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Successful forest restoration using plantation at high deer density: How neighboring vegetation drives browsing pressure and tree growth

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ABSTRACT

Browsing can be an environmental stress to forest ecosystems, where the composition and structure of plant communities depend on the balance between ungulate browsing and the ability of plants to tolerate and acclimate to this stressor. Tree planting is a management tool for restoring forest whose integrity has been compromised by the intensity and repetition of browsing. This tool may be insufficient when the stress leading to forest degradation is ongoing. Balsam fir (*Abies balsamea* (L.) Mill.) plantations are used on Anticosti Island (Quebec, Canada) to restore winter habitat for white-tailed deer (*Odocoileus virginianus* Zimmermann, 1780). To promote natural regeneration and growth of planted firs that are the staple winter forage of deer, enclosures were temporarily erected and deer densities reduced to decrease browsing pressure. The stress induced by heavy browsing at the time of fence removal and the density of competitors in regenerating cutblocks, however, could compromise fir growth and forest recruitment. Our objective was to identify factors influencing browsing intensity and balsam fir's growth following fence removal. We aimed to identify factors influencing lateral browsing intensity and number of trunk reiterations on fir at the landscape scale, including distance and size of the surrounding forests, and at the local scale through intraspecific density-dependence and interspecific associative effects. We then sought to identify the stressors most influencing balsam fir growth among browsing variables and a neighborhood crowding index (NCI). We measured browsing intensity and growth of 114 balsam firs 8 years following planting and again 2 and 4 years after dismantling two management enclosures. At the landscape scale, our results showed that when balsam fir was more than 150 m from a forest edge, the probability of browsing was close to zero and consistently a low percentage of shelter area surrounding a focal fir led to a decrease in browsing pressure. At the local scale, intensity of lateral browsing increased with the NCI of white spruce (*Picea glauca* (Moench) Voss). Fir growth was negatively influenced by the additive effects of browsing and NCI. Finally, our results showed that 19.7% (95 %CI: 4.5%, 42.6%) of the effect of the surrounding vegetation on growth was mediated by browsing. The success of forest ecosystem restoration through planting depends on density of neighboring tree species that can generate environmental stress by influencing growth indirectly through browsing as well as directly through competition for resources.

1. Introduction

Ungulates can impose a disturbance to forest ecosystems, affecting the composition and structure of plant communities (Côté et al., 2004). The net effect of herbivory depends on the balance between ungulate foraging and the ability of plants to recover from browsing (Augustine and McNaughton, 1998). The worldwide proliferation and range expansion of several cervid (hereafter deer) species present numerous challenges for ecosystem conservation (Côté et al., 2004). Browsing by cervids reduces vegetation biomass and favors resistant or tolerant

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plants (Royo and Carson, 2006). Regeneration and recruitment failure can shift successional pathways to more open environments (Barrette et al., 2014; De Vriendt et al., 2021; Tanentzap et al., 2011) or to environments dominated by browse resistant species (Augustine and McNaughton, 1998; Hidding et al., 2013). Such a shift in plant communities may alter ecosystem functions (Côté et al., 2004), which can have cascading effects on other animals (Suominen et al., 2006). Reducing deer densities does not always allow the return of natural regeneration, especially when browsing has occurred over a long period of time and depleted both the abundance of reproductive individuals and the available seed bank (Rooney et al., 2002; Rooney and Waller, 2003). When browsing prevents colonization of native forest species, plantations can be used to restore forest ecosystems (Parrotta et al., 1997; Thiffault et al., 2013). Plantations often require protection from browsing, though, as deer can put great pressure on growth and survival of planted seedlings during their early growth (Hackworth et al., 2018).

Abundance and quality of nutritional resources in regenerating forests are particularly attractive to deer (Massé and Côté, 2012a; Moser et al., 2006)., This high resource density found in regenerating forests, including those in plantation systems, can also provide benefits for regeneration facing herbivory. A high abundance of resources may diminish browsing impacts by diluting its effects on all individuals (Otway et al., 2005). Plant neighborhoods can also influence herbivore selection of a focal plant species, a phenomenon known as associational effects (Underwood et al., 2014). Associational effects can decrease (Atsatt and O' Dowd, 1976; Tahvanainen and Root, 1972) or increase (Bergvall et al., 2006; Thomas, 1986) the browsing pressure experienced by planted individuals. Browsing is modulated by associational effects, the strength of which is induced by the nature of neighboring species, their density and distance to each other (Champagne et al., 2016; Underwood et al., 2014). Plant neighborhood can, however, exert a competitive effect on planted tree individuals. The strength of competition for environmental resources depends on the spatial distribution of neighboring trees, abundance, size, and neighboring species, and influences tree growth and survival (Canham et al., 2006, 2004). While many studies have assessed the short- (Faure-Lacroix et al., 2013; Jobidon, 2000; Thiffault et al., 2012) and mid-term (Brousseau et al., 2017; Wagner and Robinson, 2006) effects of competition and browsing on planted trees, there is still a need to measure the cumulative effect of competition and browsing on the capacity of planted trees to form a new forest canopy.

Additionally, silviculture directly alters stand- and landscape-level composition, structure and heterogeneity, thus influencing deer foraging behavior (Massé and Côté, 2012b), plant competition (Jobidon, 2000), and ultimately regeneration success (Barrette et al., 2014). Clearcut harvesting creates a sharply delineated edge between the forest matrix and regeneration areas. Natural or artificial regeneration suffers more damages near forested edges than in open areas (Alverson et al., 1988). Forest patches near forest edges provide escape cover when deer perceive a risk (Kuijper et al., 2013).

Our objective was to evaluate the factors influencing browsing by white-tailed deer (*Odocoileus virginianus* Zimmermann, 1780) on planted balsam fir (*Abies balsamea* (L.) Mill.), and determine the overall effect of herbivory and stem neighborhood on tree growth on Anticosti Island, Quebec (Canada). First, we examined which factors mostly influence browsing intensity at the landscape scale. Specifically, we posited that browsing intensity in regenerating stands is highest closer to the edge with intact forest and diminishes as distance from that edge increases (Champagne et al., 2018; Massé and Côté, 2012b). We wanted to identify and measure the strength of inter- and intraspecific effects of surrounding vegetation on fir. We posited that browsing on a focal fir is a trade-off between factors acting at the landscape scale (proximity to forest edges and area of surrounding shelter stands) and at the local scale (such as the surrounding vegetation).

Second, we aimed to estimate the relative effect of both browsing and competition stressors on balsam fir growth. Because browsing pressure varies with density of neighboring tree species around fir (Champagne et al., 2020), we expected that the effect of neighboring trees density on fir growth would be mediated by browsing. We predicted that neighboring trees have a direct negative impact on growth, but an indirect positive impact mediated by browsing. However, an indirect positive impact could be mediated by browsing intensity when neighboring firs create a resource dilution effect (*sensu* Otway et al. 2005) or when other tree species create an associational or neighbor contrast defence (*sensu* Champagne et al. 2016). In the case of resource dilution effect, the browsing pressure is distributed among all consumed plants. Therefore, when these plants are present in high abundance, the pressure experienced by each of them is reduced (Otway et al. 2005). Regarding neighbor contrast defense and associational defense, the focal plant is surrounded by other plant species that the browsers select or avoid. In both cases, this results in a reduction in the intensity of browsing pressure experienced by the focal plant (Champagne et al. 2016). Furthermore, when neighboring trees create an associational or neighbor contrast susceptibility (*sensu* Champagne et al. 2016), the indirect effect on growth could be negative. Associational susceptibility occurs when neighboring plants are selected but also attract browsers to the focal plant, while neighbor contrast susceptibility occurs when avoidance of a neighboring plant concentrates browsing on the focal plant (Champagne et al. 2016). Finally, we anticipated that combining the effects of browsing and neighboring tree would have better predictive power of fir growth than considering these factors independently.

2. Material and methods

2.1. Study area

We conducted our study on Anticosti Island, a large forested island (7,943 km^2) located in the western Gulf of St. Lawrence, Quebec, Canada (49°28′ N, 63°00′ W). The climate is subpolar sub-humid with an average annual precipitation of 1 005 mm (Gouvernement du Québec, 2022). The average annual temperature is 1.9 °C with cool and short summers (the average growing season is 171 days); minimum temperatures in winter (mean temperature in January: −10.7 °C) are higher than those of the mainland (Gouvernement du Québec, 2022). The fossiliferous limestone bedrock of the island is shaped in a gently angled plateau with forested plains and hillsides interspersed with peatlands (Grondin et al. 2007). Forests belong to the eastern balsam fir–paper birch (*Betula papyrifera* Marshall) bioclimatic domain (Saucier et al., 2009) and are dominated by mature stands of balsam fir, white spruce (*Picea glauca* (Moench) Voss), and black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.).

In the late 19th century, ca. 220 white-tailed deer were introduced to the island (Newsom, 1937). In 2006, the deer population was estimated at $>$ 20 deer/km^2 (Rochette and Gingras, 2007). In the absence of predators, deer population on the island is mainly regulated by the availability of resources in winter (Massé and Côté, 2012b). <5% of the island's deer population is harvested annually by sport hunters, a rate insufficient to ensure population control (Simard et al. 2010). The browsing pressure is sufficient to inhibit regeneration of the most selected species (Tremblay et al., 2007). Chronic browsing has altered the structure and composition of Anticosti forests, resulting in the near extirpation of the shrub (Potvin et al., 2003), in the decrease of the abundance of flowers and fruiting plants of the herbaceous layer (Pellerin et al., 2006; Bachand et al., 2015) and in the depletion of deciduous species, making balsam fir the primary winter forage of deer (Lefort et al., 2007). The dependence of deer on fir has resulted in strong browsing pressure on fir regeneration, leading to a modification of natural successional pathways towards white spruce stands (Barrette et al., 2014). The only other large herbivore species present on the island is the moose (*Alces alces* Linnaeus, 1758), but their density is very low and their impact on vegetation is minor compared to white-tailed deer (Potvin et al. 2003). Snow-shoe hare (*Lepus americanus* Erxleben, 1777)

Table 1
History of management enclosures used to protect balsam fir (*Abies balsamea* (L.) Mill.) regeneration from high white-tailed deer (*Odocoileus virginianus* Zimmermann, 1780) density on Anticosti Island (Québec, Canada).

Enclosure	Km 27	Lac Claude
Coordinates	49°51′ N, 64°10′ W	49°54′ N, 64°17′ W
Area	4.4 km^2	5.7 km^2
Years of clear cut	1999 and 2002	2003 and 2004
Years of closure	2004	2004
Years of planting	2006	2006 and 2007
Years of dismantling	2016	2018

is also present on the island, but the damage it causes to the trees is limited to the lower branches. Furthermore, balsam fir does not play as central role in its diet as it does for white-tailed deer.

A forest management plan was implemented in the late 1990 s to promote fir regeneration. Large fenced areas of several km^2 (management enclosures) were erected around harvested areas with the objective of emulating natural disturbance and restoring the regeneration dynamics of balsam fir (Côté et al., 2014). White-tailed deer are present within the enclosures, but their density has been greatly reduced by sport hunting to encourage the establishment and recruitment of fir. In addition, planting of nursery-grown fir seedlings was conducted in areas where the stocking of balsam fir seedlings was too low to allow the natural regeneration of the stand. Once the fir trees reached sufficient height to escape deer browsing (estimated at 2.25 m based on Potvin, 1995), the enclosures were dismantled (Côté et al., 2014). We conducted our study in two management enclosures that protected regenerating balsam fir forests for 12 (Km 27) and 14 (Lac Claude) years (Table 1).

2.2. Data collection

In each of the two enclosures, we randomly positioned 19 circular plots of 400 m^2 within the regeneration areas. In each plot we marked the 10 largest fir trees in 2012. It was not possible to distinguish whether the selected fir trees were from natural regeneration or planted. In 2020, we randomly selected three focal firs of the 10 marked trees per plot and calculated their growth rate over 8 years (2012–2020). Each focal fir represents an observational unit. Our study period began six years after the first fir plantings and ended two (Lac Claude) and four (Km 27) years after the removal of fences from the management enclosures (Table 1).

2.2.1. Browsing

In 2012, we collected two browsing variables: the occurrence (presence/absence of at least one browsed stem) of apical and lateral browsing. In 2020, we quantified cumulative apical browsing and estimated lateral browsing intensity. We counted the number of times a new vertical growth axis has formed from lateral buds or branches following the removal of the apical dominance of the primary axis to obtain the number of reiterations (Boudreau LeBlanc, 2018). To assess the intensity of lateral browsing in 2020, we circled around each focal fir tree and inspected the branches by classifying each tree according to the leaf and twig volume browsed in 5 categories (0% no browsing, 1–25%, 26–50%, 51–75% and 76–100%).

2.2.2. Landscape characteristics

Using forestry maps, we calculated the distance of each focal fir tree to the nearest forest edge. We classified stands according to their potential for use as winter shelter habitat by deer based on Hébert et al. (2013) The stands that we considered as likely to provide shelter for deer during winter are those with a height of over 7 m, a canopy closure > 40%, and composed of either white or black spruce stands over 40 years old or balsam fir stands over 20 years old. We analyzed the area of shelter around each plot over 6-ha (radius = 138 m), corresponding to the size of the core areas used by white-tailed deer on Anticosti during winter (Massé and Côté, 2012b).

2.2.3. Neighborhood crowding

We measured the regenerating tree community in a 5 m radius (78.54 m^2) plot centered around each focal tree. We sampled only neighboring saplings and trees taller than 50 cm because below 50 cm, the snow cover hides the trees (Potvin, 1995) and we aimed to include only nearby trees that could cause associational effects. Balsam fir and white birch (two browsed species) as well as white and black spruce (two avoided species) represented 98% of the species sampled; the other present species were tamarack (*Larix laricina* (Du Roi) K. Koch), American mountain-ash (*Sorbus americana* Marshall), and Pennsylvania cherry (*Prunus pensylvanica* L. f.), but in very low abundances. We measured their height, diameter at ground level and distance from the focal fir. Using these data we calculated Hegyi's (1974) competition index:

$$NCI_i = \sum_{\substack{j=1 \\ j \neq i}}^{n} \frac{d_j}{d_i L_{ij}}$$

where, d_i and d_j are the diameter at ground level of the stem of focal fir i and neighboring tree j, respectively, and L_{ij} is the distance between i and j.

The competition index approximates several different mechanisms: on the one hand, competition mechanisms for resources experienced by the focal tree (e.g., light, water, nutrients) and on the other hand, density dependence mechanisms that influence browsing. We thus prefer to name this index "neighborhood crowding index" (NCI), a name that does not solely refer to the competition mechanism. We included dead trees in the calculation of the NCI. We also recalculated the NCI after excluding dead trees but obtained similar results (not shown hereafter).

2.2.4. Balsam fir growth

Using height and ground level diameter data of the 114 focal balsam fir trees measured in 2012 and 2020, we calculated a volume index (v) for each year:

$$v_t = \frac{h_i \, x \, \pi}{3} x \left(\frac{d_i}{2}\right)^2$$

where, h_i: height of the focal fir and d_i: diameter of the stem at ground level. This index was then used to calculate saplings relative growth as a function of their size, thus allowing us to compare the growth of plants whose initial size and age differed. The relative growth rate measures the production capacity of a plant (Pommerening and Muszta, 2016). The Relative Growth Rate in volume (RGR_v) (Pommerening and Muszta, 2015) of each fir tree was calculated as:

$$RGR_v = \frac{log(v_{2020}) - log(v_{2012})}{t_{2020} - t_{2012}}$$

where t is the year of measurement.

2.3. Statistical analyses

To achieve our first objective of evaluating the factors influencing browsing intensity by white-tailed deer on balsam fir, we used the intensity of lateral browsing and the number of stem reiterations as

response variables. We excluded one observation of a dead fir for which it was difficult to correctly quantify the intensity of browsing experienced in the past (n = 113). Intensity of lateral browsing, measured as the percentage of leaf and twig volume browsed, was normalized using a logit transformation. We modeled intensity of browsing according to two hypotheses corresponding to landscape scale and local scale (see below). Potential explanatory variables used for the landscape scale were distance to the nearest forest edge and areas of shelter stand over 6-ha around the focal fir. Potential explanatory variables for the local scale were the total neighborhood crowding index and the neighborhood crowding index by species (for *A. balsamea*, *P. glauca*, *P. mariana* and *B. papyrifera*).

To achieve our second objective of evaluating the factors influencing the growth of fir, we used RGR_v as a response variable. Potential explanatory variables used to represent browsing were the occurrence of apical and lateral browsing on focal fir trees in 2012 and the intensity of lateral browsing and number of reiterations measured in 2020. We used NCI as a potential explanatory variable representing neighborhood crowding.

All statistical analyses were performed in R (R Core Team, 2020). Continuous covariates were standardized by subtracting their mean and dividing by the standard deviation (Gelman and Hill, 2007). We calculated Spearman's rank correlation coefficients before model selection to detect collinearity among factors. All factors with a correlation coefficient > 0.7 were studied in separate candidate models. To achieve our objectives of evaluating the factors influencing browsing intensity by white-tailed deer on balsam fir and growth, we used a three-stage process to refine our choice of explanatory models (Rosenblatt et al., 2021).

1. We identified the most supported models using a landscape scale and a local scale model selection for browsing intensity, as well as a browsing and a neighborhood crowding model selection for RGR_v. We used Akaike's information criterion (Akaike, 1998) corrected for small sample size (AICc) with a delta AICc < 2 threshold to determine the best supported models using the AICcmodavg package (Mazerolle, 2020).
2. We compared the most supported models from the different model selections based on their AICc to determine which of the landscape or local scales plays a more determining role in the browsing intensity of deer. Similarly, we compared the AICc of the most supported browsing model with the one from the NCI model to determine if growth was more influenced by a top-down or bottom-up effect.
3. We evaluated the additive effect of the most supported models. A final set of models was considered with the most supported models and a combination of effects included in these models. Potential interactions between effects were also investigated. Consistently, model selection was based on AICc.

We fit linear mixed-effects models to estimate the intensity of lateral browsing using the lme() function of packages nlme (Pinheiro et al., 2020). We fit negative binomial generalized fixed-effects models to estimate the number of reiterations using the glm.nb() function of MASS (Venables and Ripley, 2002) and model coefficients were exponentiated to be interpreted in terms of incidence rate ratios. We fit linear fixed-effects models to estimate RGR_v using the lm() function of the R stats package (R Core Team, 2020). Spatial autocorrelation was tested by means of a Moran I test (Moran, 1948), using the R package DHARMa (Hartig, 2022). The intensity of lateral browsing was the only response variable showing spatial correlation. For this response variable, the dependency structure was addressed by incorporating a spatial correlation structure. Models with exponential, Gaussian, and spherical correlation structures were separately fitted and the model with the Gaussian structure showed the lowest Akaike Information Criterion (AIC) and was used for the selection of candidate models. We verified residuals from models for normality and homoscedasticity assumptions using standard graphical approaches.

Finally, we tested the hypothesis that effect of neighborhood crowding on growth of focal firs could be mediated by lateral browsing intensity. We performed a mediation analysis to explore the underlying mechanisms by which the neighborhood crowding trees influence RGR_v through lateral browsing intensity, a potential mediator variable. Lateral browsing intensity was normalized using a logit transformation, then a set of linear fixed-effects models were fitted to estimate the mediation effects (Baron and Kenny 1986). The proportion of mediation effect was quantified and associated with a 95% bias-corrected and accelerated bootstrap confidence interval based on 1000 bootstrapped samples, using the R package mediation (Tingley et al. 2014).

3. Results

Among the set of potentially explanatory factors, only two factors, distance to the edge and shelter area, were found to be highly correlated ($r = -0.93$). Not surprisingly, distance to the edge decreased with the increase in shelter area. Consequently, these two factors were included in separate candidate models to avoid any collinearity that could otherwise biased parameter estimation and led to inflated standard errors on estimates.

3.1. Browsing intensity

Browsing intensity on focal fir trees remained relatively low over time; of the 113 focal fir trees, only 12 had more than 50% lateral browsing and 23 had more than one stem reiteration indicating successive apical browsing. In 2020, 14 years after planting, 84% of the focal firs attained or exceeded $\geq$ 225 cm in height (Appendix A – Fig. A1), at which point, the top of the tree can be considered free of

Table 2
Candidate models and model selection results for variables influencing white-tailed deer-induced (*Odocoileus virginianus* Zimmermann, 1780) lateral browsing intensity on balsam fir (*Abies balsamea* (L.) Mill.) at landscape and local scales using AICc, in a habitat restoration context on Anticosti Island (Québec, Canada). Lateral browsing intensity was analyzed after a logit transformation using linear mixed-effects models with spatial autocorrelation structure and plot as a random variable.

Candidate models for landscape-scale	K	AICc	ΔAICc	Weight	R^2
edge distance	6	495.66	0.00	0.51	0.09
shelter area	6	496.05	0.39	0.42	0.09
Null model	5	499.83	4.17	0.06	–
Candidate models for local-scale	**K**	**AICc**	**ΔAICc**	**Weight**	**R^2**
white spruce NCI	6	488.67	0.00	0.74	0.12
white spruce NCI + black spruce NCI + white birch NCI	8	492.71	4.04	0.10	0.12
balsam fir NCI + white spruce NCI + black spruce NCI + white birch NCI	9	492.93	4.26	0.09	0.13
total NCI	6	493.74	5.07	0.06	0.07
white birch NCI	6	496.65	7.98	0.01	0.04
Null model	5	499.83	11.16	0.00	–
black spruce NCI	6	501.29	12.62	0.00	0.01
balsam fir NCI	6	501.97	13.30	0.00	0.00
Candidate models for landscape and local	**K**	**AICc**	**ΔAICc**	**Weight**	**R^2**
shelter area + white spruce NCI	7	484.09	0.00	0.61	0.20
edge distance + white spruce NCI	7	485.35	1.26	0.32	0.20
white spruce NCI	6	488.67	4.58	0.06	0.12
edge distance	6	495.66	11.57	0.00	0.09
shelter area	6	496.05	11.96	0.00	0.09
Null model	5	499.83	15.74	0.00	–

K = number of estimated parameters for each model, AICc = Akaike information criterion with correction for small sample size, R^2 = coefficient of determination - marginal Nakagawa's R2 for mixed-effects models.
R^2 are provided for information only; models were compared using AIC.

Table 3
Coefficient of best supported models (ΔAICc < 2) explaining lateral browsing intensity and number of stem reiterations on balsam fir (*Abies balsamea* (L.) Mill.) in management enclosure plantations on Anticosti Island (Québec, Canada) and under heavy browsing pressure by white-tailed deer (*Odocoileus virginianus* Zimmermann, 1780).

	Lateral browsing intensity[a] Estimate (95 %CI)		Number of stem reiterations[b] Estimate (95 %CI)	
	Model 1	Model 2	Model 1	Model 2
White spruce NCI	0.83 (0.43, 1.23)	0.79 (0.38, 1.19)	–	–
Shelter area	0.70 (0.19, 1.21)	–	0.45 (0.18, 0.73)	–
Edge distance	–	−0.64 (1.16, −0.13)	–	−0.49 (−0.82, −0.16)
ΔAICc	0.00	1.26	0.00	2.08
R^2	0.20	0.20	0.17	0.14

CI = confidence interval, AICc = Akaike information criteria with correction for small sample size, R^2 = coefficient of determination - marginal Nakagawa's R2 for lateral browsing intensity and Nagelkerke's R^2 for number of stem reiterations, R^2 are provided for information only; models were compared using AIC. a: Linear mixed-effects models with spatial autocorrelation structure and plot as a random variable. b: Negative binomial models. All continuous variables were standardized.

browsing risk (Potvin, 1995).

The first step of the three-stage model selection process identified two best supported models at the landscape scale, the first including the distance to the nearest forest edge and the second the percentage of shelter area habitat within 6-ha (Table 2). The most supported model at the local scale was a univariate model composed of the NCI calculated exclusively from neighboring white spruce trees (Table 2).

In the second step, the comparison of AICc scores of the most supported models (ΔAICc < 2) showed that lateral browsing intensity was mainly driven by the local effect of white spruce NCI (AICc = 488.67) compared to landscape effects such as distance to edge (AICc = 495.66) and shelter area (AICc = 496.05; Table 2).

The third and last step of the selection process including the most supported models at the landscape and local scales as well as models combining these same models yielded two models with similar fit (Tables 2 and 3). With the first model, we found lateral browsing on fir intensified when seedlings were found surrounded by a large area of shelter habitat closer to a forest edge and in dense white spruce neighborhoods (Fig. 1a and 1b). A second model was also composed of spruce NCI and forest edge lateral browsing on spruce intensified when seedlings were found closer to a forest edge (Fig. 1c). When a balsam fir was more than 150 m from a forest edge, the probability of browsing was close to zero and consistently a low percentage of shelter area surrounding a focal fir led to a decrease in browsing pressure (Fig. 1b and 1c).

For the number of stem reiterations, the local explanatory variables did not yield a better supported model than the null model (Table 4). In contrast, at the landscape scale, model selection supported two models (Table 4), both playing a similar role as distance to the edge and shelter area were found to be highly correlated (r = −0.93). The first model showed that the percentage of shelter area within 6-ha around each balsam fir induced at least a 57% increase (Incidence Rate Ratio (IRR) = exp(0.45) = 1.57) in the predicted number of stem reiterations for each standard deviation increase in shelter area (Table 3, Appendix B – Fig. B1). The second model showed that the number of reiterations decreased with the distance to the edge, the model predicting a 45% decrease in the number of stem reiterations for each standard deviation increase in distance to the edge (IRR = exp(−0.59) = 0.55).

3.2. Balsam fir growth

The first model selection with the goal of identifying which browsing models had the greatest influence on RGR_v, showed that all tested browsing models had a better fit than the null model (ΔAICc with null model > 2), and the most supported model consisted of only one variable: the intensity of lateral browsing (Table 5). Comparison between the AICc of the intensity of lateral browsing model and the NCI model showed that this browsing variable slightly influenced growth more than the NCI (ΔAICc = 2.77) (Table 5).

Final model selection showed that RGR_v was negatively influenced by both intensity of lateral browsing (coef = −0.04, 95 %CI: −0.05, −0.02) and neighborhood crowding (coef = −0.03, 95 %CI: −0.05, −0.02) (Table 5, Fig. 2). We obtained similar results by analyzing the growth in height (Appendix C). Variables included in the best model explained 42% of the total variance in RGR_v (Multiple R^2 = 0.42).

The analysis of direct and indirect effects of NCI on balsam fir growth excluded a complete mediation by lateral browsing index (Table 6). Instead, a partial mediation was observed with an indirect effect of neighborhood crowding through lateral browsing representing 19.7% (95 %CI: 4.5%, 42.6%) of the total effect induced by NCI.

Similar results were observed in mediation analyses including growth in height as the dependent variable (Appendix C) and/or NCI calculated only by considering the neighboring white spruce as an independent variable (Appendix D – Table D1).

4. Discussion

We examined factors affecting browsing intensity and balsam fir growth in restoration plantations on Anticosti Island after white-tailed deer were given back access to previously fenced areas. At the landscape scale, the presence, proximity, and area of forest stands providing cover in winter influenced browsing intensity. At the local scale, density-dependent effects of neighboring trees influenced only lateral browsing intensity. Combined effects of browsing and neighborhood crowding better predicted fir growth than the single effects of these factors.

4.1. Browsing intensity

Browsing intensity increased with the proximity and size of forest stands providing cover. Our results indicate that the intensity of browsing, apical or lateral, was higher near forest edges and increased with the area of shelter habitat, and of spruce stands, over a 6-ha area around the focal fir. Our study confirms the presence of an edge effect on white-tailed deer foraging behavior on Anticosti Island, as reported by Champagne et al. (2018) in a context similar to the recently dismantled management enclosures we studied. Deer on the island select conifer edges in winter presumably to increase access to forage resources in adjacent clearcuts while minimizing the cost of locomotion involved in moving through deep snow cover (Massé and Côté, 2012b). In contrast with our results, Casabon and Pothier (2007) found that distance to edge did not influence browsing behavior on naturally regenerating seedlings on Anticosti Island. This suggests that the plantation forestry approach used in our study to promote fir provided deer with a sufficiently large amount of food to allow them to adopt a more conservative foraging behavior than the conditions experienced in the study by Casabon and Pothier (2007) in unfenced cutblocks. The harsh winters of 2015 and 2018 decreased the deer population on the island (Direction de la gestion de la faune de la Côte-Nord, 2019) and may have created a deer-forage ratio favorable to the observation of conservative foraging behavior. Additionally, we found browsing on fir intensified when shelter area was considered at the 6-ha scale. In unpublished results, we observed that equivalent models considering shelter habitats over a 30-

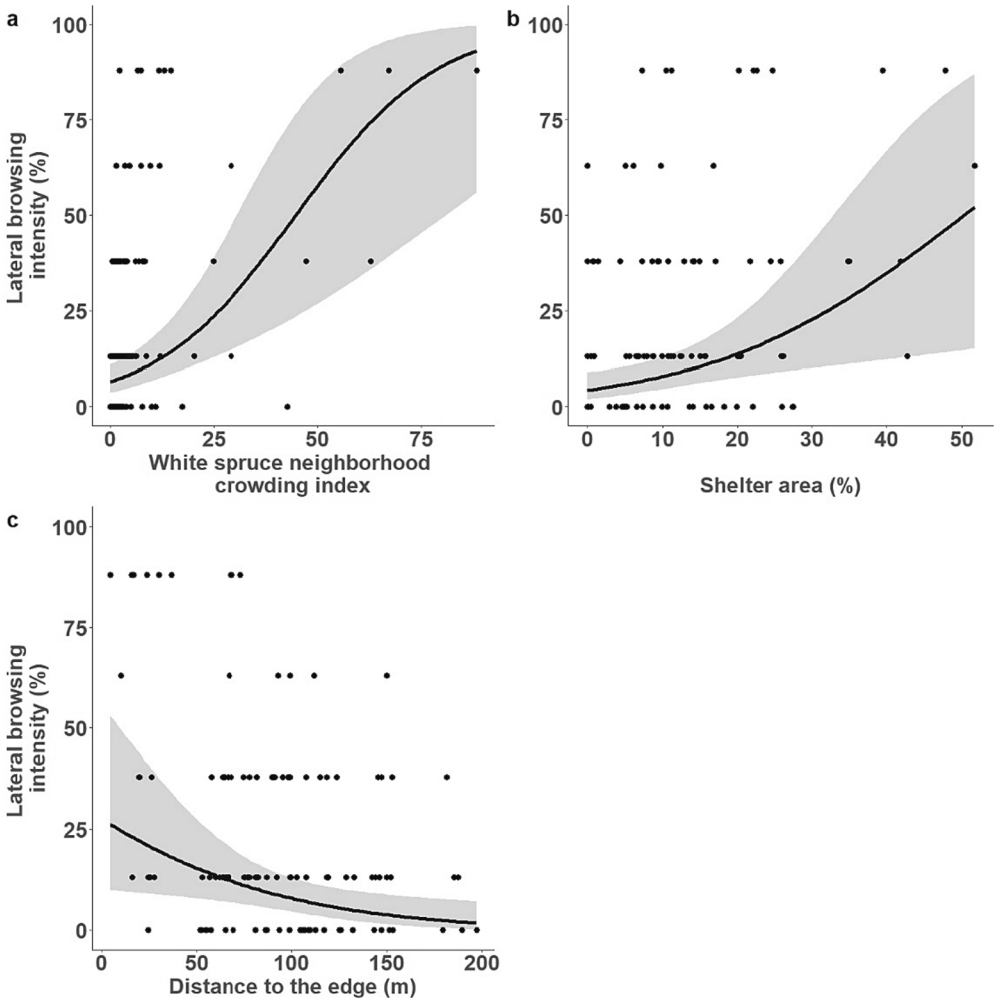

Fig. 1. Variables influencing white-tailed deer (*Odocoileus virginianus* Zimmermann, 1780) browsing on balsam fir (*Abies balsamea* (L.) Mill.) in the context of balsam fir restoration on Anticosti Island (Québec, Canada). Neighborhood crowding index from white spruce (*Picea glauca* (Moench) Voss) greater than 50 cm within a 5 m radius of the focal fir was positively related to the intensity of lateral browsing (%) (a). Area of shelter on 6-ha surrounding the focal fir tree (%) was positively related to the intensity of lateral browsing (%) (b). Distance to the nearest forest edge to the focal fir tree was negatively related to the intensity of lateral browsing (%) (c). Lines represent the predicted values (linear mixed-effects models); gray areas correspond to the 95% CI; points are the raw data.

Table 4
Candidate models and model selection results for variables influencing white-tailed deer-induced (*Odocoileus virginianus* Zimmermann, 1780) number of reiterations on balsam fir (*Abies balsamea* (L.) Mill.) at landscape and local scales using AICc, in a habitat restoration context on Anticosti Island (Québec, Canada). Number of stem reiterations was analyzed using negative binomial generalized fixed-effects model.

Candidate models for landscape-scale	K	AICc	ΔAICc	Weight	R^2
shelter area	3	258,88	0.00	0.73	0.17
edge distance	4	260,96	2.08	0.26	0.14
Null model	2	268,15	9.27	0.01	–
Candidate models for local-scale	**K**	**AICc**	**ΔAICc**	**Weight**	**R^2**
white birch NCI	3	267.83	0.00	0.20	0.04
Null model	2	268.15	0.32	0.17	–
black spruce NCI	3	268.33	0.50	0.16	0.03
total NCI	3	268.76	0.93	0.13	0.02
white spruce NCI	3	268.86	1.03	0.12	0.02
balsam fir NCI + white spruce NCI + black spruce NCI + white birch NCI	6	269.46	1.63	0.09	0.11
balsam fir NCI	3	269.87	2.04	0.07	0.01
white spruce NCI + black spruce NCI + white birch NCI	5	270.76	2.93	0.05	0.06

K = number of estimated parameters for each model, AICc = Akaike information criterion with correction for small sample size, R^2 = coefficient of determination – Nagelkerke's R^2.
R^2 are provided for information only; models were compared using AIC.

Table 5
Candidate models and model selection results for browsing and neighborhood crowding variables influencing Relative Growth Rate in volume (RGR_v) of balsam fir (*Abies balsamea* (L.) Mill.) over 8 years of growth (from 2012 to 2020) from plantations and natural regeneration on Anticosti Island (Québec, Canada) using AICc. RGR in volume was analyzed using linear mixed-effect models.

Candidate models for browsing	K	AICc	ΔAICc	Weight	R^2
lateral browsing intensity (2020)	3	−249.41	0.00	0.36	0.30
number of reiterations (2020) + lateral browsing intensity (2020)	4	−247.40	2.01	0.13	0.30
lateral browsing (2012) + lateral browsing intensity (2020)	4	−247.29	2.12	0.12	0.30
apical browsing (2012) + lateral browsing (2012) + number of reiterations (2020) + lateral browsing intensity (2020)	6	−245.98	3.43	0.06	0.32
number of reiterations (2020)	3	−216.62	32.79	0.00	0.06
apical browsing (2012) + number of reiterations (2020)	4	−215.97	33.44	0.00	0.07
Null model	2	−212.20	37.21	0.00	–
Candidate models for NCI	**K**	**AICc**	**ΔAICc**	**Weight**	**R^2**
NCI	3	−246.64	0.00	1.00	0.28
Null model	2	−212.20	34.44	0.00	–
Candidate models for browsing and NCI	**K**	**AICc**	**ΔAICc**	**Weight**	**R^2**
lateral browsing intensity + NCI	4	−268.17	0.00	1.00	0.42
lateral browsing intensity	3	−249.41	18.76	0.00	0.30
NCI	3	−246.64	21.53	0.00	0.28
Null model	2	−212.20	55.97	0.00	–

K = number of estimated parameters for each model, AICc = Akaike information criterion with correction for small sample size, R^2 = coefficient of determination – multiple R^2.
R^2 are provided for information only; models were compared using AIC.

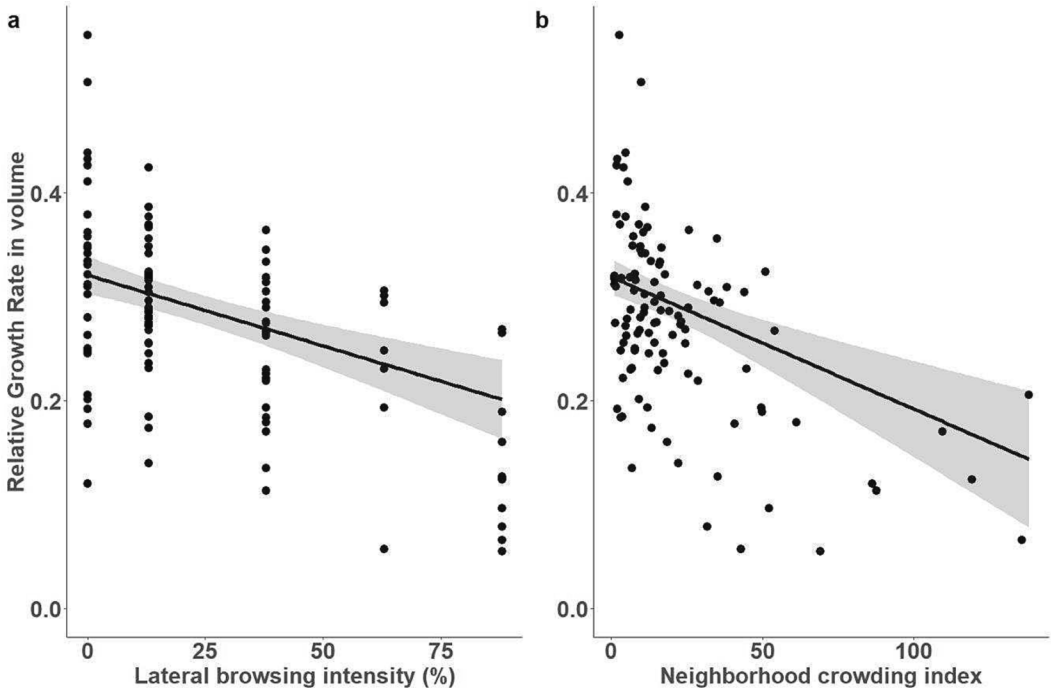

Fig. 2. Balsam fir (*Abies balsamea* (L.) Mill.) growth between 2012 and 2020 in the context of balsam fir restoration on Anticosti Island (Québec, Canada). Lateral browsing intensity (%) was negatively related to the relative growth rate in volume (RGR_v). Neighborhood crowding index from trees larger than 50 cm within a 5 m radius of the focal fir was negatively related to RGR_v (b). Lines represent predicted values from the generalized linear models; gray areas correspond to the 95% CI; points are the raw data.

ha area, which corresponds to the winter home range of deer on the island (Massé and Côté, 2012b), are less effective in predicting the intensity of browsing on firs compared to models over 6-ha areas. It is likely that the relationship between browsing and shelter habitat only exists at a fine scale, as suggested by our results on the distance to the nearest forest edge (Fig. 1), most likely due to winter snow conditions limiting deer movements.

The combined effects of edge or shelter area with white spruce neighborhood crowding better predicted lateral browsing intensity than the single effects of these factors. At the local scale, as white spruce neighborhood crowding around the focal fir tree increased, so did the intensity of lateral browsing. White spruce is a species that white-tailed deer generally avoid consuming, although it may represent a significant portion of their diet when more profitable food sources are lacking on Anticosti Island (Sauvé and Côté, 2007). In a similar context of restoration on Anticosti Island, but without planting, Champagne et al. (2020) observed a neighbor contrast susceptibility (*sensu* Bergvall et al. 2006) effect of white spruce on balsam fir, but only when white spruce

Table 6
Direct and indirect relationships between neighborhood crowding index and relative growth rate in volume between 2012 and 2020 of balsam fir (*Abies balsamea* (L.) Mill.) in the context of balsam fir restoration on Anticosti Island (Québec, Canada).

NCI	Relative Growth Rate in volume		
	Estimate	95% Bootstrap CI*	p-value
Direct Effect	$-14.5\ 10^{-4}$	($-20.8\ 10^{-4}$, $-10.7\ 10^{-4}$)	<0.001
Indirect Effect	$-3.5\ 10^{-4}$	($-8.9\ 10^{-4}$, $-0.8\ 10^{-4}$)	0.014
Total Effect	$-18.0\ 10^{-4}$	($-25.8\ 10^{-4}$, $-13.6\ 10^{-4}$)	<0.001
Percentage of indirect effect (%)	19.7	(4.5, 42.6)	0.014

*CI = confidence interval.

had a low digestible nitrogen content. White spruce in our plots may therefore have been low in foliar nitrogen, which could be a result of the low concentration of nitrogen in the soils of boreal forest (Jerabkova et al., 2006) in general, and on Anticosti Island in particular (Houde et al. 2020). We found no density-dependent relationship other than the white spruce effect. At the local scale, we did not find any factors influencing the number of reiterations, including white spruce neighborhood crowding.

4.2. Balsam fir growth

Growth, expressed in term of relative growth rate in volume, was negatively influenced by the intensity of lateral browsing and crowding by neighboring trees. Our results indicate that the intensity of lateral browsing, i.e., the repeated loss over time of photosynthetic tissue and energy reserves, is sufficient to reduce growth. Occasional browsing, even at high intensity, does not seriously affect tree growth and structure; it is the repetition over time that negatively affects these factors, as well as tree survival (Wallgren et al., 2014). Neighborhood crowding was one of the main factors negatively influencing balsam fir growth. Combined effects of browsing and neighborhood crowding index better predicted fir growth than the single effects of these explanatory variables. Our results indicate that neighboring trees had an indirect effect on growth presumably by influencing lateral browsing. The limited number of observations does not allow us to accurately gauge the strength of this indirect effect relatively to the total effect of neighborhood crowding on growth. However, despite presenting a large confidence interval, our results suggest that the indirect effect of neighborhood crowding on growth mediated by the intensity of lateral browsing was sufficiently high not to be neglected. Our results indicate that the associative susceptibility generated by white spruce had a strong enough effect on deer behavior to generate a delay in fir growth. The remaining part of the effects of neighborhood crowding of trees on growth was probably a result of the competition they generated for resources, such as light, water and soil nutrients (Brand, 1991).

We suggest that vegetation density measures such as competition indices as a proxy for the effect of competition on growth are potentially biased, especially in the presence of herbivores. These density measures are not only a proxy for competition for resources (e.g. light, water, nutrients), but also a proxy for the mechanisms by which vegetation influences herbivore foraging behavior (density dependence and associative effects). Fortunately, it is possible to determine how much of this overall effect is due to each of these mechanisms by performing a mediation analysis. In natural conditions where herbivores may interact with the experimental system, it is necessary to take browsing measurements into account to correctly partition the effect of competition and browsing generated by the surrounding vegetation. There may also be a bias in using vegetation density measurements to study the influence of resource concentration or associative effects on foraging behavior; foliar concentration of macronutrients, such as nitrogen, can be directly correlated with tree growth rate (Wang and Klinka, 1997). Variations in nutritional quality may influence associative effects and density variation effects of the resource species (Champagne et al., 2020). Our findings suggest that neighborhood crowding may indirectly affect foraging behavior through a mediator: the nutritional quality of the tree. Neighboring tree competition affects the growth of the focal tree and thus, its nutritional value (i.e. nitrogen content), which would have an effect on deer foraging behaviour.

Our results suggest that a reduction in white spruce density could benefit fir growth by reducing the direct negative effects of competition and the indirect negative effects of neighbor contrast susceptibility. Brousseau et al. (2017) attempted to reduce the effect of interspecific competition on fir plantations on Anticosti Island using a mechanical release 5 years after planting without any real benefit on growth. However, other long-term studies have shown that release usually has a positive effect on the growth of other conifer species (Bell et al., 2011; Cyr and Thiffault, 2009; Wagner and Robinson, 2006). The other competing species, except for spruce, are species consumed by deer and their regeneration is limited by browsing.

5. Conclusion

The increase and expansion of several deer species around the world poses many challenges for ecosystem conservation (Côté et al., 2004). When browsing compromises the resilience of forest ecosystems, protection of natural regeneration areas and management of deer density can be used (Beguin et al., 2016), in addition to restoration through the use of plantations (Parrotta et al., 1997; Thiffault et al., 2012). Our study allowed to identify factors that influence the success of restoration and recruitment by monitoring the growth of a focal species when the environmental stressor that led to the conservation problem for that species regained access to the area. Our results suggest that a fenced plantation restoration system paired with 10–12 years of reduced deer density allowed the recruitment of a sufficiently high amount of forage resources to induce deer foraging behavior compatible with the maintenance of forests once natural deer densities are restored. Our results showed that competing vegetation can adversely affect the growth of the focal species through a direct competitive effect and an indirect effect by increasing susceptibility to browsing. The observation that most focal fir trees reached a sufficient height to escape browsing despite that most of them were subjected to heavy browsing pressure in recent years testify to the success of the management approach on Anticosti Island, 14 years after planting. Nevertheless, longer term monitoring is necessary to ensure that the plantation sites have the capacity to form a new forest canopy composed of balsam fir despite strong white spruce regeneration. Thus, the success of forest habitat restoration through plantations depends on how well the surrounding vegetation modulates the heavy browsing pressure and growth of the planted trees.

CRediT authorship contribution statement

Baptiste Brault: Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Jean-Pierre Tremblay:** Conceptualization, Methodology, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Nelson Thiffault:** Conceptualization,

Methodology, Investigation, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Alejandro A. Royo:** Writing – review & editing. **Steeve D. Côté:** Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare no financial interests/personal relationships which may be considered as potential competing interests.

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Appendix A

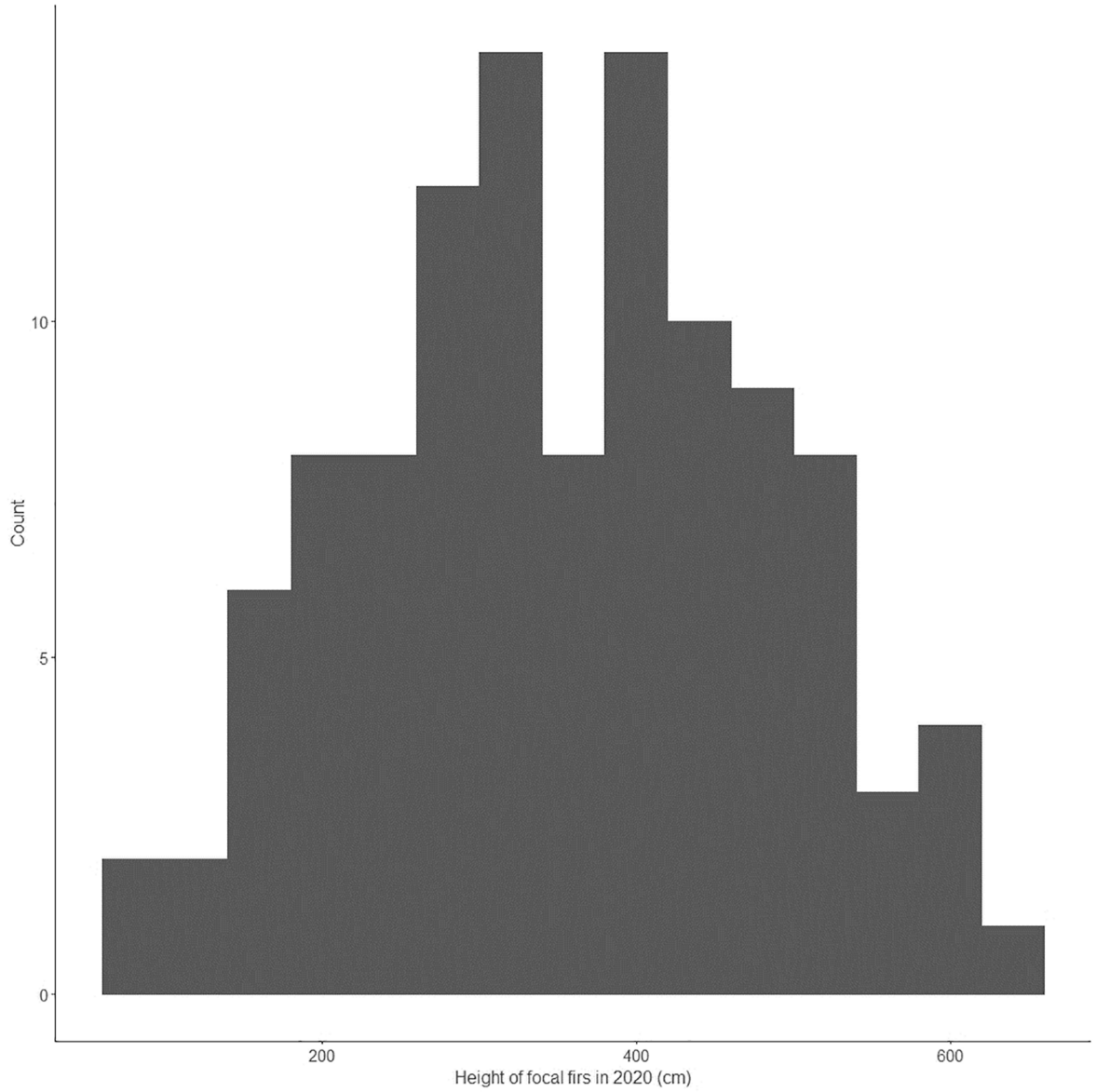

Fig. A1. Stem height frequency distribution of balsam fir (*Abies balsamea*, (L.) Mill.) over 8 years of growth (from 2012 to 2020) from plantations and natural regenerations on Anticosti Island (Québec, Canada).

Appendix B

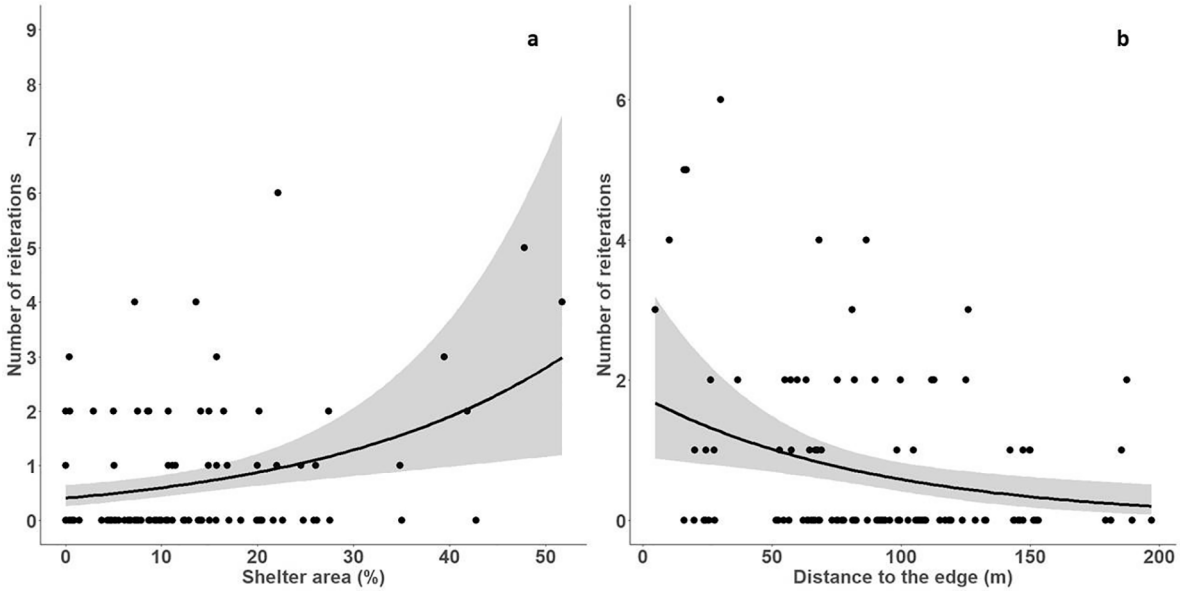

Fig. B1. Variables influencing white-tailed deer (*Odocoileus virginianus* Zimmermann, 1780) browsing on balsam fir (*Abies balsamea* (L.) Mill.) in the context of balsam fir restoration on Anticosti Island (Québec, Canada). Area of shelter on 6-ha surrounding the focal fir tree (%) was positively related to the number of stem reiterations (a). Distance to the nearest forest edge to the focal fir tree was negatively related to the number of stem reiterations (b). Lines are the predicted values (linear mixed-effects models); gray areas correspond to the 95% CI; points are the raw data.

Appendix C

We calculated the growth in height, as this variable determines the ability of the trees to escape browsing. We calculated the relative growth in height (RGH):

$$RGH = \frac{(h_{i2020} - h_{i2012})}{h_{i2012}}$$

where, h_{i2012} and h_{i2020} are the height of focal fir i in 2012 and 2020, respectively.

In order to achieve our second objective, which was to evaluate the factors influencing the growth of fir, we used RGH as a response variable. Potential explanatory variables used to represent browsing were the occurrence of apical and lateral browsing on focal fir trees in 2012 and the intensity of lateral browsing and number of reiterations measured in 2020. We used NCI as a potential explanatory variable to represent neighborhood crowding.

The first model selection based on AICc among candidate models included browsing variables potentially influencing RGH (Table C1). The second model selection was to compare a univariate model of the neighborhood crowding index and the null model (Table C1). The third model selection was based on AICc of the most supported models of the first two model selections (lowest AICc value and ΔAICc < 2), combining variables included in the most supported models from the two previous selections (Table C1). Models used are linear mixed-effect models.

Table C1
Candidate models and model selection results for browsing and neighborhood crowding variables influencing Relative Growth Height (RGH) of balsam fir (*Abies balsamea* (L.) Mill.).) over 8 years of growth (from 2012 to 2020) from plantations and natural regeneration on Anticosti Island (Québec, Canada) using AICc. RGH was analyzed using linear fixed-effects models.

Candidate models for the browsing selection	K	AICc	ΔAICc	Weight	R^2
apical browsing (2012) + lateral browsing (2012) + number of reiterations (2020) + lateral browsing intensity (2020)	6	140.52	0.00	0.56	0.35
lateral browsing (2012) + lateral browsing intensity (2020)	4	142.34	1.82	0.22	0.32
number of reiterations (2020) + lateral browsing intensity (2020)	4	143.40	2.88	0.13	0.31
lateral browsing intensity (2020)	3	144.26	3.74	0.09	0.24
number of reiterations (2020)	3	168.45	27.93	0.00	0.11
apical browsing (2012) + number of reiterations (2020)	4	168.55	28.03	0.00	0.13
Null model	2	179.46	38.94	0.00	–
Candidate models for the NCI selection	**K**	**AICc**	**ΔAICc**	**Weight**	**R^2**
NCI	3	160.23	0.00	1.00	0.18
Null model	2	179.46	19.23	0.00	–
Candidate models for the browsing and NCI selection	**K**	**AICc**	**ΔAICc**	**Weight**	**R^2**
apical browsing (2012) + lateral browsing (2012) + number of reiterations (2020) + lateral browsing intensity (2020) + NCI	7	136.24	0.00	0.57	0.39
lateral browsing (2012) + lateral browsing intensity (2020) + NCI	5	137.26	1.02	0.34	0.36
apical browsing (2012) + lateral browsing (2012) + number of reiterations (2020) + lateral browsing intensity (2020)	6	140.52	4.28	0.07	0.35

(*continued on next page*)

Table C1 (*continued*)

Candidate models for the browsing selection	K	AICc	ΔAICc	Weight	R^2
lateral browsing (2012) + lateral browsing intensity (2020)	4	142.34	6.10	0.03	0.32
NCI	3	160.23	23.99	0.00	0.13
Null model	2	179.46	43.22	0.00	–

K = number of estimated parameters for each model, AICc = Akaike information criterion with correction for small sample size, R^2 = coefficient of determination – multiple R^2.
R^2 are provided for information only; models were compared using AIC.

The first model selection with the goal of identifying the browsing models most influencing tree growth resulted in two models. Final model selection for RGH showed that both lateral browsing and neighborhood crowding negatively influenced tree growth (Table C2). Variables included in the most parsimonious model, with ΔAICc < 2, explained 36% of the total variance in RGH (Multiple $R^2 = 0.36$).

Table C2
Best parsimonious models explaining the Relative Growth in Height of balsam fir (*Abies balsamea* (L.) Mill.) over 8 years of growth (from 2012 to 2020) in management enclosure plantations on Anticosti Island (Québec, Canada) and under heavy browsing pressure by white-tailed deer (*Odocoileus virginianus* Zimmermann, 1780).

Relative Growth in Height (95 %CI)	
Browsing	
Occurrence of lateral browsing in 2012	−0.14 (−0.31, 0.03)
Lateral browsing intensity in 2020	−0.24 (−0.33, −0.15)
Competition	
NCI in 2020	−0.12 (−0.22, −0.03)
ΔAICc	1.025

CI = confidence interval, AICc = Akaike information criteria with correction for small sample size, Wt = weight. Linear models. All continuous variables were standardized.

The effect of neighborhood crowding on RGH was half the effect of lateral browsing (Fig. C1). A mean decrease of 24% in RGH was predicted over the 8-year period for 1-standard deviation change in the 2020 lateral browsing intensity, and a mean decrease of 12.5% for 1-standard deviation change in the neighborhood crowding.

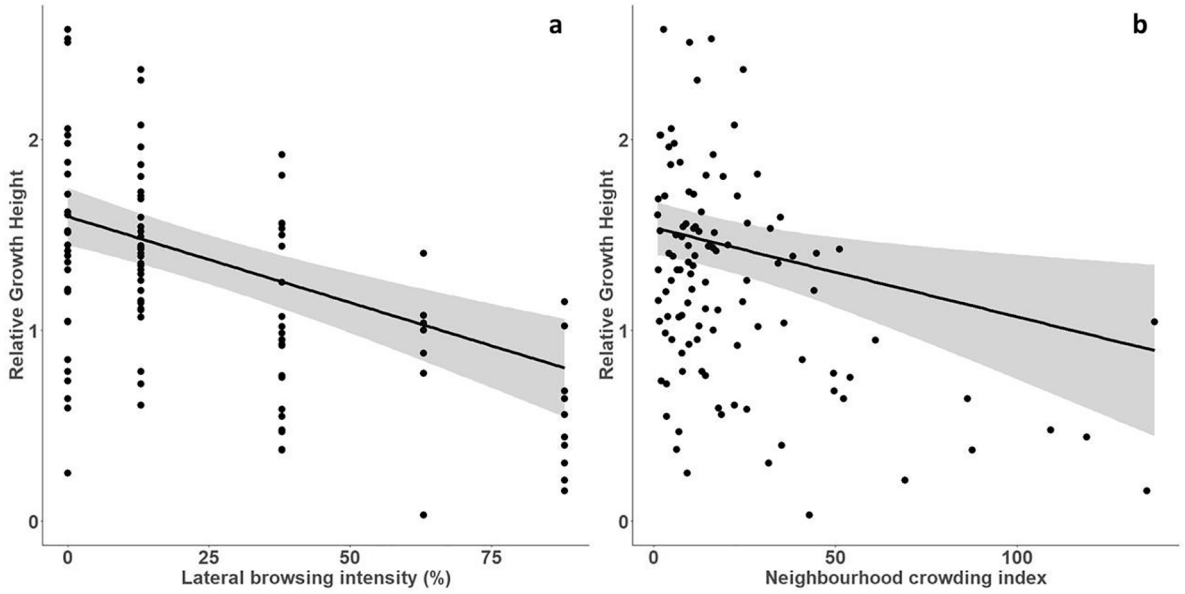

Fig. C1. Balsam fir (*Abies balsamea* (L.) Mill.) growth between 2012 and 2020 in the context of balsam fir restoration on Anticosti Island (Québec, Canada). Lateral browsing intensity (%) was negatively related to the relative height growth (RGH) (a). Neighborhood crowding index from trees larger than 50 cm within a 5 m radius of the focal fir was negatively related to RGH (b). Lines represent predicted values from generalized linear models; gray areas correspond to the 95% CI; points are the raw data.

Considering the additive effects of the models and assuming an absence of lateral browsing in 2012, a mean growth in height of only 25% was expected in presence of intensive lateral browsing (76–100%) in 2020 and a NCI = 130 resulted in a 25 cm increase for a balsam fir of 1 m in height in 2012. A mean growth in height of 166% was expected in absence of lateral browsing and neighborhood trees, resulting in a 2.66 m height in 2020 for a balsam fir of 1 m in 2012.

The analysis of direct and indirect effects of NCI on balsam fir growth excluded a complete mediation by the lateral browsing index (Table C3). Instead, a partial mediation was observed with an indirect effect of neighborhood crowding through lateral browsing representing 24.3% (95 %CI: 7.3%, 48.9%) of the total effect induced by NCI.

Table C3
Direct and indirect relationships between neighborhood crowding index (NCI) and relative growth in height of balsam fir (*Abies balsamea* (L.) Mill.) in the context of balsam fir restoration on Anticosti Island (Québec, Canada).

NCI	Relative Growth in Height		
	Estimate	95% Bootstrap CI	p-value
Direct Effect	$-64.9\ 10^{-4}$	($-95.7\ 10^{-4}$, $-43.7\ 10^{-4}$)	<0.001
Indirect Effect	$-20.8\ 10^{-4}$	($-52.6\ 10^{-4}$, $-5.6\ 10^{-4}$)	0.014
Total Effect	$-85.7\ 10^{-4}$	($-125.9\ 10^{-4}$, $-56.0\ 10^{-4}$)	<0.001
Percentage of indirect effect (%)	24.3	(7.3, 48.8)	0.014

CI = confidence interval.

Similar results were observed in mediation analyses including white spruce NCI as an independent variable (Table C4, Appendix D – Table D1). Our results showed that 27.8% (95 %CI = 12.0, 47.2) of the effect of white spruce neighborhood crowding on fir growth was mediated by lateral browsing intensity (Table C4).

Table C4
Direct and indirect relationships between white spruce neighborhood crowding index (NCI) and relative growth in height of balsam fir (*Abies balsamea* (L.) Mill.) in the context of balsam fir restoration on Anticosti Island (Québec, Canada).

White spruce NCI	Relative Growth in Height		
	Estimate	95% Bootstrap CI	p-value
Direct Effect	$-112.7\ 10^{-4}$	($-183.4\ 10^{-4}$, $-79.3\ 10^{-4}$)	<0.001
Indirect Effect	$-43.5\ 10^{-4}$	($-83.6\ 10^{-4}$, $-16.2\ 10^{-4}$)	0.002
Total Effect	$-156.1\ 10^{-4}$	($-24.1\ 10^{-4}$, $-117.5\ 10^{-4}$)	<0.001
Percentage of indirect effect (%)	27.8	(12.0, 47.2)	0.002

CI = confidence interval.

Appendix D

Table D1
Direct and indirect relationships between white spruce neighborhood crowding index (NCI) and relative growth rate in volume of balsam fir (*Abies balsamea* (L.) Mill.) in the context of balsam fir restoration on Anticosti Island (Québec, Canada).

White spruce NCI	Relative Growth Rate in volume		
	Estimate	95% Bootstrap CI	p-value
Direct Effect	$-23.4\ 10^{-4}$	($-41.4\ 10^{-4}$, $-17.7\ 10^{-4}$)	<0.001
Indirect Effect	$-7.5\ 10^{-4}$	($-15.8\ 10^{-4}$, $-3.4\ 10^{-4}$)	0.004
Total Effect	$-31.0\ 10^{-4}$	($-52.4\ 10^{-4}$, $-24.6\ 10^{-4}$)	<0.001
Percentage of indirect effect (%)	24.3	(9.8, 41.5)	0.004

CI = confidence interval.

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