



Linking moose browsing to composition and growth delays in fir dominated boreal stand

Hugo Larue^{a,b,*}, Jean-Pierre Tremblay^{a,b,c}, Martin Barrette^{b,d}

^a Département de biologie, Université Laval, 1045 avenue de la Médecine, Québec, QC G1V 0A6, Canada

^b Centre d'étude de la forêt, Montréal, QC H3C 3P8, Canada

^c Centre d'étude nordique, 2405 rue de la Terrasse, Québec, QC G1V 0A6, Canada

^d Direction de la recherche forestière, ministère des Ressources naturelles et forêts, 2700 Rue Einstein, Québec, QC G1P 3W8, Canada

ARTICLE INFO

Keywords:

Balsam fir
Regeneration
Apical stem
Lateral browsing
Seedling
Sapling
Suppression

ABSTRACT

Selective browsing by moose (*Alces alces*) can substantially alter forest regeneration by reducing the survival and growth of selected species, shifting competitive dynamics and altering stand succession. We investigated (1) whether selective browsing by moose prevents selected species from reaching later growth stages, and (2) whether balsam fir (*Abies balsamea*) sapling height growth is reduced under various intensities of apical and lateral browsing. During summer 2023, we surveyed 56 balsam fir-dominated stands cut between 2000 and 2015 in the Forêt Montmorency, in Québec, Canada. Browsing strongly influenced seedling density according to the hierarchical generalized linear mixed effects model. Highly selected species at the seedling stage, such as broadleaves, also suffered the greatest decline at sapling stages, suggesting that the selective browsing prevents broadleaves species from reaching the sapling stage. For balsam fir saplings, both apical and lateral browsing additively reduced apparent height growth, with lateral browsing having a comparable effect to apical browsing. Under high apical browsing, apparent height growth declined by a factor of 0.79 [95 % CI= 0.70: 0.90] compared with unbrowsed individuals. Our findings demonstrate that moose browsing not only reshapes species composition but also delays the growth of surviving saplings, highlighting the need to incorporate browsing pressure when predicting forest growth and yield and for ensuring the implementation of adaptive management strategies.

1. Introduction

Stand growth is affected by abiotic environmental conditions and biotic factors such as competition or herbivory (Maes et al., 2019). Selective browsing by large cervids may stress individual trees and indirectly alter not only interspecific competition (Tremblay et al., 2007), but also the growth of browsed trees (Wallgren et al., 2014). Although browsing is known to influence tree stand composition and structure, its impact on early stand development is often neglected in yield models (Nappi, 2013). This gap results in the uncertainty of stand growth predictions, especially in areas heavily impacted by large cervids, which can alter stand composition and growth and hinder sustainable forest management (Pachana, 2016; Peng, 2000). In this study, we investigated how moose (*Alces alces*) can influence potential stand growth through alteration of species recruitment and subsequent stem growth following clearcutting in balsam fir (*Abies balsamea*) dominated stands.

We thus provide a preliminary step toward improving yield models to integrate early biotic stressors.

Moose occupy habitats that balance forage availability and shelter, with food selection shifting seasonally. They frequent forage-rich habitat types near mature stands that provide shelter (Snaith and Beazley, 2004; Crête, 1977; Lenarz et al., 2011), feeding on plants that provide a favorable balance of macronutrients (Spitzer et al., 2024). In summer, they will primarily select, among other plants, leaves from palatable deciduous trees such as willows (*Salix sp.*) and birches (*Betula spp.*; Bowyer et al., 2003). During winter, they usually settle in winter yards and feed on twigs from both deciduous and coniferous species, mostly balsam fir in North America (Bowyer et al., 2003) or Scots pine (*Pinus sylvestris*) in Northern Europe (Danell et al., 1991). Through this selective and seasonally variable foraging behavior, moose can modulate the survival and growth of tree species local population at early developmental stages.

* Corresponding author at: Département de biologie, Université Laval, 1045 avenue de la Médecine, Québec, QC G1V 0A6, Canada
E-mail address: hugo.larue.1@ulaval.ca (H. Larue).

<https://doi.org/10.1016/j.foreco.2026.123619>

Received 16 December 2025; Received in revised form 9 February 2026; Accepted 11 February 2026

Available online 14 February 2026

0378-1127/© 2026 Elsevier B.V. All rights are reserved, including those for text and data mining, AI training, and similar technologies.

Selective browsing can alter the speed of forest stand succession as it modifies the seedlings species composition. Moose can reduce the abundance of seedling species they selectively consume (De Vriendt et al., 2021; Smith et al., 2010) and prevent them from reaching a more advanced growth stage (Gosse et al., 2011; De Vriendt et al., 2023). Under low to moderate browsing pressure, moose primarily consume shade-intolerant deciduous species (Danell et al., 1985), which are mostly early succession species in boreal forests. By modifying competitive interactions in favor of browse-resistant species (Holt and Bonsall, 2017), they act as a release treatment from competitors for late-succession species, thereby accelerating stand succession (Brousseau et al., 2017; De Vriendt et al., 2020; Posner and Jordan, 2002). At high population densities, browsing pressure may shift toward less selected late-succession species (De Vriendt et al., 2021), slowing down stand succession (Gosse et al., 2011; Smith et al., 2010). When browsing is particularly severe during the first years following harvest, moose have been shown to induce alternative successional pathways by changing the final stand composition (sensu Hidding et al., 2013; Andreozzi et al., 2014; De Vriendt et al., 2021). These early-stage impacts shape the initial stand composition, strongly influencing successional speed and pathways (Rijal et al., 2022; Kuuluvainen and Gauthier, 2018; Andreozzi et al., 2014).

Once trees have transitioned to the sapling stage, moose can continue to directly affect their growth by removing meristems and structural tissues, as well as photosynthetic tissues. Cumulative removal of structural tissues like apical stems appears to be the type of browsing inducing the most damage to trees and the greatest delays in tree growth as they remove annual growth increments (Bergqvist et al., 2003; Wallgren et al., 2014). Sapling trees are also vulnerable to lateral browsing. While moderate lateral thinning can stimulate height growth (Koga et al., 2002; McCarthy and Weetman, 2007), heavy thinning can reduce growth due to reduced photosynthetic capacity (Margolis et al., 1988). Severe lateral browsing is therefore expected to negatively affect growth (Brault et al., 2023). Finally, the combined effects of apical and lateral browsing on growth remains poorly understood, with the latter often neglected despite its potential negative impacts on growth.

Our objective was to evaluate the effects of moose browsing on stand composition and growth delays of individual balsam fir by investigating seedling composition and sapling growth naturally regenerated after clearcutting. First, we evaluated browsing effects on seedling composition 8–23 years after a clearcut in balsam fir forest stands. Then, we assessed browsing effects on growth of saplings that survived the seedling stage, thus providing a more integrated understanding of how browsing influences stand growth dynamics. We hypothesized that selective browsing of seedlings is a driver of stand composition, thereby influencing successional dynamics by slowing stand succession as browsing pressure shifts from shade-intolerant deciduous species toward balsam fir. We also hypothesized that apical and lateral browsing induces growth delays in balsam fir saplings, with greater delays under higher browsing pressure. These findings are essential for improving stand growth predictions and for developing adaptive management strategies that mitigate the impacts of moose browsing on stand development. To test our hypotheses, we evaluated stand composition and growth in balsam fir stands in Québec, Canada, under heavy browsing pressure due to the increase in moose density in recent decades.

2. Materials and methods

2.1. Study area

We conducted this study during summer 2023 at the Forêt Montmorency, Université Laval teaching and research forest located in the Laurentian Massif, Québec, Canada (41° 12' N, -71° 11' W). The 66 km² central area of the Forêt Montmorency features a plateau at an altitude of 700 m, dotted with rounded peaks reaching 1000 m in elevation (Bouliane et al., 2014). The study area is located in the eastern balsam

fir-paper birch bioclimatic domain (Morneau, 2021). The humid climate with high precipitation and long fire return intervals has favored the establishment of balsam fir dominated stands (Bouliane et al., 2014). White spruce (*Picea glauca*), paper birch (*Betula papyrifera*), black spruce (*Picea mariana*) and trembling aspen (*Populus tremuloides*) are also present. The main natural disturbances are outbreaks of spruce budworm (*Choristoneura fumiferana*), hemlock looper (*Lambdina fiscellaria*) and windthrow (Bouliane et al., 2014).

The main vertebrate herbivores in the Forêt Montmorency are moose and snowshoe hare (*Lepus americanus*) with rare observations of white-tailed deer (*Odocoileus virginianus*). The most recent aerial moose survey in the Forêt Montmorency was carried out in 2023 and estimated an overall density of 3.6 (SE=0.4) mooses per 10 km² (Grenier-Potvin and Roy, 2023). Moose populations in this region exhibited a marked increasing trends in the decade preceding our studies based on observations-per-unit-effort models (Côté-Vaillancourt et al., 2016). The moose population density was estimated from aerial surveys at 10.6 ± 7.4 individuals per 10 km² in 2004 and 14.8 ± 1.5 individuals per 10 km² in 2013 (Langevin and Bastien, 2013). Sport hunting has been banned at Forêt Montmorency since 1986 (Bouliane et al., 2014). The main predators of moose in our study area are the gray wolf (*Canis lupus*) and the black bear (*Ursus americanus*; Bouliane et al., 2014).

2.2. Sampling design

Between the first week of June and the first week of August, we investigated 56 randomly selected stands (mean area = 3.6 ± 3.4 ha) out of 285 established from natural regeneration after clearcutting between 2000 and 2015. We used a LiDAR-derived canopy height model with 1 m² resolution (Ministère des ressources naturelles et des forêts, 2019) to evaluate the variation in tree height within each stand. Proportionally to this variation, we allocate two to four plots per stand. We chose to focus on height variation obtained from LiDAR to distribute plots in balsam fir forest stands because it is central to our second objective regarding sapling height growth, but the height measurements used to calculate sapling growth was obtained in the field as described in Section 2.3.2.

We randomly distributed plots (n = 162) composed of concentric circles with a radius of 5.64 m (100 m²) and 3.57 m (40 m²) for measuring trees (diameter at breast height (DBH) ≥ 10 cm) and saplings (1 cm ≤ DBH < 10 cm), respectively, reflecting differences in stem density among size classes. For every plot, we tallied seedlings (DBH < 1 cm and height > 30 cm) in 4 subplots with a radius of 1.13 m (4 m²). Subplots were systematically distributed along the four cardinal directions at 5.64 m from the plot center.

2.3. Data collection and processing

2.3.1. Seedling species composition

We counted seedling abundance of all species present in subplots. We combined *Sorbus americana* (n individual = 415) with deciduous species with a low abundance (*Acer spicatum* [n = 60], *Prunus pensylvanica* [n = 33], *Lonicera canadensis* [n = 9], *Alnus rugosa* [n = 4], and *Acer rubra* [n = 2]) into a single category (other deciduous), as their small numbers preclude forming individual categories. We decided to keep balsam fir (n = 2293) and paper birch (n = 465) in a separate category since they were the most abundant species. Despite the low number of spruces (*Picea spp.*, [n = 59]), they constitute a distinct group of species that we could not logically pool with balsam fir.

For quantifying browsing pressure at the subplot-scale, we calculated the proportion of seedlings stems browsed in every subplot (here-after browsing proportion). We differentiated moose from snowshoe hare browsing by examining the characteristic marks on the twigs. Snowshoe hares typically leave a sharp diagonal cut, while moose tend to leave a ragged, broken tip (Zhou et al., 2017). Among all seedlings measured, only 52 (20 balsam fir, 17 paper birch, 15 other deciduous) showed signs of hare browsing, and these were spread across 40 subplots. Hare

browsing was thus negligible and we did not account for this factor in our analysis. Given that there are no known white-tailed deer wintering areas within our study location (Bouliane et al., 2014), the risk of mistaking their browsing for that of moose was minimal.

To account for competition from other plants, we visually estimated the horizontal cover of raspberry (*Rubus idaeus*) in sapling plots ($r = 3.57$ m). We only measured competition from raspberry because, in our study area, raspberry is a pioneer species frequently competing for space and resources with seedling species mentioned above. Besides competition, we also measured slope orientation ($N = 0^\circ \leq \text{aspect} < 45^\circ$ and $\geq 315^\circ$, $E = 45^\circ \leq \text{aspect} < 135^\circ$, $S = 135^\circ \leq \text{aspect} < 225^\circ$, $W = 225^\circ \leq \text{aspect} < 315^\circ$) and inclination (degrees) obtained from a digital elevation model (Ministère des ressources naturelles et des forêts, 2019), while stand area (ha) and stand age (year) came from Ministère des ressources naturelles et des forêts (2016). With the same database (Ministère des ressources naturelles et des forêts, 2016), we estimated the distance to the nearest mature forest edge (hereafter distance to shelter) for each plot using the `st_distance` function of the `sf` package (Pebesma and Bivand, 2023) in R software (v4.2.1; R Core Team, 2022).

2.3.2. Sapling apparent height growth

We recorded each stem in trees and samplings plots. We used a vertex (Haglöf, vertex 5, Sweden) to estimate trees and saplings height (to the next centimeter) which we divided by the age of the stand to obtain their apparent height growth (m/year). We measured DBH (2 cm classes) to distinguish saplings from trees. For quantifying browsing pressure at the stem-scale, we used two complementary metrics describing apical and lateral browsing. For apical browsing pressure, we categorized browsing-induced architecture of each saplings following Keigley et al. (2003) and modified according to LeBlanc-Boudreau et al. (2018) to better suit balsam fir architecture. We translated architecture into cumulative apical browsing pressure categories: unbrowsed (Uninterrupted-growth-type), low (Released-type; Figure S1), high (Retrogressed and Arrested-type; Figure S2 and S3). We grouped the retrogressed- and arrested-type for analyses because there were very few instances of retrogressed-type architecture. For lateral browsing pressure, we counted the number of lateral branches browsed by moose controlled for tree height (i.e. the number of branches browsed per m of stem height).

To account for stem-level differences in growth potential within plots, we measured suppression by counting the number of neighboring stems overtopping each sapling. We then ran a regression of height as a function of suppression (centered and scaled) and took the residuals of this regression as the variable representing competition. As a result, suppression is no longer a number of stems, but rather a relative index of height for a given level of suppression, here-after referred to as release index.

2.4. Statistical analysis

2.4.1. Seedlings species composition

We evaluated the relative importance of moose browsing, slope inclination and orientation, stand area and age, distance to shelter and raspberry cover on woody seedlings species composition, (i.e., count of stems). Because we had count of stems from four categories (balsam fir, paper birch spruces and other deciduous), we used a hierarchical generalized linear mixed effects model (HGLME; Warton, 2022). Unlike conventional multivariate analysis, HGLME models allow conducting a multivariate analysis while including random variables to account for the hierarchy of the sampling design. Warton (2022) proposes modeling counts as a function of species, with species in interaction with each explanatory variables, thereby providing the effect of each explanatory variable on the abundance of a given species. We used the R package `glmmTMB` (Brooks et al., 2017) with the function `glmmTMB`, fitting a

negative binomial family (log link) to correct for overdispersion and for zero inflation (Brooks et al., 2017). We also included plots nested in stand as random intercepts. We standardized (centered and scaled) numerical explanatory variables to facilitate the interpretation of effects on various scales (proportion, degrees, ha, years, m, percentage). We conducted the statistical analysis on the scale of density of seedlings in 4 m^2 subplots, but we converted the estimates presented in Table 1 in terms of density of seedlings per ha to ease interpretation (Table 1). We had two subplots with extreme values for the density of other deciduous seedlings (54 and 135,000 stem/ha) and for slope inclination (28°). We compared a model with the original values and another with the extreme values removed (Zuur et al., 2010). The effects were similar, but the model with the extreme values had the deviation test significant (KS test: $p = 0.021$). We therefore kept the model without the extreme data for analysis.

2.4.2. Sapling apparent height growth

To evaluate the simple, additive and multiplicative effects of cumulative apical browsing pressure and lateral browsing pressure on apparent height growth (height/stand age) of balsam fir saplings, we built candidate models (Table 2) using generalized linear mixed effects models, with plots nested in stands as a random intercept and a Gamma family (log link). We included our release index as a covariate to account for competition from neighboring stems. Because we compared models with nested fixed effects, but with the same random structure, we used the Akaike Information Criterion (AIC) and AIC weight with maximum likelihood estimation to identify the most parsimonious models (i.e. all models within a $\Delta \text{AIC} \leq 6$ and a cumulative AIC weight ≥ 0.95 ; Zuur et al., 2009; Harrison et al., 2018).

For both analyses, we developed models using the `glmmTMB` function of the `glmmTMB` package (Brooks et al., 2017). We used the DHARMA package to visually assess the conformity of assumptions (Hartig et al., 2024). For both analyses, we performed post-hoc tests using `emmeans` function (pairwise option) of the `emmeans` package for categorical data (i.e. species, slope orientation and cumulative apical browsing pressure, to test for differences among the other values of the same category; Lenth et al., 2024). For both analyses, we present the back-transformed data on the response-scale by exponentiating the link-scale data. All statistical analyses were performed using R software (v4.2.1; R Core Team, 2022).

3. Results

3.1. Seedlings species composition

Balsam fir was the most abundant naturally regenerated seedling species with an average of 7000 [95 % confidence intervals (CI) = 5075: 9750] seedlings per ha when all other standardized predictors of the model were equal to 0 (i.e. their mean). Paper birch, spruce spp. and other deciduous had lower density of 1820 [863: 3802], 70 [10: 195] and 2100 [1015: 4290] seedlings per ha on average, respectively (Table 1). All pairwise comparisons between species were statistically significant ($9.30 < Z < 16.21$, all p values < 0.001), except for paper birch compare to other deciduous ($Z = 1.62$, $p = 0.37$).

Across all species except paper birch, the proportion of browsed stems per subplot had the strongest impact on seedling density (Table 1). Indeed, it is the predictor for which the effect on the density of balsam fir, spruces and other deciduous deviates the most from 1 (null effect) ($-6.24 < Z < 5.51$, all p values < 0.008). The results of the post-hoc test show that the differences between the slope orientation values were not significant.

To investigate whether moose constrains the transition of certain species to a more developed growth stage, we plotted the proportion of each species by growth stages (Fig. 1). We observed that paper birch and

Table 1

Coefficients and 95 % confidence intervals (CI) of variables contributing to explain the density of seedlings (diameter at breast height <1 cm and height >30 cm) in stands established between 2000 and 2015 after clearcutting in the Forêt Montmorency (Québec, Canada). The coefficients were computed using a hierarchical generalized linear mixed effect model. The intercept represents the density (n/ha) of each species when all other standardized model parameters are equal to 0 and slope orientation equal East. Effect sizes (estimates) are given at the response-scale which represents the incidence rate ratio (i.e., the factor by which the mean density increase (above 1) or decrease (below 1) with an increase of one unit of the explanatory variable). Coefficients for which the 95 % CI did not overlap 1, or 0 for the intercept, are shown in bold, indicating estimates that differ from these reference values.

| Variable | Balsam fir | | Paper birch | | Spruces | | Other deciduous | |
|-----------------------------|-------------|---------------------|-------------|---------------------|-------------|---------------------|-----------------|---------------------|
| | estimate | 95 % CI | estimate | 95 % CI | estimate | 95 % CI | estimate | 95 % CI |
| (Intercept) | 7000 | [5075: 9750] | 1820 | [863: 3802] | 70 | [10: 195] | 2100 | [1015: 4290] |
| Stand age | 1.20 | [0.99: 1.46] | 0.59 | [0.47: 0.74] | 0.94 | [0.59: 1.52] | 1.13 | [0.89: 1.43] |
| Proportion of stems browsed | 0.67 | [0.59: 0.76] | 1.23 | [1.05: 1.43] | 0.41 | [0.26: 0.65] | 1.55 | [1.32: 1.82] |
| Stand area | 1.08 | [0.94: 1.25] | 0.97 | [0.81: 1.15] | 0.60 | [0.36: 1.01] | 1.06 | [0.89: 1.27] |
| Slope inclination | 0.84 | [0.72: 0.97] | 1.08 | [0.90: 1.31] | 0.72 | [0.49: 1.06] | 0.73 | [0.60: 0.87] |
| Slope orientation West | 1.31 | [0.90: 1.90] | 0.95 | [0.61: 1.49] | 2.44 | [0.76: 7.77] | 0.81 | [0.53: 1.23] |
| Slope orientation South | 1.34 | [0.87: 2.03] | 1.23 | [0.74: 2.08] | 5.64 | [1.75: 18.36] | 0.50 | [0.30: 0.84] |
| Distance to shelter | 1.06 | [0.92: 1.22] | 1.04 | [0.89: 1.22] | 1.20 | [0.82: 1.75] | 1.09 | [0.92: 1.30] |
| Raspberry | 1.12 | [0.92: 1.35] | 0.73 | [0.59: 0.90] | 0.72 | [0.44: 1.17] | 1.14 | [0.90: 1.43] |

Table 2

Summary of candidate models tested to evaluate the additive and multiplicative effects of browsing variables (cumulative apical browsing pressure and lateral browsing pressure) and competition (release index) on apparent height growth (height/stand age) of balsam fir (*Abies balsamea*) sapling (1 cm ≤ diameter at breast height < 10 cm) in stands (n = 162 plots) established between 2000 and 2015 after clearcutting in the Forêt Montmorency (Québec, Canada).

| Candidate model | Intercept | release index | Cumulative apical browsing pressure | Lateral browsing pressure | Cumulative apical browsing pressure X Lateral browsing pressure | AIC | Δ AIC | AIC weight |
|-----------------|-----------|---------------|-------------------------------------|---------------------------|---|---------|--------|------------|
| m3 | X | X | X | X | | -7745.0 | 0.0 | 0.82 |
| m_full | X | X | X | X | X | -7741.9 | 3.1 | 0.18 |
| m2 | X | X | | X | | -6832.4 | 912.7 | 0.00 |
| m1 | X | X | X | | | -6746.6 | 998.5 | 0.00 |
| m_null | X | | | | | -6661.0 | 1084.0 | 0.00 |

other deciduous stems were almost absent from the sapling and tree stages.

3.2. Sapling apparent height growth

Balsam fir apparent height growth was additively influenced by cumulative apical browsing pressure, lateral browsing pressure and release index according to the model with the lowest AIC (Table 2). The model including a multiplicative effect of cumulative apical browsing and lateral browsing (m_full) was partly supported with a Δ AIC = 3.1, but the AIC weight was considerably lower: the m_full had 4.6 times less support than the m3 when comparing the evidence ratio (Table 2).

Apparent height growth of balsam fir saplings with low cumulative apical browsing pressure was 0.94 [0.90: 0.99] time that of unbrowsed saplings (intercept) and apparent height growth of balsam fir saplings with high cumulative apical browsing pressure was 0.79 [0.70: 0.90] time that of unbrowsed saplings (Fig. 2a). All pairwise comparisons between cumulative apical browsing pressures were statistically significant (2.7 < Z < 3.7, all p values < 0.02). Apparent height growth also decreased by 0.988 [0.985: 0.991] for each additional branch pruned per m of height (Fig. 2b). Finally, apparent height growth increases by a factor of 1.26 [1.23: 1.27] with every unit increase of release index.

4. Discussion

We evaluated the effects of moose browsing on composition and growth delays of balsam fir-dominated stands by investigating seedling composition and sapling growth along a chronosequence from 8 to 23 years after clearcut. This approach represents a preliminary step toward integrating browsing effects into forest growth predictions in Québec, Canada. Browsing exerted a strong influence on seedling density for

three of the four species (or group of species) analyzed, exceeding the effect of the other measured variables. Furthermore, we demonstrated that the most heavily browsed species at the seedling stage, paper birch and other deciduous species, had almost completely disappeared at the sapling and tree stages. This supports our hypothesis that moose browsing alters initial species composition and influences successional dynamics by preventing selected species from reaching a more advanced stage (Heikkilä et al., 2003). At the sapling stage, we demonstrated that apparent height growth of balsam fir saplings decreased with increasing cumulative apical browsing pressure and number of branches pruned, supporting our second hypothesis. Our results reveal an additive effect of cumulative apical browsing pressure and lateral browsing pressure. Our results also show an increase in apparent height growth with increasing values of the release index, which is the parameter with the largest effect size in our model. This result is consistent with the well-established effect of competition on height growth (Ruel, 1992; Soubeyrand et al., 2024). However, we do not interpret this effect further, as the release index was included solely to control for underlying competitive differences among saplings.

Our analysis of seedling species composition indicated that the density of balsam fir and spruces decreased as the proportion of browsed stems increased, while the density of paper birch and other deciduous species increased. Although our multivariate analysis could be interpreted as a negative effect of moose browsing on coniferous species and a positive one on deciduous species, we rather consider this result as an indication that moose were selecting subplots with the highest density of broadleaved seedlings. This result is consistent with the findings of Smith et al. (2010) in Nova Scotia, Canada, who reported that the highest levels of browsing occurred in the densest paper birch stands.

Despite deciduous seedlings densities reaching almost 4000 stems per ha, virtually none were recruited as saplings. Competition from

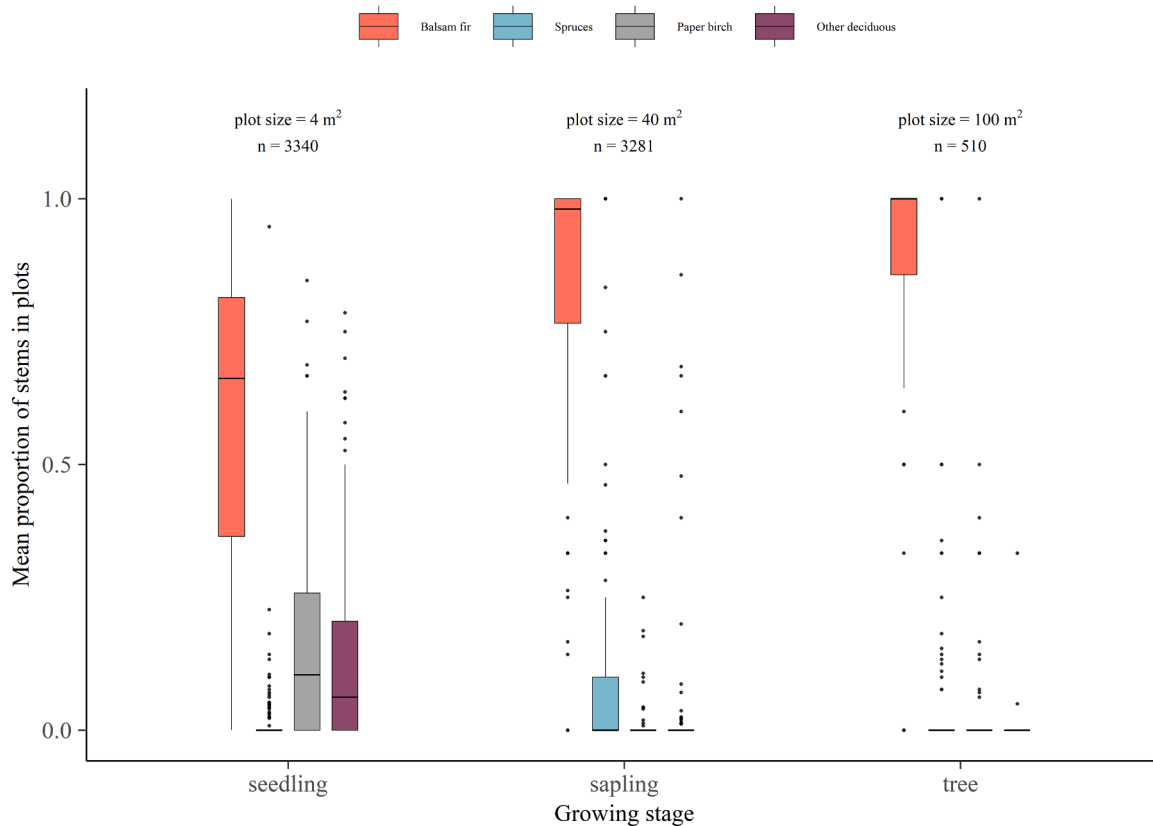


Fig. 1. Proportion of species (n = number of individual) present in plots (boxplots) across growth stages (seedlings: diameter at breast height (DBH) < 1 cm and height > 30 cm, saplings: 1 cm ≤ DBH < 10 cm and trees: DBH ≥ 10 cm) in stands established between 2000 and 2015 after clearcutting in the Forêt Montmorency (Québec, Canada).

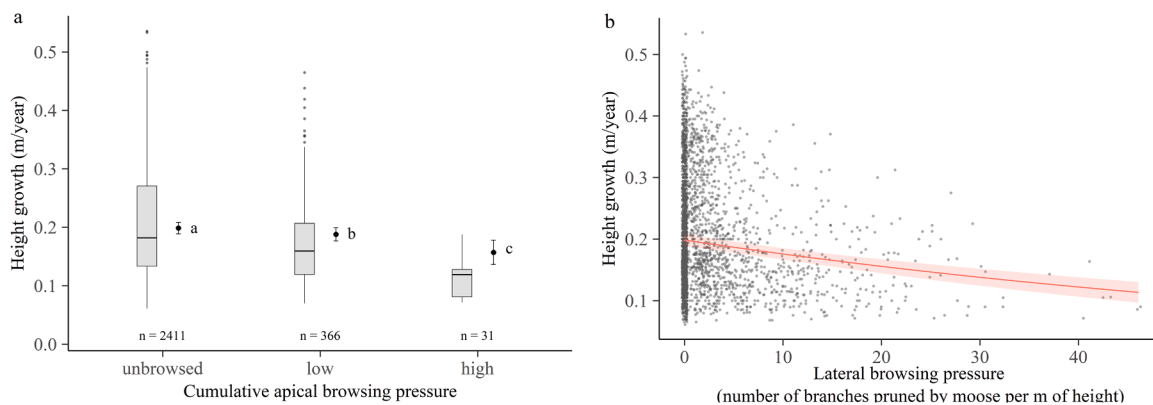


Fig. 2. a) Observed values (gray boxplots) and predicted values (black points) with their 95 % confidence intervals (error bars) of balsam fir (*Abies balsamea*) sapling (1 cm ≤ diameter at breast height < 10 cm) apparent height growth (tree height divided by stand age in summer 2023) in relation with cumulative apical browsing pressure (based on architectural classes taken from Keigley et al., 2003). The letters represent the result of the post-hoc test b) Predicted mean (red line) with 95 % confidence intervals (ribbon) and observed values (dots) of balsam fir sapling apparent height growth in relation with the number of lateral twigs browsed by moose, per m of height. Saplings were measured in stands established between 2000 and 2015 after clearcutting in the Forêt Montmorency (Québec, Canada).

deciduous species is often an issue following harvest in eastern boreal forest (Ménard et al., 2019). In Québec province, herbicide spraying has been banished in forest since 2000 and mechanical brushing is usually used to control competition, yet it was not used in any of the stands we surveyed. Competition from deciduous species used to be a concern at Forêt Montmorency, but no control has been prescribed after 2007 (Bouliane, comm. pers.). Other situation where cervids have precluded the recruitment of selected species have been reported elsewhere (deer:

Tremblay et al., 2007; moose: Gosse et al., 2011; De Vriendt et al., 2020). Selective browsing may thus act as a species specific filter allowing the recruitment of resistant species to the sapling stage but retaining browse sensitive species at the seedling stage. These results suggest that moose accelerates stand succession toward coniferous dominated stands under the moderate moose density observed in our study area (Kielland and Bryant, 1998). From a forest management perspective, this may seem desirable as it promotes a more rapid

progression towards a fir stand, but this can occur with a price for wildlife species with specific needs (Cardinal et al., 2012; Chollet and Martin, 2013). Under higher population densities, we could expect browsing pressure to shift toward balsam fir (White et al., 2021; De Vriendt et al., 2021).

Field-based browsing assessments are limited by the inability to account for stems that have already disappeared (Villemaire-Côté et al., 2022). As an example, our gradient of browsing intensity extended from 0 % to 100 % of stem browsed in a subplot, but a score of 0 could either mean that no stem was browsed or that there was no stem at all. The latter may reflect very heavy browsing pressure that eliminated all previously available stems. This limitation could be amplified by our measurement protocol where seedlings smaller than 30 cm were ignored to maximize our sampling effort considering that smaller seedlings are typically below lower moose browsing reach. Thus, we could not measure the effect of browsing if it occurred below 30 cm. As a result, our current estimates may underestimate the true effect of browsing. Furthermore, we did not directly test the effect of moose preventing selected seedlings from reaching the sapling stage, nor moose-induced mortality, as this would have involved tracking individual stems over several years. Instead, we used a chronosequence encompassing stands originating from clearcuts conducted 8–23 years ago as an alternative to a long term study where individual trees are monitored for several years (Angst and Kupferschmid, 2023). Still, our results show that major changes in composition and recruitment can occur at the transition from seedling to sapling stages due to moose browsing, emphasizing the need for the seedlings stage to be included in models predicting stand growth and yield given its critical role in the succession speed and stand development (Rijal et al., 2022).

Moreover, growth of balsam fir saplings can be considerably slowed by browsing, particularly in moose winter yards where browsing is intense and extended (LeBlanc-Boudreau et al., 2018). This is supported by our results, which further revealed an additive instead of a multiplicative effect of cumulative apical browsing pressure and lateral browsing pressure. This could be due to the very few measurements made on heavily browsed balsam fir stems, reducing the number of observations required for having enough statistical power to test interactions (Harrison et al., 2018). Regarding lateral browsing, our results showed that if the number of branches pruned is relatively high, its effect size can be of similar magnitude to that of apical browsing. However, its effect may last longer because lateral branches remain available for browsing after the apical bud is out of the moose's reach. Accordingly, we could extend the traditional threshold of 3 m height from which the stem is considered free to grow (Telfer, 1974; Potvin, 1995; Frerker et al., 2013).

Many young balsam fir sapling that we measured where exposed to moose browsing over only a few years. Considering that these young stems are the most vulnerable to browsing as they are easily accessible, and that stems previously browsed by moose are more likely to be rebrowsed (Mathisen et al., 2017), the long-term impact remains to be measured on younger stems (Angst and Kupferschmid, 2023). This potentially major impact could be perpetuated over time, causing an underestimation of its effect if they are only measured at young age (Wallgren et al., 2014).

5. Management implications

We demonstrated a growth delay on individual stems caused by moose browsing. The next step is to scale up our results to estimate growth delay at the stand scale and its effect on the prediction of potential forest yield at the landscape scale. Future studies should focus on integrating the effect of initial composition changes and the loss of individual growth on the long-term growth and yield models of forest stands. Once these models have been built, forest managers will be able to incorporate browse measurements (proportion of stems browsed in subplots for seedlings, cumulative apical browsing pressure and lateral

browsing pressure for saplings) into their field inventories to obtain an estimate of the long-term growth delay of forest stands. In areas where moose population densities are high, this will be a useful tool to contribute to sustainable forest management.

We could obtain a good indicator of browsing pressure at the stand level if we combine our results with those of aerial inventories. Considering the low proportion of heavily browsed stems, both apically and laterally, stand growth delay in our study area is likely to be low. However, browsing pressure is not spatially uniform; if we were to sample exclusively in winter yards, where browsing pressure is particularly intense, we will likely observe a higher proportion of heavily browsed stems. Moreover, we could spatialize these impacts according to the number and spatial distribution of winter yards within a given area. We could use this information alongside moose population surveys as these measures are both accessible and regularly conducted.

CRedit authorship contribution statement

LaRue Hugo: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation. **Tremblay Jean-Pierre:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Barrette Martin:** Writing – review & editing, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

Our research was funded by the Ministère des Ressources naturelles et Forêt (MRNF), the Ministère de l'Environnement, de la Lutte contre les changements climatiques, Faunes et Parcs (MELCCFP), the Bureau du forestier en chef, the Société des établissements de plein air du Québec (SEPAQ) and the Nation Huronne-Wendat. Special thanks to É.P. Laplante, M. Letellier-Bao and A. Higgins for their help in the fieldwork and data collection. We are grateful to S. Hamel and É. Thiffault and two anonymous referees for their comments on a previous version of the manuscript.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2026.123619](https://doi.org/10.1016/j.foreco.2026.123619).

Data availability

I am currently in the process of making the data public and available for sharing.

References

- Andreozzi, H.A., Pekins, P.J., Langlais, M.L., 2014. Impact of moose browsing on forest regeneration in Northeast Vermont. *Alces* 50, 67–79.
- Angst, J.K., Kupferschmid, A.D., 2023. Assessing browsing impact in beech forests: the importance of tree responses after browsing. *Diversity* 15, 1–22. <https://doi.org/10.3390/d15020262>.
- Bergqvist, G., Bergström, R., Edenius, L., 2003. Effects of moose (*Alces alces*) rebrowsing on damage development in young stands of Scots pine (*Pinus sylvestris*). *For. Ecol. Manag.* 176, 397–403. [https://doi.org/10.1016/S0378-1127\(02\)00288-8](https://doi.org/10.1016/S0378-1127(02)00288-8).
- Bouliane, J., Bélanger, L., Pineault, P., Sansregret, H., 2014. Plan d'aménagement forestier intégré tactique. (https://www.foretmontmorency.ca/assets/documents/PAFI-T_FMA.pdf).
- Bowyer, R., Ballenberghe, V., Kie, J., 2003. Moose (*Alces alces*), in: *Hoofed Mammals*. pp. 931–964.

- Brault, B., Tremblay, J.-P., Thiffault, N., Royo, A.A., Côté, S.D., 2023. Successful forest restoration using plantation at high deer density: How neighboring vegetation drives browsing pressure and tree growth. *For. Ecol. Manag.* 549, 121458. <https://doi.org/10.1016/j.foreco.2023.121458>.
- Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Machler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R. J.* 9, 378–400. <https://doi.org/10.32614/RJ-2017-066>.
- Brousseau, M., Thiffault, N., Beguin, J., Roy, V., Tremblay, J.-P., 2017. Deer browsing outweighs the effects of site preparation and mechanical release on balsam fir seedlings performance: implications to forest management. *For. Ecol. Manag.* 405, 360–366. <https://doi.org/10.1016/j.foreco.2017.09.024>.
- Cardinal, E., Martin, J.-L., Tremblay, J.-P., Côté, S.D., 2012. An experimental study of how variation in deer density affects vegetation and songbird assemblages of recently harvested boreal forests. *Can. J. Zool.* 90, 704–713. <https://doi.org/10.1139/z2012-037>.
- Chollet, S., Martin, J., 2013. Declining woodland birds in North America: should we blame Bambi? *Divers. Distrib.* 19, 481–483. <https://doi.org/10.1111/ddi.12003>.
- Côté-Vaillancourt, D., Tremblay, J.-P., Solberg, E., 2016. collabOR: estimation des tendances démographiques des populations d'originaux de la Seigneurie de Beaupré par une approche de science collaborative (mémoire). Université Laval, Québec.
- Crête, M., 1977. Importance de la coupe forestière sur l'habitat hivernal de l'original dans le sud-ouest du Québec. *Can. J. For. Res.* 7, 241–257. <https://doi.org/10.1139/x77-034>.
- Danell, K., Huss-Danell, K., Bergstrom, R., 1985. Interactions between browsing moose and two species of birch in Sweden. *Ecology* 66, 1867–1878. <https://doi.org/10.2307/2937382>.
- Danell, K., Niemela, P., Varvikko, T., Vuorisalo, T., 1991. Moose browsing on Scots pine along a gradient of plant productivity. *Ecology* 72, 1624–1633. <https://doi.org/10.2307/1940962>.
- De Vriendt, L., Barrette, M., Kolstad, A.L., Vuorinen, K., Speed, J.D.M., Lavoie, S., Tremblay, J.-P., 2023. Heavy browsing pressure by moose (*Alces alces*) can interfere with the objectives of ecosystem-based forest management. *For. Ecol. Manag.* 549, 121483. <https://doi.org/10.1016/j.foreco.2023.121483>.
- De Vriendt, L., Lavoie, S., Barrette, M., Tremblay, J.-P., 2021. From delayed succession to alternative successional trajectory: How different moose browsing pressures contribute to forest dynamics following clear-cutting. *J. Veg. Sci.* 32, 1–11. <https://doi.org/10.1111/jvs.12945>.
- De Vriendt, L., Thiffault, N., Royo, A.A., Barrette, M., Tremblay, J.-P., 2020. Moose browsing tends spruce plantations more efficiently than a single mechanical release. *Forests* 11, 1138. <https://doi.org/10.3390/f11111138>.
- Frerker, K., Sonnier, G., Waller, D.M., 2013. Browsing rates and ratios provide reliable indices of ungulate impacts on forest plant communities. *For. Ecol. Manag.* 291, 55–64. <https://doi.org/10.1016/j.foreco.2012.11.041>.
- Gosse, J., Hermanutz, L., McLaren, B., Deering, P., Knight, T., 2011. Degradation of boreal forests by nonnative herbivores in Newfoundland's national parks: recommendations for ecosystem restoration. *Nat. Areas J.* 31, 331–339. <https://doi.org/10.3375/043.031.0403>.
- Grenier-Potvin, A., Roy, G., 2023. Inventaire aérien de la population d'originaux (*Alces alces*) de la Forêt Montmorency et du Camp Mercier - Hiver 2023. Québec, ministère de l'Environnement et de la Lutte contre les changements climatiques, de la Forêt et des Parcs. 4p.
- Harrison, X.A., Donaldson, L., Correa-Cano, M.E., Evans, J., Fisher, D.N., Goodwin, C.E.D., Robinson, B.S., Hodgson, D.J., Inger, R., 2018. A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ* 6, e4794. <https://doi.org/10.7717/peerj.4794>.
- Hartig, F., Lohse, L., Leite, M. de S., 2024. DHARMA: Residual diagnostics for hierarchical (multi-level/mixed) regression models. (Version 0.4.7). (<https://cran.r-project.org/web/packages/DHARMA/index.html>).
- Heikkilä, R., Hokkanen, P., Kooiman, M., Aygüney, N., Bassoulet, C., 2003. The impact of moose browsing on tree species composition in Finland. *Alces* 39, 203–213.
- Hidding, B., Tremblay, J.-P., Côté, S.D., 2013. A large herbivore triggers alternative successional trajectories in the boreal forest. *Ecology* 94, 2852–2860. <https://doi.org/10.1890/12-2015.1>.
- Holt, R.D., Bonsall, M.B., 2017. Apparent competition. *Annu. Rev. Ecol. Evol. Syst.* 48, 447–471. <https://doi.org/10.1146/annurev-ecolsys-110316-022628>.
- Keigley, R.B., Frisina, M.R., Fager, C., 2003. A method for determining the onset year of intense browsing. *J. Range Manag.* 56, 33–38. <https://doi.org/10.2307/4003878>.
- Kielland, K., Bryant, J.P., 1998. Moose herbivory in taiga: effects on biogeochemistry and vegetation dynamics in primary succession. *Oikos* 82, 377–383. <https://doi.org/10.2307/3546979>.
- Koga, S., Zhang, S.Y., Bégin, J., 2002. Effects of precommercial thinning on annual radial growth and wood density in balsam fir (*Abies balsamea*). *Wood Fiber Sci.* 34, 625–642. (<https://wfs.wst.org/index.php/wfs/article/view/329>).
- Kuuluvainen, T., Gauthier, S., 2018. Young and old forest in the boreal: critical stages of ecosystem dynamics and management under global change. *For. Ecosyst.* 5, 26. <https://doi.org/10.1186/s40663-018-0142-2>.
- Langevin, B., Bastien, H., 2013. Inventaire aérien de l'original dans la zone de chasse 27 à l'hiver 2013. Québec Minist. ère Des. Ressour. Nat. 16p. (https://www.seigneuriedebaupre.ca/documents/contenu/fsc_071_1_2_1.pdf).
- LeBlanc-Boudreau, A., Tremblay, J.-P., Boudreau, S., 2018. Croissance et architecture du sapin baumier en réponse au broutement de l'original (mémoire). Université Laval, Québec.
- Lenarz, M.S., Wright, R., Schrage, M.W., Edwards, A.J., 2011. Compositional analysis of moose habitat in northeastern Minnesota. *Alces* 47, 135–149. (<https://www.alcesjournal.org/index.php/alces/article/view/89>).
- Lenth, R.V., Banfai, B., Bolker, B., Buerkner, P., Giné-Vázquez, I., Herve, M., Jung, M., Love, J., Miguez, F., Piskowski, J., Riebl, H., Singmann, H., 2024. emmeans: Estimated marginal means, aka least-squares means. (version 1.10.5). (<https://cloud.r-project.org/web/packages/emmeans/index.html>).
- Maes, S.L., Perring, M.P., Vanhellefont, M., Depauw, L., Van den Bulcke, J., Brümelis, G., Brunet, J., Decocq, G., den Ouden, J., Härdtle, W., Hédl, R., Heinken, T., Heinrichs, S., Jaroszewicz, B., Kopecký, M., Máliš, F., Wulf, M., Verheyen, K., 2019. Environmental drivers interactively affect individual tree growth across temperate European forests. *Glob. Change Biol.* 25, 201–217. <https://doi.org/10.1111/gcb.14493>.
- Margolis, H.A., Gagnon, R.R., Pothier, D., Pineau, M., 1988. The adjustment of growth, sapwood area, heartwood area, and sapwood saturated permeability of balsam fir after different intensities of pruning. *Can. J. For. Res.* 18, 723–727. <https://doi.org/10.1139/x88-110>.
- Mathisen, K.M., Milner, J.M., Skarpe, C., 2017. Moose–tree interactions: rebrowsing is common across tree species. *BMC Ecol.* 17, 1–15. <https://doi.org/10.1186/s12898-017-0122-3>.
- McCarthy, J., Weetman, G., 2007. Self-thinning dynamics in a balsam fir (*Abies balsamea* (L.) Mill.) insect-mediated boreal forest chronosequence. *For. Ecol. Manag.* 241, 295–309. <https://doi.org/10.1016/j.foreco.2007.01.001>.
- Ménard, L.-P., Ruel, J.-C., Thiffault, N., 2019. Abundance and impacts of competing species on conifer regeneration following careful logging in the Eastern Canadian boreal forest. *Forests* 10, 177. <https://doi.org/10.3390/f10020177>.
- Ministère des ressources naturelles et des forêts, 2016. Carte écoforestière à l'échelle 1: 20 000 en format PDF. Données Québec. (<https://www.donneesquebec.ca/recherche/dataset/carte-ecoforestiere-pdf>).
- Ministère des ressources naturelles et des forêts, 2019. Modèles numériques de terrain à l'échelle de 1/20 000. Données Québec. (<https://www.donneesquebec.ca/recherche/dataset/modeles-numeriques-d-altitude-a-1-echelle-de-1-20-000>).
- Morneau, C., 2021. Classification écologique du territoire québécois. Québec, ministère des forêts, de la faune et des parcs. 11p. (<https://mfpp.gouv.qc.ca/nos-publications/classification-ecologique-territoire-quebecois/>).
- Nappi, A., 2013. Perturbations naturelles. Fascicule 1.5. Dans Bureau du forestier en chef. Manuel de détermination des possibilités forestières 2013-2018. Gouvernement du Québec, Roberval, QC, pp. 29–39.
- Pachana, P., 2016. Forest stands volume estimation by using Finnish multi-source national forest inventory in Stoilowe Mountains National Park. *Folia For. Pol. Ser. A* 58, 3–12. <https://doi.org/10.1515/ffp-2016-0001>.
- Pebesma, E., Bivand, R., 2023. Spatial Data Science: With Applications in R. Chapman and Hall/CRC, New York. <https://doi.org/10.1201/9780429459016>.
- Peng, C., 2000. Understanding the role of forest simulation models in sustainable forest management. *Environ. Impact Assess. Rev.* 20, 481–501. [https://doi.org/10.1016/S0195-9255\(99\)00044-X](https://doi.org/10.1016/S0195-9255(99)00044-X).
- Posner, S.D., Jordan, P.A., 2002. Competitive effects on plantation white spruce saplings from shrubs that are important browse for moose. *For. Sci.* 48, 283–289. <https://doi.org/10.1093/forestscience/48.2.283>.
- Potvin, F., 1995. L'inventaire du brouet: revue des méthodes et description de deux techniques. *Minist. ère De. l'Environ. Et. De. la Faune Québec Can.*
- R Core Team, 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. (version 4.2.1). (<https://www.R-project.org/>).
- Rijal, B., Power, H., Auger, L., Guillemette, F., Bédard, S., Schneider, R., 2022. Development of tree recruitment models for 10 species groups in the sugar maple-dominated mixed forests of eastern Canada. *Can. J. For. Res.* 53, 134–150. <https://doi.org/10.1139/cjfr-2022-0111>.
- Ruel, J.-C., 1992. Impact de la compétition exercée par le framboisier (*Rubusidaeus* L.) et les feuillus de lumière sur la croissance du sapin (*Abies balsamea* (L.) Mill.) en régénération. *Can. J. For. Res.* 22, 1408–1416. <https://doi.org/10.1139/x92-187>.
- Smith, C., Beazley, K., Duinker, P., Harper, K.A., 2010. The impact of moose (*Alces alces andersoni*) on forest regeneration following a severe spruce budworm outbreak in the Cape Breton Highlands, Nova Scotia, Canada. *Alces* 46, 135–150.
- Snaith, T.V., Beazley, K.F., 2004. The distribution, status and habitat associations of moose in mainland Nova Scotia. *PNSIS* 42, 263–317. (<https://DalSpace.library.dal.ca/handle/10222/70932>).
- Soubeyrand, M., Marchand, P., Duchesne, L., Bergeron, Y., Gennaretti, F., 2024. Interactions between climate, soil and competition drive tree growth in Quebec forests. *For. Ecol. Manag.* 555, 121731. <https://doi.org/10.1016/j.foreco.2024.121731>.
- Spitzer, R., Ericson, M., Felton, A.M., Heim, M., Raubenheimer, D., Solberg, E.J., Wam, H.K., Rolandsen, C.M., 2024. Camera collars reveal macronutrient balancing in free-ranging male moose during summer. *Ecol. Evol.* 14, e70192. <https://doi.org/10.1002/ece3.70192>.
- Telfer, E.S., 1974. Logging as a factor in wildlife ecology in the boreal forest. *For. Chron.* 50, 186–190. <https://doi.org/10.5558/ffc50186-5>.
- Tremblay, J.-P., Huot, J., Potvin, F., 2007. Density-related effects of deer browsing on the regeneration dynamics of boreal forests. *J. Appl. Ecol.* 44, 552–562. <https://doi.org/10.1111/j.1365-2664.2007.01290.x>.
- Villemaine-Côté, O., Ruel, J.-C., Tremblay, J.-P., 2022. Reduction in local white-tailed deer abundance allows the positive response of northern white cedar regeneration to gap dynamics. *Can. J. For. Res.* 52, 1383–1397. <https://doi.org/10.1139/cjfr-2022-0063>.
- Wallgren, M., Bergquist, J., Bergström, R., Eriksson, S., 2014. Effects of timing, duration, and intensity of simulated browsing on Scots pine growth and stem quality. *Scand. J. For. Res.* 29, 734–746. <https://doi.org/10.1080/02827581.2014.960896>.

- Warton, D.I., 2022. More than one response variable: multivariate analysis. In: *Eco-Stats: Data Analysis in Ecology, Methods in Statistical Ecology*. Springer, Cham, pp. 267–293.
- White, S., Zhu, X., Meng, F., Taylor, S., Bourque, C.P.-A., 2021. Intensive moose browsing and small-scale domestic woodcutting impacts on forest successional trajectories in Gros Morne National Park, Canada. *For. Chron.* 97, 1–11. <https://doi.org/10.5558/tfc2021-025>.
- Zhou, J., Prugh, L., D. Tape, K., Kofinas, G., Kielland, K., 2017. The role of vegetation structure in controlling distributions of vertebrate herbivores in arctic Alaska. *Arct. Antarct. Alp. Res.* 49, 291–304. <https://doi.org/10.1657/AAAR0016-058>.
- Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems: data exploration. *Methods Ecol. Evol.* 1, 3–14. <https://doi.org/10.1111/j.2041-210X.2009.00001.x>.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed effects modelling for nested data. In: Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M. (Eds.), *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York, NY, pp. 101–142. https://doi.org/10.1007/978-0-387-87458-6_5.