1 **Compositional and functional trajectories of herbaceous communities**

2 **after deer density control in clearcut boreal forests**

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24   **Abstract:** Overabundant populations of large herbivores have strong persistent effects on forest

25   composition, structure and function. However the mechanism through which plant communities

26   recover their original composition and function after herbivore management remains poorly

27   understood. We assessed the temporal trajectories of the herbaceous communities in *Abies balsamea*

28   (L.) Mill. and *Picea glauca* (Moech) stands on Anticosti Island (Quebec, Canada) over eight years,

29   following clearcutting and deer management. The impact of deer exclusion or reduction to 7.5 and

30   15 deer $\cdot$ km^{-2} was compared with benchmark *in situ* deer densities (27 and 56 deer $\cdot$ km^{-2}). Effects

31   of deer management treatments on plant species and functional trait assemblages over time were

32   assessed using Principal Response Curves. Although complete deer exclusion seemed necessary to

33   modify species composition from that occurring under intense browsing, a reduced density of 7.5

34   deer $\cdot$ km^{2} was sufficient to induce significant changes in functional trait assemblages of

35   regenerating stands. For instance, reduced deer densities favored plants with brightly colored

36   flowers and compound inflorescences pollinated by animals and producing large seeds and fleshy

37   fruits dispersed by animals. We conclude that the boreal forest's herbaceous communities are

38   resilient to chronic browsing when deer population reduction and forest clearcutting are applied in

39   synergy.

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), 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) as well as the potential impoverishment of seed banks (Maron and Crone 2006), may even push the forest toward an alternative successional trajectory (*sensu* Suding 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 (natural density) is usually compared to 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). Considering plants in terms of functional traits may facilitate 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 as well as 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.

63   In this study, we used Anticosti Island as a laboratory to investigate the capacity of forest

64   herbaceous communities to re-establish after long-term intense browsing pressure. Anticosti is a

65   predator-free island supporting a white-tailed deer (*Odocoileus virginianus* Zimm.) population that

66   became overabundant (> 20 deer · km^{-2}) about 30 years after the introduction of 220 individuals in

67   1896-97. Since then, most disturbed *Abies balsamea* stands have been replaced by *Picea glauca*

68   (Moench) Voss stands and several shrub and herb species have become locally extinct (Potvin et al.

69   2003). Since 1995, large fenced areas have been clearcut, preserving soils and advance regeneration;

70   to increase light and stimulate young *Abies* growth since this species represents a critical food

71   resource on the island for deer survival in winter (Beaupré et al. 2004). In 2001, an extensive

72   experiment was established in a mosaic of forests and clearcut areas to evaluate the impact of four

73   different deer densities (0, 7.5, 15 deer · km^{-2} and *in situ*: 27-56 deer · km^{-2}) on plant succession.

74   Using Principal Response Curves analyses (van den Brink and ter Braak 1999), we compared the

75   temporal trajectory of the herbaceous plant community on clearcut areas under different deer

76   densities both from a compositional (species) and a functional (traits) perspective.

77   **Material and Methods**

78   **Study area**

79   Anticosti Island (7943 km^2) is located in the Gulf of St. Lawrence in Quebec, Canada (49°28'N,

80   63°00'W). The climate is classified as cold maritime, with a total annual precipitation of 917 ± 130

81   mm (mean ± SD), one third of which falls as snow, and mean temperatures varying from a minimum

82   of −11.5 ± 1.9 °C in February to a maximum of 16.1 ± 1.1 °C in July (Environment Canada, 2006).

83   Anticosti's forests belong to the boreal zone and are part of the eastern *Abies balsamea − Betula*

84   *papyrifera* Marsh. bioclimatic region (Saucier et al. 2009). These forests were originally dominated

85   by *Abies balsamea*, *Picea mariana* (Mill.) Britton, Sterns & Poggenb. and *Picea glauca*, with

86   deciduous tree species, such as *Betula papyrifera*, *Populus tremuloide*s Michx., and *Populus*

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87   *balsamifera* L. occurring sporadically. Stands that regenerated after the 1930s are now dominated

88   by *Picea glauca*, while in clearcut stands under chronic deer browsing, white-tailed deer has

89   eliminated competing species resulting in *Picea* barrens (Barrette et al. 2014). Moose (*Alces alces*

90   L.) is the only other introduced large browser that has survived on Anticosti Island, but its density is

91   very low (0.04 moose · km^{-2}; Beaupré et al. 2004) and its impact on the vegetation minimal (Potvin

92   et al., 2003). The indigenous black bear (*Ursus americanus*) was abundant on the island at the time

93   of deer introduction, but became extinct around the year 2000 (Côté 2005).

94   **Experimental design**

95   Our study used the infrastructure of an experiment on deer density control established in 2001

96   on sites with both intact and clearcut forested areas (Tremblay et al. 2006). As plant responses in the

97   forests were slow (Hidding et al. 2012), we chose to focus on clearcut areas in the current study. We

98   tested four deer densities replicated in three blocks located 4 to 71 km apart. Each block consisted of

99   three large fenced areas in which deer densities were controlled: all deer were removed from 10 ha

100   exclosures, whereas three deer were stocked in both 40 ha (7.5 deer · km^{-2}) and 20 ha (15 deer · km^{-}

101   ^{2}) enclosures. An unfenced experimental unit at *in situ* density (27 to 56 deer · km^{-2} estimated from

102   pellets counts; see Tremblay et al. 2006 for details) was associated with each block. To maintain

103   experimental deer density, we culled all deer from fenced areas in late autumn each year and

104   monitored tracks in winter. New individuals (mainly yearlings) were stocked in enclosures each

105   spring from 2002 to 2009. At the time the experiment was established (2001), all trees >9 cm in

106   diameter at breast height were removed from about 70% of the surface of each experimental unit,

107   leaving about 30% mature *Abies balsamea* forest fragments.

108   **Sampling procedures**

109   We surveyed herbaceous plant communities in 20 permanent quadrats (10 × 10 m) that had

110   been randomly positioned in clearcut areas of each of the 12 experimental units (four deer densities

111   × three blocks). We estimated the cover of each herbaceous species (including ferns) in two 1 × 1 m

112   sub-quadrats randomly located in each permanent quadrat, two, six and eight years after the

113   beginning of deer control. The cover of each species was evaluated according to 12 classes (<1, 1-5,

114   6-15, 16-25, 26-35, 36-45, 46-55, 56-65, 66-75, 76-85, 86-95, 96-100%). We removed rare species

115   (found in only one sub-quadrat) from the database for subsequent analyses.

116   **Plant traits**

117   We described each species in terms of its functional traits, including biological traits related to

118   morphology, reproduction and dispersal, as well as traits related to resources used by plants (Violle

119   et al. 2007) and plant origin (indigenous or exotic). We selected 14 traits (Table 1) that have been

120   previously associated with herbivore density (Bachand et al. 2014a). Trait values (Table S1) were

121   gathered from the TOPIC database (http://topic.rncan.gc.ca) and from a literature review.

122   **Statistical analyses**

123   We used Principal Response Curves analysis (PRC; van den Brink and ter Braak 1999) to

124   compare the post-clearcutting trajectory of plant species assemblages in stands with deer excluded

125   or at reduced density to that in stands with *in situ* deer density. This type of redundancy analysis

126   (RDA) expresses attributes (species or traits composition) of a given treatment (deer density) as a

127   deviation from a comparison benchmark along a time axis (Lepš and Šmilauer 2003). Our PRC

128   analysis displays three curves, each representing the trajectory of the species or trait community

129   over time at a specific deer density, using the *in situ* density as the point of reference. We tested the

130   significance of the RDA axes using 999 Monte Carlo permutation tests (alpha value set to 0.05).

131   We conducted a second PRC analysis using functional traits rather than species identity. For

132   this, we first calculated the community weighted mean value (CWM) for each trait as the mean of

133   trait values in the community weighted by the relative abundance of the species for each site

134   (Garnier et al. 2004). Both PRC were followed by post-hoc comparisons of curves at year eight after

135   treatment establishment, with Monte Carlo permutations (n=999). In order to respect the

136   comparisonwise error of 0.05, a Šidák correction was applied to each pairwise comparison (Šidák

137   1967). Since we had four treatments, the *p* value for each pair was determined to be 0.0085. For the

138   above analyses, we applied a Hellinger transformation to control for double absence of species

139   between two sites (Legendre and Gallagher 2001). We performed all statistical analyses using R

140   version 2.15.2 (R Development Core Team, Vienna, Austria).

141   **Results and Discussion**

142   **Species composition**

143   Deer density management led to rapid changes in the composition of the herbaceous community

144   in clearcut areas, as the three curves corresponding to density exclusion and reduction were already

145   lower than the *in situ* density benchmark two years after treatment establishment (Fig. 1). However,

146   changes slowed after six years, and only plots in deer exclosures had a significantly different species

147   composition than plots under intensive browsing (*in situ* density) during the final year of the

148   experiment (Table 2, Fig. 1). Indeed, a small density reduction (15 deer $\cdot$ km^{-2}) led to a distinct plant

149   temporal pathway from that observed under intensive browsing, but further reduction, even to 7.5

150   deer $\cdot$ km^{-2}, was insufficient to significantly alter plant communities over a period of eight years

151   after clearcutting. More time would be required to determine whether plant communities under the

152   intermediate deer densities tested could eventually emerge from the apparent stable state achieved at

153   year six and further diverge from those affected by intensive browsing.

154   The positive score of **Poaceae** spp., *Pteridium aquilinum* (L.) Kuhn, *Cirsium arvense* (L.)

155   Scopoli, *Carex* spp. and *Gymnocarpium dryopteris* (L.) Newman, *Mitella nuda* L. and *Equisetum*

156   spp. along the right vertical axis of the PRC indicates that these species benefited from the

157   conditions generated by heavy browsing at *in situ* deer density, notably via the suppression of

158   competitive species (Fig. 1). Graminoid plants (including *Carex* spp.) usually thrive under high deer

159   density (Fisichelli et al. 2013), likely due to their basal meristems, high shoot densities and capacity

160   for compensatory growth (Ferraro and Oesterheld 2002). Although pteridophytes could constitute an

161   alternative foraging choice at very high deer browsing intensity (Rooney 2009), their palatability is

162   usually considered low due to the presence of defense metabolites, such as a high concentration of

163   tannins (Jones and Firn 1979). This could explain the association of *P. aquilinum*, *G. dryopteris* and

164   *Equisetum* spp. with *in situ* deer density on Anticosti. Furthermore, decline (Perrin et al. 2011) and

165   even elimination (Kelly 2000) of ferns has often occurred following deer exclusion, a trend that has

166   been associated with increased competition from recovering species sensitive to browsing. *Cirsium*

167   *arvense* has the advantage of possessing physical defenses, which are generally recognized to be

168   efficient protection against herbivores, though its greater abundance under high herbivore density

169   has been mainly associated to competitive release (Edwards et al. 2000). Despite the presence of

170   physical defenses, *Cirsium* species could contribute to deer diet (Austin and Urness 1983),

171   especially after the first frosts of the fall, and its seeds can be hooked to herbivore fur and dispersed

172   around, which may contribute to its occurrence under high herbivore densities.

173   Under reduced browsing pressure, palatable species with lower tolerance to browsing, such as

174   *Chamerion angustifolium* (L.) Holub., *Rubus pubescens* Raf., or *Cornus canadensis* L., were the

175   main species responsible for the temporal trajectories of communities (Fig. 1). *Chamerion*

176   *angustifolium* is a highly palatable species that has recently been identified as a biological indicator

177   of low deer density in clearcut boreal forests ($\leq$ 7.5 deer · km^{-2}; Bachand et al. 2014b). Although *C.*

178   *angustifolium* is not known to create a long-term seed bank (Thompson et al. 1993), its seeds can be

179   dispersed over hundreds of kilometers (Solbreck and Andersson 1987), which could explain how it

180   can establish in Anticosti deer exclosures despite its quasi-absence from unmanaged areas of the

181   island. *Rubus* spp are known to thrive after clearcutting (Horsley et al. 2003), and their positive

182   response to reduced deer density might reflect their sensitivity to competition with graminoids and

183   other spiny plants like *Cirsium* at high deer densities. *Rubus* spines are also rather soft at the early

184   stages of its development, and early browsing at high density might prevent the development of full

185   plant height and the associated defense structure. Among the seven species identified as drivers of

186   temporal trajectories after deer density reduction (Fig. 1), three were species associated to mature

187   boreal forests: *Cornus canadensis*, *Linnaea borealis* L., and *Maianthemum canadense* Desf.

188   Clearcutting has been shown to be a disturbance essential for catalyzing compositional changes after

189   deer density reduction (Tremblay et al. 2007), but our study shows that it may also benefit closed

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

191   **Traits composition**

192   The above changes in species composition of herbaceous communities were mirrored in their

193   functional trait composition, with curves showing similar trajectories after deer management: rapid

194   changes in functional traits were observable between two and six years after treatment was initiated,

195   followed by almost constant trait assemblages after six years (Fig. 2). However, the functional

196   components of herbaceous communities seemed more resilient than their species composition *per*

197   *se*. Indeed, it seems unnecessary to completely exclude deer to achieve a significant change in plant

198   trait communities, as plots with a density of 7.5 deer $\cdot$ km^{-2} were significantly different from those

199   under *in situ* densities after eight years of succession (Table 2). On this point, our findings concur

200   with those of Tremblay et al. (2006), who also observed that the biomass of dominant/preferred

201   herbaceous species recovered rapidly at densities under 7.5 deer $\cdot$ km^{-2}. The plant traits favored

202   under densities equal to or higher than 15 deer $\cdot$ km^{-2} included wind- or gravity-dispersed seeds,

203   erect foliage, storage organs, exotic origin, as well as vegetative propagation and self- and abiotic

204   pollination (Fig. 2). Most of these traits have previously been identified as efficient strategies for

205   ensuring persistence under foraging pressure by large herbivores (e.g., Wiegmann and Waller 2006),

206   and as potentially having significant cascading effects on other taxa (Nuttle et al. 2011), notably on

207   pollinators by making plants less attractive to them (Vázquez and Simberloff 2004). On the other

208   hand, reducing deer density favored species with brightly colored flowers and compound

209   inflorescences pollinated by animals and producing large seeds and fleshy fruits, dispersed by birds

210   or other animals (Fig. 2). Plant species found under reduced deer density therefore seem to have the

211   capacity to allocate resources to sexual reproductive structures. Investment in flowers attractive to

212   pollinators and in fleshy fruits attractive to birds may indicate that the recovery of these forest

213   systems after deer control is not limited to plant species but also involved other taxa indirectly

214   through the change of plant trait communities. Recent studies on Anticosti Island have indeed shown

215   that total abundance, richness and diversity of songbirds increased at deer densities ≤ 7.5 deer $\cdot$ km^{-2}

216   due to higher abundance of *Betula papyrifera* (Cardinal et al. 2012). Insects responded to plant

217   regeneration under reduced deer densities according to their degree of dependence on plants, with

218   the fastest response by Lepidoptera, a moderate response by Apoidea and Syrphidae, and no

219   response by Carabidae (Brousseau et al. 2013). In addition, brightly colored flowers in studied

220   stands generally represented palatable species (Table S1) associated with pollinators. The resilience

221   of plant communities after deer control should thus foster higher trophic guilds, notably pollinators

222   and seed dispersers, but the magnitude of this relationship has yet to be determined (Bachand et al.

223   2014a). Our study is based on averaged traits from the literature and further investigation would be

224   needed to assess the ability of species to flower and produce fruits along different deer densities,

225   which could reflect plasticity within species and reveal some mechanistic adaptation of plants to

226   persist or recover after intense browsing.

227   The majority of the traits analyzed in our study were binary traits describing aerial plant parts.

228   Using numerical traits, such as specific leaf area; traits relevant to herbivory, such as nitrogen

229   content of leaves, proportion of fibers and secondary metabolites or digestibility; and integrating

230   root traits, such as specific root depth or nitrogen content, could provide further insight into the

231   resilience of individual ecosystem functionality (e.g., nutrient cycle or soil stability; Cornelissen et

232   al. 2003). The use of a reference ecosystem may also help to assess whether a system is recovering

233   functionality. For example, Aubin et al. (2008) pointed out the need for specific forestry practices to

234   accelerate the regeneration of an herbaceous community functionally similar to that of natural old

235   growth forests. Yet, reference ecosystems are lacking on Anticosti Island, as deer have been

236   affecting all forest stands for more than 100 years. Setting up reference ecosystems on the mainland

237   would pose comparison problems, since the response of functional traits may still be context-

238   dependent, in that the behaviour of common species with unusual attributes might lead to a different

239   trait composition after a change in grazing regime (Pakeman 2004). Although comparison with a

240   reference ecosystem is impossible for many areas under large herbivore pressure, as on Anticosti,

241   demonstrating that succession can lead to species assemblages and functional communities distinct

242   from those on sites subjected to intensive browsing, provides evidence of ecosystem resilience.

243   Interpreting the species and functional traits responsible for these trajectories can further increase

244   our confidence in this resilience.

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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	Millimeters
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

Table 2. Statistical differences between curves at year eight after the establishment of deer control treatments. Post-hoc comparisons of curves were performed with Monte Carlo permutations (n=999). In order to respect the comparisonwise error of 0.05, a Šidák correction was applied to each pairwise comparison (Šidák 1967). Since we had four treatments, the p value for each pair was determined to be 0.0085.

Comparison	F	df	p-value
Species composition			
In situ vs 15 deer $\cdot$ km^{-2}	2.581	1/12	0.160
In situ vs 7.5 deer $\cdot$ km^{-2}	5.516	1/12	0.017
In situ vs 0 deer $\cdot$ km^{-2}	6.772	1/12	$p<0.001$*
15 deer $\cdot$ km^{-2} vs 7.5 deer $\cdot$ km^{-2}	1.891	1/12	0.490
15 deer $\cdot$ km^{-2} vs 0 deer $\cdot$ km^{-2}	2.509	1/12	0.230
7.5 deer $\cdot$ km^{-2} vs 0 deer $\cdot$ km^{-2}	0.901	1/12	0.800
Trait composition			
In situ vs 15 deer $\cdot$ km^{-2}	2.908	1/12	0.059
In situ vs 7.5 deer $\cdot$ km^{-2}	4.293	1/12	$p<0.001$*
In situ vs 0 deer $\cdot$ km^{-2}	6.217	1/12	$p<0.001$*
15 deer $\cdot$ km^{-2} vs 7.5 deer $\cdot$ km^{-2}	2.511	1/12	0.130
15 deer $\cdot$ km^{-2} vs 0 deer $\cdot$ km^{-2}	3.926	1/12	0.005*
7.5 deer $\cdot$ km^{-2} vs deer $\cdot$ km^{-2}	3.610	1/12	0.020

1 # Compositional and functional trajectories of herbaceous communities

2 # after deer density control in clearcut boreal forests

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24 **Abstract:** Overabundant populations of large herbivores have strong persistent effects on forest

25 composition, structure and function. **However** the mechanism **through** which plant communities

26 recover their original composition and function after herbivore management remains poorly

27 understood. We assessed the **temporal trajectories** of the herbaceous communities in *Abies*

28 *balsamea* (L.) Mill. **and *Picea glauca* (Moech)** stands on Anticosti Island (Quebec, Canada) over

29 eight years, following clearcutting and deer management. The impact of deer exclusion or reduction

30 to 7.5 and 15 deer $\cdot$ km^{-2} was compared with benchmark *in situ* deer densities (27 and 56 deer $\cdot$ km^{-}

31 ^{2}). Effects of deer management treatments on plant species and functional trait assemblages over

32 time were assessed using Principal Response Curves. Although complete deer exclusion seemed

33 necessary to modify species composition from that occurring under intense browsing, a reduced

34 density of 7.5 deer $\cdot$ km^{2} was sufficient to induce significant changes in functional trait assemblages

35 of regenerating stands. For instance, reduced deer densities favored plants with brightly colored

36 flowers and compound inflorescences pollinated by animals and producing large seeds and fleshy

37 fruits dispersed by animals. We conclude that the boreal forest's herbaceous communities are

38 resilient to chronic browsing when deer population reduction and forest clearcutting are applied in

39 synergy.

2

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), 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) as well as the potential impoverishment of seed banks (Maron and Crone 2006), may even push the forest toward an alternative successional trajectory (*sensu* Suding 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 (natural density) is usually compared to 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). Considering plants in terms of functional traits may facilitate 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 as well as 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.

64   In this study, we used Anticosti Island as a laboratory to investigate the capacity of forest

65   herbaceous communities to re-establish after long-term intense browsing pressure. Anticosti is a

66   predator-free island supporting a white-tailed deer (*Odocoileus virginianus* Zimm.) population that

67   became overabundant (> 20 deer · km^{-2}) about 30 years after the introduction of 220 individuals in

68   1896-97. Since then, **most disturbed** *Abies balsamea* stands have been replaced by *Picea glauca*

69   (Moench) Voss stands and several shrub and herb species have become locally extinct (Potvin et al.

70   2003). Since 1995, large fenced areas have been clearcut, preserving soils and **advance**

71   **regeneration;** to increase light and stimulate young *Abies* growth since this species represents a

72   critical food resource on the island for deer survival in winter (Beaupré et al. 2004). In 2001, an

73   extensive experiment was established in a mosaic of forests and clearcut areas to evaluate the impact

74   of four different deer densities (0, 7.5, 15 deer · km^{-2} and *in situ*: 27-56 deer · km^{-2}) on plant

75   succession. Using Principal Response Curves analyses (van den Brink and ter Braak 1999), we

76   compared the **temporal trajectory** of the herbaceous plant community on clearcut areas under

77   different deer densities both from a compositional (species) and a functional (traits) perspective.

78   **Material and Methods**

79   **Study area**

80   Anticosti Island (7943 km^{2}) is located in the Gulf of St. Lawrence in Quebec, Canada (49°28'N,

81   63°00'W). The climate is classified as cold maritime, with a total annual precipitation of 917 ± 130

82   mm (mean ± SD), one third of which falls as snow, and mean temperatures varying from a minimum

83   of –11.5 ± 1.9 °C in February to a maximum of 16.1 ± 1.1 °C in July (Environment Canada, 2006).

84   Anticosti's forests belong to the boreal zone and are part of the eastern *Abies balsamea – Betula*

85   *papyrifera* Marsh. bioclimatic region (Saucier et al. 2009). These forests were **originally dominated**

86   by *Abies balsamea*, *Picea mariana* (Mill.) Britton, Sterns & Poggenb. and *Picea glauca*, with

87   deciduous tree species, such as *Betula papyrifera*, *Populus tremuloide*s Michx., and *Populus*

4

88 *balsamifera* L. occurring sporadically. **Stands that regenerated after the 1930s are now**

89 **dominated by *Picea glauca*, while in clearcut stands under chronic deer browsing, white-tailed**

90 **deer has eliminated competing species resulting in *Picea* barrens (Barrette et al. 2014).** Moose

91 (*Alces alces* L.) is the only other introduced large browser that has survived on Anticosti **I**sland, but

92 its density is very low (0.04 moose $\cdot$ km^{-2}; Beaupré et al. 2004) and its impact on the vegetation

93 minimal (Potvin et al., 2003). The indigenous black bear (*Ursus americanus*) was abundant on the

94 island at the time of deer introduction, but became extinct around the year 2000 (Côté 2005).

95 **Experimental design**

96 Our study used the infrastructure of an experiment on deer density control established in 2001

97 on sites **with both intact and clearcut forested areas** (Tremblay et al. 2006). As plant responses in

98 the forests were slow (Hidding et al. 2012), we chose to focus on clearcut areas in the current study.

99 We tested four deer densities replicated in three blocks located 4 to 71 km apart. Each block

100 consisted of three large fenced areas in which deer densities were controlled: all deer were removed

101 from 10 ha exclosures, whereas three deer were stocked in both 40 ha (7.5 deer $\cdot$ km^{-2}) and 20 ha

102 (15 deer $\cdot$ km^{-2}) enclosures. An unfenced experimental unit at *in situ* density (27 to 56 deer $\cdot$ km^{-2}

103 estimated from pellets counts; see Tremblay et al. 2006 for details) was associated with each block.

104 To maintain experimental deer density, we culled all deer from fenced areas in late autumn each

105 year and monitored tracks in winter. New individuals (mainly yearlings) were stocked in enclosures

106 each spring from 2002 to 2009. At the time the experiment was established (2001), all trees >9 cm

107 in diameter at breast height were removed from about 70% of the surface of each experimental unit,

108 leaving about 30% mature *Abies balsamea* forest fragments.

109 **Sampling procedures**

110 We surveyed herbaceous plant communities in 20 permanent quadrats (10 × 10 m) that had

111 been randomly positioned in clearcut areas of each of the 12 experimental units (four deer densities

112   × three blocks). We estimated the cover of each herbaceous species (including ferns) in two 1 × 1 m

113   sub-quadrats randomly located in each permanent quadrat, two, six and eight years after the

114   beginning of deer control. The cover of each species was evaluated according to 12 classes **(<1, 1-5,**

115   **6-15, 16-25, 26-35, 36-45, 46-55, 56-65, 66-75, 76-85, 86-95, 96-100%)**. We removed rare species

116   (found in only one sub-quadrat) from the database for subsequent analyses.

117   **Plant traits**

118   We described each species in terms of its functional traits, including biological traits related to

119   morphology, reproduction and dispersal, as well as traits related to resources used by plants (Violle

120   et al. 2007) and plant origin (indigenous or exotic). We selected 14 traits (Table 1) that have been

121   previously associated with herbivore density (Bachand et al. 2014a). Trait values (**Table S1**) were

122   gathered from the TOPIC database (http://topic.rncan.gc.ca) and from a literature review.

123   **Statistical analyses**

124   We used Principal Response Curves analysis (PRC; van den Brink and ter Braak 1999) to

125   compare the post-clearcutting trajectory of plant species assemblages in stands with deer excluded

126   or at reduced density to that in stands with *in situ* deer density. This type of redundancy analysis

127   (RDA) expresses attributes (species or traits composition) of a given treatment (deer density) as a

128   deviation from a comparison benchmark along a time axis (Lepš and Šmilauer 2003). Our PRC

129   analysis displays three curves, each representing the trajectory of the species or trait community

130   over time at a specific deer density, using the *in situ* density as the point of reference. We tested the

131   significance of the RDA axes using 999 Monte Carlo permutation tests (alpha value set to 0.05).

132   We conducted a second PRC analysis using functional traits rather than species identity. For

133   this, we first calculated the community weighted mean value (CWM) for each trait as the mean of

134   trait values in the community weighted by the relative abundance of the species for each site

135   (Garnier et al. 2004). Both PRC were followed by post-hoc comparisons of curves at year eight after

136 treatment establishment, with Monte Carlo permutations (n=999). In order to respect the

137 comparisonwise error of 0.05, a Šidák correction was applied to each pairwise comparison (Šidák

138 1967). Since we had four treatments, the *p* value for each pair was determined to be 0.0085. For the

139 above analyses, we applied a Hellinger transformation to control for double absence of species

140 between two sites (Legendre and Gallagher 2001). We performed all statistical analyses using R

141 version 2.15.2 (R Development Core Team, Vienna, Austria).

142 **Results and Discussion**

143 **Species composition**

144 Deer density management led to rapid changes in the composition of the herbaceous community

145 in clearcut areas, as the three curves corresponding to density exclusion and reduction were already

146 lower than the *in situ* density benchmark two years after treatment establishment (Fig. 1). However,

147 changes slowed after six years, and only plots in deer exclosures had a significantly different species

148 composition than plots under intensive browsing (*in situ* density) during the final year of the

149 experiment (Table 2, Fig. 1). Indeed, a small density reduction (15 deer $\cdot$ km^{-2}) led to a distinct plant

150 **temporal pathway** from that observed under intensive browsing, but further reduction, even to 7.5

151 deer $\cdot$ km^{-2}, was insufficient to significantly alter plant communities over a period of eight years

152 after clearcutting. More time would be required to determine whether plant communities under the

153 intermediate deer densities tested could eventually emerge from the apparent stable state achieved at

154 year six and further diverge from those affected by intensive browsing.

155 The positive score of ***Poaceae*** spp., *Pteridium aquilinum* (L.) Kuhn, *Cirsium arvense* (L.)

156 Scopoli, *Carex* spp. and *Gymnocarpium dryopteris* (L.) Newman, *Mitella nuda* L. and *Equisetum*

157 spp. along the right vertical axis of the PRC indicates that these species benefited from the

158 conditions generated by heavy browsing at *in situ* deer density, **notably via the suppression of**

159 **competitive species** (Fig. 1). Graminoid plants (including *Carex* spp.) usually thrive under high

7

160   deer density (Fisichelli et al. 2013), likely due to their basal meristems, high shoot densities and

161   capacity for compensatory growth (Ferraro and Oesterheld 2002). Although pteridophytes could

162   constitute an alternative foraging choice at very high deer browsing intensity (Rooney 2009), their

163   palatability is usually considered low due to the presence of defense metabolites, such as a high

164   concentration of tannins (Jones and Firn 1979). This could explain the association of *P. aquilinum*,

165   *G. dryopteris* and *Equisetum* spp. with *in situ* deer density on Anticosti. Furthermore, decline (Perrin

166   et al. 2011) and even elimination (Kelly 2000) of ferns has often occurred following deer exclusion,

167   a trend that has been associated with increased competition from recovering species sensitive to

168   browsing. *Cirsium arvense* has the advantage of possessing physical defenses, which are generally

169   recognized to be efficient protection against herbivores, though its greater abundance under high

170   herbivore density has been mainly associated to competitive release (Edwards et al. 2000). **Despite**

171   **the presence of physical defenses, *Cirsium* species could contribute to deer diet (Austin and**

172   **Urness 1983), especially after the first frosts of the fall, and its seeds can be hooked to**

173   **herbivore fur and dispersed around, which may contribute to its occurrence under high**

174   **herbivore densities.**

175   Under reduced browsing pressure, palatable species with lower tolerance to browsing, such as

176   *Chamerion angustifolium* (L.) Holub., *Rubus pubescens* Raf., or *Cornus canadensis* L., were the

177   main species responsible for the **temporal trajectories** of communities (Fig. 1). *Chamerion*

178   *angustifolium* is a highly palatable species that has recently been identified as a biological indicator

179   of low deer density in clearcut boreal forests (≤ 7.5 deer $\cdot$ km^{-2}; Bachand et al. 2014b). Although *C.*

180   *angustifolium* is not known to create a long-term seed bank (Thompson et al. 1993), its seeds can be

181   dispersed over hundreds of kilometers (Solbreck and Andersson 1987), which could explain how it

182   can establish in Anticosti deer exclosures despite its quasi-absence from unmanaged areas of the

183   island. *Rubus* spp are known to thrive after clearcutting (Horsley et al. 2003), and their positive

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184 response to reduced deer density might reflect their sensitivity to competition with **graminoids** and

185 other spiny plants like *Cirsium* at high deer densities. *Rubus* spines are also rather soft at the early

186 stages of its development, and early browsing at high density might prevent the development of full

187 plant height and the associated defense structure. Among the seven species identified as drivers of

188 **temporal trajectories** after deer density reduction (Fig. 1), three were species associated to mature

189 boreal forests: *Cornus canadensis*, *Linnaea borealis* L., and *Maianthemum canadense* Desf.

190 Clearcutting has been shown to be a disturbance essential for catalyzing compositional changes after

191 deer density reduction (Tremblay et al. 2007), but our study shows that it may also benefit closed

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

193 **Traits composition**

194 The above changes in species composition of herbaceous communities were mirrored in their

195 functional trait composition, with curves showing similar trajectories after deer management: rapid

196 changes in functional traits were observable between two and six years after treatment was initiated,

197 followed by almost constant trait assemblages after six years (Fig. 2). However, the functional

198 components of herbaceous communities seemed more resilient than their species composition *per*

199 *se*. Indeed, it seems unnecessary to completely exclude deer to achieve a significant change in plant

200 trait communities, as plots with a density of 7.5 deer $\cdot$ km^{-2} were significantly different from those

201 under *in situ* densities after eight years of succession (Table 2). On this point, our findings concur

202 with those of Tremblay et al. (2006), who also observed that the biomass of dominant/preferred

203 herbaceous species recovered rapidly at densities under 7.5 deer $\cdot$ km^{-2}. The plant traits favored

204 under densities equal to or higher than 15 deer $\cdot$ km^{-2} included wind- or gravity-dispersed seeds,

205 erect foliage, storage organs, exotic origin, as well as vegetative propagation and self- and abiotic

206 pollination (Fig. 2). Most of these traits have previously been identified as efficient strategies for

207 ensuring persistence under foraging pressure by large herbivores (e.g., Wiegmann and Waller 2006),

9

208   and as potentially having significant cascading effects on other taxa (**Nuttle et al. 2011**), notably on

209   pollinators by making plants less attractive to them (Vázquez and Simberloff 2004). On the other

210   hand, reducing deer density favored species with brightly colored flowers and **compound**

211   **inflorescences** pollinated by animals and producing large seeds and fleshy fruits, dispersed by birds

212   or other animals (Fig. 2). **Plant species found under reduced deer density therefore seem to have**

213   **the capacity to allocate resources to sexual reproductive structures.** Investment in flowers

214   attractive to pollinators and in fleshy fruits attractive to birds may indicate that the recovery of these

215   forest systems **after deer control** is not limited to plant species **but also involved other taxa**

216   **indirectly through the change of plant trait communities**. Recent studies on Anticosti Island have

217   indeed shown that total abundance, richness and diversity of songbirds increased at deer densities ≤

218   7.5 deer · km^{-2} due to higher abundance of *Betula papyrifera* (Cardinal et al. 2012). Insects

219   responded to plant regeneration under reduced deer densities according to their degree of

220   dependence on plants, with the fastest response by Lepidoptera, a moderate response by Apoidea

221   and Syrphidae, and no response by Carabidae (Brousseau et al. 2013). In addition, brightly colored

222   flowers in studied stands generally represented palatable species (**Table S1**) associated with

223   pollinators. The resilience of plant communities after deer control should thus foster higher trophic

224   guilds, notably pollinators and seed dispersers, but the magnitude of this relationship has yet to be

225   determined (Bachand et al. 2014a). **Our study is based on averaged traits from the literature and**

226   **further investigation would be needed to assess the ability of species to flower and produce**

227   **fruits along different deer densities, which could reflect plasticity within species and reveal**

228   **some mechanistic adaptation of plants to persist or recover after intense browsing.**

229   The majority of the traits analyzed in our study were binary traits describing aerial plant parts.

230   Using numerical traits, such as specific leaf area; traits relevant to herbivory, such as nitrogen

231   content of leaves, proportion of fibers and secondary metabolites or digestibility; and integrating

232   root traits, such as specific root depth or nitrogen content, could provide further insight into the

233   resilience of individual ecosystem functionality (e.g., nutrient cycle or soil stability; Cornelissen et

234   al. 2003). The use of a reference ecosystem may also help to assess whether a system is recovering

235   functionality. For example, Aubin et al. (2008) pointed out the need for specific forestry practices to

236   accelerate the regeneration of an herbaceous community functionally similar to that of natural old

237   growth forests. Yet, reference ecosystems are lacking on Anticosti Island, as deer have been

238   affecting all forest stands for more than 100 years. Setting up reference ecosystems on the mainland

239   would pose comparison problems, since the response of functional traits may still be context-

240   dependent, in that the behaviour of common species with unusual attributes might lead to a different

241   trait composition after a change in grazing regime (Pakeman 2004). Although comparison with a

242   reference ecosystem is impossible for many areas under large herbivore pressure, as on Anticosti,

243   demonstrating that succession can lead to species assemblages and functional communities distinct

244   from those on sites subjected to intensive browsing, provides evidence of ecosystem resilience.

245   Interpreting the species and functional traits responsible for these trajectories can further increase

246   our confidence in this resilience.

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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	millimeters
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

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Table 2. Statistical differences between curves at year eight after the establishment of deer control treatments. Post-hoc comparisons of curves were performed with Monte Carlo permutations (n=999). In order to respect the comparisonwise error of 0.05, a Šidák correction was applied to each pairwise comparison (Šidák 1967). Since we had four treatments, the *p* value for each pair was determined to be 0.0085.

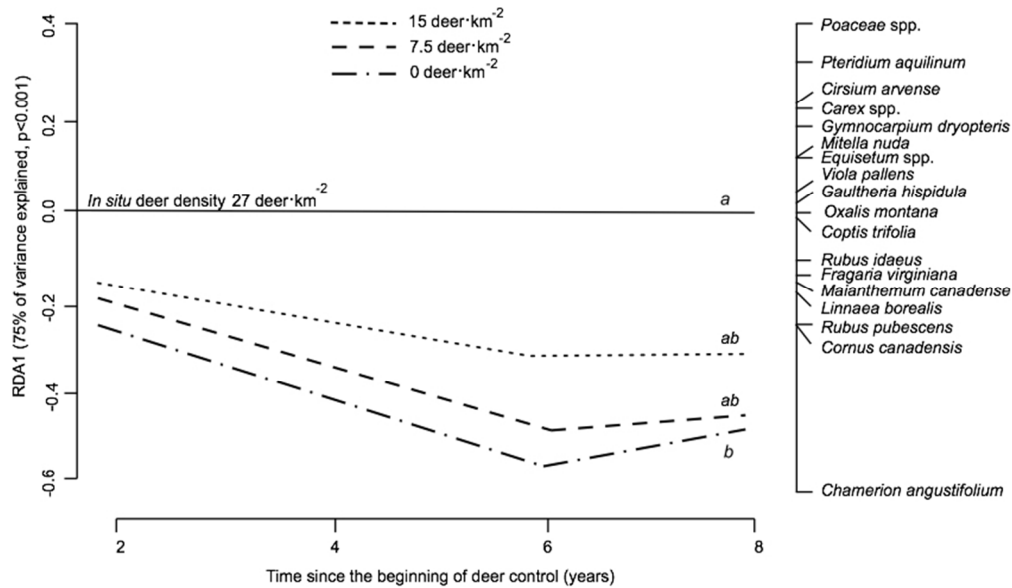| Comparison	F	df	*p*-value
Species composition			
In situ vs 15 deer $\cdot$ km^{-2}	2.581	1/12	0.160
In situ vs 7.5 deer $\cdot$ km^{-2}	5.516	1/12	0.017
In situ vs 0 deer $\cdot$ km^{-2}	6.772	1/12	*p*<0.001*
15 deer $\cdot$ km^{-2} vs 7.5 deer $\cdot$ km^{-2}	1.891	1/12	0.490
15 deer $\cdot$ km^{-2} vs 0 deer $\cdot$ km^{-2}	2.509	1/12	0.230
7.5 deer $\cdot$ km^{-2} vs 0 deer $\cdot$ km^{-2}	0.901	1/12	0.800
Trait composition			
In situ vs 15 deer $\cdot$ km^{-2}	2.908	1/12	0.059
In situ vs 7.5 deer $\cdot$ km^{-2}	4.293	1/12	*p*<0.001*
In situ vs 0 deer $\cdot$ km^{-2}	6.217	1/12	*p*<0.001*
15 deer $\cdot$ km^{-2} vs 7.5 deer $\cdot$ km^{-2}	2.511	1/12	0.130
15 deer $\cdot$ km^{-2} vs 0 deer $\cdot$ km^{-2}	3.926	1/12	0.005*
7.5 deer $\cdot$ km^{-2} vs deer $\cdot$ km^{-2}	3.610	1/12	0.020

Fig. 1. Principal Response Curves showing the temporal trajectory in species composition of herbaceous communities of Abies balsamea stands after clearcutting at different levels of reduced deer density as compared to in situ deer density. The principal response curves with the same letter are not significantly different eight years after deer density control, following post-hoc comparisons of curves with Monte Carlo permutations (n=999) and a Šidák correction (see 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.
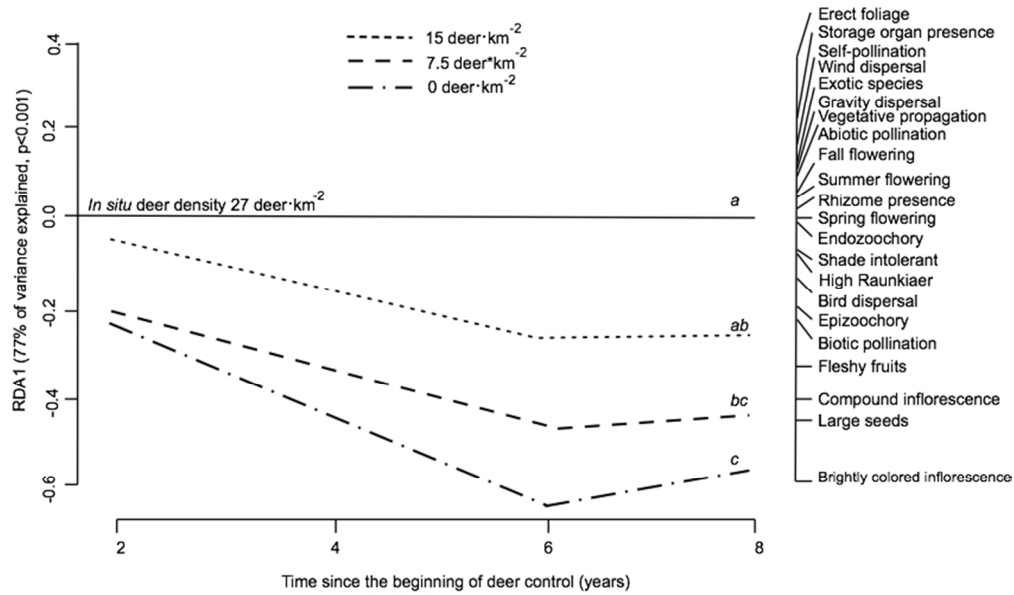213x139mm (100 x 100 DPI)

Fig. 2. Principal Response Curves showing the temporal trajectory in species traits of herbaceous plant communities of Abies balsamea stands after clearcutting at different levels of reduced deer density as compared to in situ deer density. The principal response curves with the same letter are not significantly different eight years after deer density control, following post-hoc comparisons of curves with Monte Carlo permutations (n=999) and a Šidák correction (see 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.
213x140mm (100 x 100 DPI)