft at the early stages of its development, and early browsing at high deer densities might prevent the development of full plant height and the associated defense structure. Among the seven species identified as drivers of temporal trajectories after deer density reduction (Fig. 1), three were species associated with mature boreal forests, namely, *C. canadensis*, *Linnaea borealis* L., and *Maianthemum canadense* Desf. Clear-cutting has been shown to be a disturbance essential for catalyzing compositional changes after deer density reduction (Tremblay et al. 2007); however, our study shows that it may also benefit closed-

Fig. 1. Principal response curves showing the temporal trajectory in species composition of herbaceous communities of *Abies balsamea* stands after clear-cutting at different levels of reduced deer density compared with in situ deer density. The principal response curves with the same lowercase letter are not significantly different 8 years after deer density control, following post-hoc comparisons of curves with Monte Carlo permutations ($n = 999$) and a Šidák correction (see Materials and methods). The respective scores of the most dominant species are displayed along the right-side vertical axis, indicating how strongly each species is correlated with the temporal patterns displayed by the curves, thus illustrating the main drivers of the temporal trajectories.

Table 2. Statistical differences between curves at year 8 after the establishment of deer control treatments.

Comparison	F	df	p value
Species composition			
In situ vs 15 deer·km⁻²	2.581	1, 12	0.160
In situ vs 7.5 deer·km⁻²	5.516	1, 12	0.017
In situ vs 0 deer·km⁻²	6.772	1, 12	<0.001*
15 deer·km⁻² vs 7.5 deer·km⁻²	1.891	1, 12	0.490
15 deer·km⁻² vs 0 deer·km⁻²	2.509	1, 12	0.230
7.5 deer·km⁻² vs 0 deer·km⁻²	0.901	1, 12	0.800
Trait composition			
In situ vs 15 deer·km⁻²	2.908	1, 12	0.059
In situ vs 7.5 deer·km⁻²	4.293	1, 12	<0.001*
In situ vs 0 deer·km⁻²	6.217	1, 12	<0.001*
15 deer·km⁻² vs 7.5 deer·km⁻²	2.511	1, 12	0.130
15 deer·km⁻² vs 0 deer·km⁻²	3.926	1, 12	0.005*
7.5 deer·km⁻² vs 0 deer·km⁻²	3.610	1, 12	0.020

Note: Post-hoc comparisons of curves were performed using Monte Carlo permutations ($n = 999$). To respect the comparisonwise error of 0.05, a Šidák correction was applied to each pairwise comparison (Šidák 1967). Because we had four treatments, the p value for each pair was determined to be 0.0085. An asterisk (*) denotes statistical significance. df, degrees of freedom, expressed as "numerator, denominator".

canopy species and promote resilience of understory plant communities in *A. balsamea* forests.

Trait composition

The above changes in species composition of herbaceous communities were mirrored in their functional trait composition, with curves showing similar trajectories after deer management; rapid changes in functional traits were observable between 2 and 6 years after treatment was initiated, followed by almost constant trait assemblages after 6 years (Fig. 2). However, the functional components of herbaceous communities seemed to be more resilient than their species composition per se. Indeed, it seems un-

necessary to completely exclude deer to achieve a significant change in plant trait communities, as plots with a density of 7.5 deer·km⁻² were significantly different from those under in situ densities after 8 years of succession (Table 2). On this point, our findings concur with those of Tremblay et al. (2006), who also observed that the biomass of dominant and preferred herbaceous species recovered rapidly at densities under 7.5 deer·km⁻². The plant traits favored under densities equal to or higher than 15 deer·km⁻² included wind- or gravity-dispersed seeds, erect foliage, storage organs, exotic origin, vegetative propagation, and self-pollination and abiotic pollination (Fig. 2). Most of these traits have been previously identified as efficient strategies for ensuring persistence under foraging pressure by large herbivores (e.g., Wiegmann and Waller 2006) and as potentially having significant cascading effects on other taxa (Nuttle et al. 2011), notably on pollinators by making plants less attractive to them (Vázquez and Simberloff 2004). On the other hand, reducing the deer density favored species with brightly colored flowers and compound inflorescences pollinated by animals and producing large seeds and fleshy fruits, dispersed by birds or other animals (Fig. 2). Therefore, plant species found under reduced deer densities seem to have the capacity to allocate resources to sexual reproductive structures. Investment in flowers attractive to pollinators and in fleshy fruits attractive to birds may indicate that the recovery of these forest systems after deer control is not limited to plant species but also involves other taxa indirectly through the change of plant trait communities. Recent studies on Anticosti Island have indeed shown that total abundance, richness, and diversity of songbirds increased at deer densities ≤7.5 deer·km⁻² due to a higher abundance of *B. papyrifera* (Cardinal et al. 2012). Insects responded to plant regeneration under reduced deer densities according to their degree of dependence on plants, with the fastest response by Lepidoptera, a moderate response by Apoidea and Syrphidae, and no response by Carabidae (Brousseau et al. 2013). In addition, brightly colored flowers in the studied stands gener-

Fig. 2. Principal response curves showing the temporal trajectory in species traits of herbaceous plant communities of *Abies balsamea* stands after clear-cutting at different levels of reduced deer density compared with in situ deer density. The principal response curves with the same lowercase letter are not significantly different 8 years after deer density control, following post-hoc comparisons of curves with Monte Carlo permutations (n = 999) and a Šidák correction (see Materials and methods). The respective scores of plant traits are displayed along the right-side vertical axis, indicating how strongly each trait is correlated with the temporal patterns displayed by the curves, thus illustrating the main drivers of the temporal trajectories.
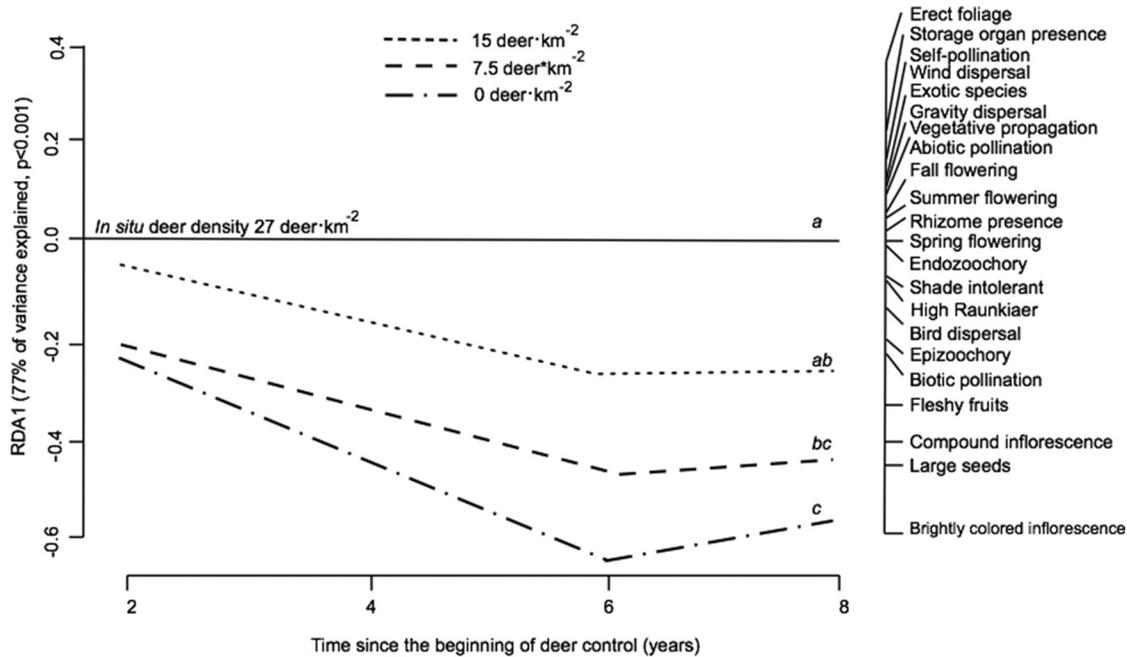
ally represented palatable species (Supplementary Table S1[1]) associated with pollinators. The resilience of plant communities after deer control should thus foster higher trophic guilds, notably pollinators and seed dispersers, but the magnitude of this relationship has yet to be determined (Bachand et al. 2014a). Our study is based on averaged traits from the literature, and further investigation would be needed to assess the ability of species to flower and produce fruits along different deer densities, which could reflect plasticity within species and reveal some mechanistic adaptation of plants to persist or recover after intense browsing.

The majority of the traits analyzed in our study were binary traits describing aerial plant parts. Using numerical traits such as specific leaf area, traits relevant to herbivory such as nitrogen content of leaves, proportion of fibers, and secondary metabolites or digestibility, and integrating root traits such as specific root depth or nitrogen content could provide further insight into the resilience of individual ecosystem functionality (e.g., nutrient cycle or soil stability; Cornelissen et al. 2003). The use of a reference ecosystem may also help to assess whether a system is recovering functionality. For example, Aubin et al. (2008) pointed out the need for specific forestry practices to accelerate the regeneration of an herbaceous community functionally similar to that of natural old-growth forests. Yet, reference ecosystems are lacking on Anticosti Island, as deer have been affecting all forest stands for more than 100 years. Setting up reference ecosystems on the mainland would pose comparison problems, as the response of functional traits may still be context dependent in that the behaviour of common species with unusual attributes might lead to a different trait composition after a change in grazing regime (Pakeman 2004). Although comparison with a reference ecosystem is impossible for many areas under pressure from large herbivores, as on Anticosti Island, demonstrating that succession can lead to species assemblages and functional communities distinct from those on sites subjected to intensive browsing provides evidence of ecosystem resilience. Interpreting the species and functional traits

responsible for these trajectories can further increase our confidence in this resilience.

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