


RESEARCH ARTICLE

Cumulative effects of spruce budworm and moose herbivory on boreal forest ecosystems

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Handling Editor: Clare McArthur**Abstract**

1. Ungulate herbivory is a key natural disturbance in many ecosystems. In forest ecosystems, ungulate herbivory often co-occurs with other disturbances yet there are few studies looking at the cumulative impacts of ungulates and other natural disturbances on forest dynamics.
2. We report on an 18-year experiment to investigate the combined effects of introduced, non-native moose and native spruce budworm herbivory on balsam fir forest recruitment and regeneration. Specifically, we measured inputs into early life-history components of balsam fir dominant boreal forest ecosystems such as seed density, seedbed quality, seedling and sapling height and density, as well as adult density in eight paired moose exclosure and control sites across a spruce budworm disturbance gradient (i.e. no outbreak, recent outbreak, old outbreak) that resulted in closed, partially open and open canopies.
3. Piecewise structural equation models (SEMs) revealed a strong negative effect of spruce budworm disturbance on balsam fir adult density and indirect effects of this budworm disturbance on balsam fir seedling and sapling density mediated through adult density. We observed a similar pattern of budworm disturbance effects on balsam fir seed density with the lowest densities in sites with open canopy, then partially open and closed canopies. As expected, the SEM showed a positive effect of bryophyte seedbed cover on balsam fir seedling density. The SEM showed support for a positive effect of moose exclusion on balsam fir sapling height and density. Specifically, saplings were on average taller and denser in exclosure than control plots and these differences are most pronounced at sites with partially open canopies created by spruce budworm disturbance and undisturbed or closed canopy sites. Overall, we show evidence for cumulative and interactive effects of spruce budworm and moose herbivory on all life stages of balsam fir and such effects are negatively affecting regeneration of balsam fir forests.
4. Human activities are creating conditions that facilitate the expansion and increased impacts of herbivores on boreal ecosystem functioning. A greater understanding of how ungulate herbivory interacts with other disturbances is needed to improve our predictions of forest ecosystem dynamics under global change.

KEYWORDS

alternative stable state, boreal forest, deer, disturbance, forest dynamics, legacy effect, regime shift, ungulate

1 | INTRODUCTION

Phytophagous insects, particularly taxa that experience outbreak dynamics over large spatial extents (e.g. spruce budworm *Choristoneura* sp.) have long been considered important natural disturbances (Mattson & Addy, 1975). Insect outbreaks can influence plant biodiversity and species coexistence, and community productivity, with implications for ecosystem services provided by forests (Kurz et al., 2008; Mattson & Addy, 1975). Research over the past two decades has also clearly demonstrated that ungulate species can act as key forest disturbances (reviewed in Bernes et al., 2018; Côté et al., 2014; Forbes et al., 2019) with several studies linking high ungulate densities to ecosystem transitions (Hidding et al., 2013; McInnes et al., 1992). In forest ecosystems, ungulate herbivory often co-occurs with disturbances such as insect outbreaks, yet there are few studies looking at the interactive impacts of ungulates and other natural disturbances on forest dynamics (but see Conway & Johnstone, 2017; Nuttle et al., 2013; Royo et al., 2010).

Ungulates, such as moose *Alces alces*, whitetail deer *Odocoileus virginianus*, sika deer *Cervus nippon* and red deer *Cervus elaphus*, can influence ecosystems via direct and indirect mechanisms (see reviews in Bernes et al., 2018; Forbes et al., 2019; Pastor et al., 2006; Schrama et al., 2013). Direct effects include selective feeding on palatable plant species providing a competitive advantage to unpalatable species (Ellis & Leroux, 2017; Hidding et al., 2013; Royo et al., 2010). Indirect effects of selective feeding, trampling and excreta include changes in litter quantity and quality and changes in soil structure, fauna and function, which can cascade back to influence plant production (Daskin & Pringle, 2016; Kardol et al., 2014; Lagerström et al., 2011; Schrama et al., 2013). The severity of impacts of ungulates on forest ecosystems, however, is often mediated by other human (e.g. forestry; Kolstad et al., 2018; Tremblay et al., 2007) and natural (e.g. insect outbreaks; Ellis & Leroux, 2017; MacSween et al., 2019) disturbances.

Insect outbreaks are important disturbances in boreal forests of North America and Fennoscandia (Pickett & White, 1985). In balsam fir *Abies balsamea* dominated boreal forests, these natural disturbances cause significant adult tree removal or die-off, which provides open canopies and conditions for fast growing, palatable species to thrive (Côté et al., 2014). Abundant food paired with low densities of natural predators can lead to high ungulate densities and subsequent high direct and indirect effects on boreal forest functioning (Ellis & Leroux, 2017).

Unlike most boreal forest trees, balsam fir regenerates via 'advanced regeneration', germinating into closed canopy stands forming a dense understorey of saplings (McLaren et al., 2009). Unimpeded growth is crucial at this stage, without overbrowsing by herbivores

such as moose, to ensure minimal density to close the canopy gap and regenerate the stand (Kneeshaw & Bergeron, 1998). These saplings will remain in this arrested stage until there is an opening in the canopy, usually a result of native insect herbivory such as spruce budworm and/or windfall, into which these saplings grow (Charron & Hermanutz, 2016; McCarthy & Weetnam, 2007). Balsam fir dominant boreal landscapes are therefore a mosaic of various aged stands, limiting the size of natural disturbances to small to medium canopy openings. Recruitment relies directly on seed production, rather than a seed bank, as seeds are viable for only 1 year (Gosse et al., 2011; Houle & Payette, 1991). Balsam fir reaches maturity at approximately 20 years, and if there are insufficient adult trees to produce seed, there will be a direct response: a lack of recruitment, because there is no buffering ability of a seed bank (Gosse et al., 2011). Another potential recruitment limitation is the availability of optimal seedbed, composed of feathermosses (*Dicranum* sp., *Hylocomium splendens*, *Pleurozium schreberi*, *Ptilium crista-castrensis* and *Rhytidiadelphus* sp.) and low growing plants such as bunchberry *Cornus canadensis*, without the presence of leaf litter, grasses or shrubs such as *Kalmia angustifolia* (Charron & Hermanutz, 2017; McLaren & Janke, 1996). Therefore, there are numerous stages of the balsam fir life cycle that may result in failed regeneration; however, few studies have focused on herbivory effects on the germination recruitment phase to understand how it may affect the regeneration trajectory and the occurrence of alternative states (Hidding et al., 2013).

To test the combined effects of moose herbivory and spruce budworm disturbance on balsam fir dominant forest regeneration, we measure forest components in sites with and without moose herbivory after 18 years (1998–2016) across a budworm disturbance gradient [i.e. no outbreak, recent outbreak (i.e. 1990s), old outbreak (i.e. 1970s)] that results in canopy openings of various sizes. To address the crucial lack of understanding on the potential recruitment limitation of balsam fir and how it affects regeneration, we measure inputs into early life-history components of fir dominant forest ecosystems such as seed density, seedbed quality, seedling and sapling height and density as well as adult density. We hypothesize that spruce budworm and moose herbivory will act in tandem to have negative impacts on balsam fir regeneration. Spruce budworm preferentially kill adult fir trees 70 years and older, while moose restrict the transition from fir sapling to adults via browsing. Moose impacts can therefore lead to an indirect loss of seed productivity and seedling recruitment. Given the duration of the experiment relative to balsam fir longevity (max. 200 years), we expect a difference in adult balsam fir density and seed rain across our spruce budworm disturbance gradient but no direct moose impact on the adult life stage, and therefore seed production of fir. We test the following predictions:

areas with open spruce budworm canopy gaps will have (a) lower adult balsam fir and seed density and (b) lower seedbed quality than areas with closed or less disturbed canopies. In addition, we predict that in areas with high moose browsing (i.e. controls) (c) balsam fir seedling density and height will be lower, and (d) balsam fir sapling density and height will be lower than in areas with low moose browsing (i.e. exclosures). We hypothesize that these direct moose effects on seedlings and saplings will be influenced by the indirect effect of spruce budworm disturbance on adult balsam fir density and canopy opening. Given the lack of studies investigating combined effects of insect herbivory and ungulate herbivory on forest recruitment (but see Charron & Hermanutz, 2017; Gosse et al., 2011), we base our predictions on recent evidence of combined effects of forestry and moose (Kolstad et al., 2018; Speed et al., 2014) or deer browsing (Dufresne et al., 2009; Hidding et al., 2013) and fire/windfall and ungulate browsing (Conway & Johnstone, 2017; Nuttle et al., 2013, 2014) on components of forest understorey.

2 | MATERIALS AND METHODS

2.1 | Study site

The study took place in Terra Nova National Park (TNNP; 48°30'N, 54°00'W), a protected area of 40,000 ha under maritime climate, located on the east coast of the island of Newfoundland, Canada. Balsam fir is a dominant component of eastern Boreal forests, and in Newfoundland is the major tree species, accounting for 50% of the tree volume (Meades & Roberts, 1992). TNNP boreal forest is dominated by balsam fir, black spruce *Picea mariana* and mixed hardwood forests. Historically, natural disturbances such as insect outbreaks and severe wind events, triggered balsam fir stand regeneration. Between the late 1970s to early 1980s, 1,300 ha of TNNP forest experienced insect outbreaks, and 23 ha were affected in the 1990s. These spruce budworm outbreaks are distributed as patches

of various sizes occurring mainly in the balsam fir dominated areas of TNNP.

In 1878 and 1904, moose were introduced to the island of Newfoundland (Pimlott, 1959). Since wolf extirpation in the 1930s (Pimlott, 1959), the moose population has thrived and increased to a level higher than carrying capacity in many parts of the island. Spruce budworm outbreaks have created optimal conditions for forage species growth and moose populations have increased in areas affected by the recent budworm outbreaks in and around TNNP (Gosse et al., 2011).

2.2 | Experimental design

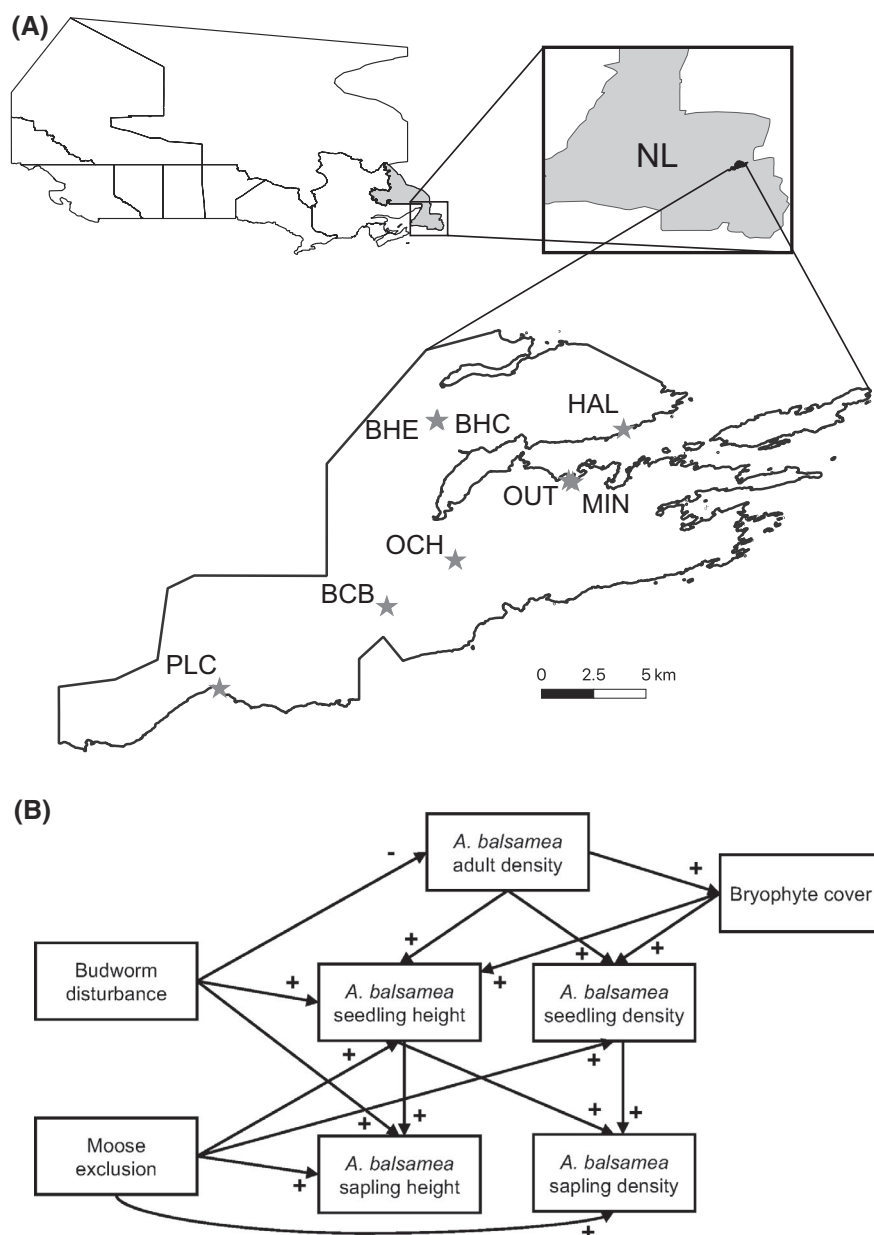
In the fall of 1998, eight pairs of moose exclosure and control plots were established along a gradient of spruce budworm disturbance intensity, in an effort to assess the interaction between spruce budworm and moose herbivory on forest regeneration (Table 1; Figure 1A). Disturbance intensity can be characterized in many different ways (Pickett & White, 1985), and here we define intensity by canopy cover, at the start of the study, created by disturbance as this trait has been found to correlate with various factors influencing boreal forest recovery (Charron & Hermanutz, 2016, 2017). Note that canopy opening created by spruce budworm in this study system correlates with the age of disturbance and the gap size created from the disturbance (Table 1). Plots are 25 × 25 m with five 5 × 5 m sub-plots distributed along a diagonal and nested, 2 × 2 m and 1 × 1 m quadrats for survey purposes. A 5 m wide buffer zone was included around the exclosure plot so that the fencing was 35 m on each side (Figure A1). Fencing effectively excluded moose, but allowed access to other small herbivores (e.g. hares, red squirrels). There are no deer on the island and native woodland caribou *Rangifer tarandus caribou* do not frequent the areas surrounding the experimental plots.

The exclosures were erected in balsam fir dominated stands in the following budworm disturbance recovery stages (Table 1): (a)

TABLE 1 Description of eight experimental sites. Description of eight sites used for the moose exclusion experiment implemented in 1997–1998 in Terra Nova National Park, Newfoundland, Canada. Old insect outbreaks occurred in the 1970–1980s and new insect outbreaks occurred in the 1990s. We used budworm disturbance patch openness at the start of the study in 1998 to characterize disturbance in our analysis as previous empirical evidence (e.g. Charron & Hermanutz, 2016) suggests that patch openness is an important predictor of forest regeneration and moose effects post disturbance. Current disturbance size (2018) reported here was estimated from Google Earth images

Site	Site ID	Disturbance stage at establishment	Disturbance Openness	Disturbance size (ha)
Hall's Beach	HAL	Mature forest	Closed	0
Outport Trail	OUT	Mature forest	Closed	0
Minchin's Cove	MIN	New insect outbreak	Partial	2.12
Platter's Cove	PLC	New insect outbreak	Partial	0
Bread Cove Brook	BCB	Old insect outbreak	Partial	3.35
Ochre Hill	OCH	Old insect outbreak	Partial	5.53
Blue Hill Centre	BHC	Old insect outbreak	Open	82
Blue Hill Edge	BHE	Old insect outbreak	Open	82

FIGURE 1 (A) Study area with eight paired moose exclosure/control sites in balsam fir forests along a gradient of spruce budworm outbreak in Terra Nova National Park, Newfoundland and Labrador (NL), Canada. See Table 1 for site names and characteristics. (B) Conceptual diagram showing predicted effects of spruce budworm disturbance and moose exclusion on components of balsam fir life history. Direction of predicted effect is denoted + (positive) or - (negative) where arrows join boxes. These predicted relationships are the basis for a piecewise structural equation model—see main text for details and Table 2 and Figure 2 for results



mature, non-disturbed forest stand with closed canopies ($n = 2$; gap size: 0 ha), (b) small gaps created by insect disturbance during the 1970s and 1990s spruce budworm outbreaks with partially open canopies ($n = 4$; gap size: 0–5.53 ha) and (c) large gaps created by insect disturbance during the 1970s spruce budworm outbreak with open canopies ($n = 2$; gap size: 82 ha). As exclosures were erected post-budworm outbreak, our inference is on the legacy effects (i.e. long-term, sensu Cuddington, 2011) of sustained moose herbivory following outbreak and not on the short-term response of forests to moose herbivory following outbreak.

As budworm disturbance cannot be externally manipulated and we are interested in long-term forest regeneration, our approach to investigating combined effects of budworm and moose involved placing moose exclosures along a gradient of observed budworm disturbance. While we have low replication across treatments, the exclosures are large with multiple subplots per plot to characterize

internal variability and we continue to monitor our treatments over a relatively long period (18 years). Large-scale, long-term experiments are rare, inherently difficult to conduct and such experiments often have low replication but fill important knowledge gaps about ecosystem and landscape processes (Carpenter et al., 1995).

2.3 | Data collection

We collected data on the different adult, seedling, sapling balsam fir life stages and seedbed in 2016, 18 years after the initial experimental moose exclusion. Because of the mast year behaviour of balsam fir, seed productivity was highly variable. We collected data from the last masting event in our study system, 2015. Following Houle (1999) we define a balsam fir mast year as years where seed production is >100 seeds/m². We measured balsam

TABLE 2 Piecewise structural equation model results. Results of a piecewise structural equation model to test the effects of budworm disturbance and moose exclusion on balsam fir forests. Note that budworm disturbance is measured using canopy openness (i.e. open, partial, closed) created by budworm. Site was always included as a random intercept in models. Coefficient estimates for each level of the categorical variables are provided. Std estimate: standardized coefficient estimate, Raw estimate: non-standardized coefficient estimate, SE = standard error of coefficient estimate, df = degrees of freedom, and p = p -value with statistical significance denoted as *** <0.001, * <0.01, * <0.05. See Figure 2 for model fits (i.e. marginal and conditional R^2)

Response	Predictor	Standardized estimate	Raw estimate	SE	df	p
<i>A. balsamea</i> adult density	Budworm disturbance = closed		0.07	0.008	7	<0.001***
	Budworm disturbance = partial		0.01	0.005	5	0.053
	Budworm disturbance = open		0.004	0.008	5	0.96
<i>A. balsamea</i> seedling density	<i>A. balsamea</i> adult density	0.528	34.22	7.627	69	<0.001***
	Bryophyte cover	0.30	0.022	0.006	69	0.001***
	Moose exclusion				1	0.906
	Moose exclusion = control		0.986	0.267	7	0.008**
	Moose exclusion = enclosure		1.02	0.267	7	0.007**
<i>A. balsamea</i> seedling height	<i>A. balsamea</i> adult density	-0.162	-51.323	107.30	69	0.634
	Bryophyte cover	0.007	0.003	0.04	69	0.948
	Moose exclusion = control		15.664	1.697	5	<0.001***
	Moose exclusion = enclosure		13.744	1.729	5	<0.001***
	Budworm disturbance = closed		18.815	5.551	7	0.012*
	Budworm disturbance = partial		18.70	2.229	5	<0.001***
	Budworm disturbance = open		6.598	3.764	5	0.140
<i>A. balsamea</i> sapling density	<i>A. balsamea</i> seedling density	0.43	0.185	0.040	69	<0.001***
	<i>A. balsamea</i> seedling height	0.30	0.026	0.008	69	0.001**
	Moose exclusion = control		0.156	0.112	7	0.204
	Moose exclusion = enclosure		0.71	0.112	7	<0.001***
<i>A. balsamea</i> sapling height	<i>A. balsamea</i> seedling height	-0.037	-0.158	0.431	70	0.716
	Moose exclusion = control		27.606	7.809	5	0.017*
	Moose exclusion = enclosure		61.228	7.865	5	<0.001***
	Budworm disturbance = closed		24.392	13.505	7	0.114
	Budworm disturbance = partial		66.0184	9.667	5	0.001**
	Budworm disturbance = open		42.84	13.919	5	0.028*
Bryophyte cover	<i>A. balsamea</i> adult density	0.203	179.274	163.938	71	0.278

fir life stage components as density and height (for seedlings and saplings; Table A1).

To test prediction (a) we recorded the density of live balsam fir adults in 25 × 25 m plots. Adult trees were defined as >10 cm DBH

individuals (Table A1). To characterize spruce budworm impacts on balsam fir seed density, we placed seed traps in all control plots at all sites (Table A1) and collected and counted total number of seeds per m² per control plot. We only collected seed data from control

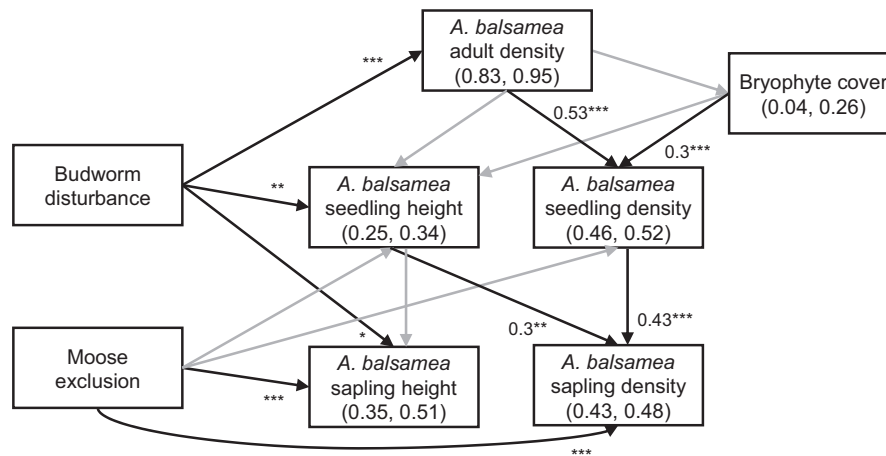


FIGURE 2 Results of piecewise structural equation model analysis to test the effects of budworm disturbance and moose exclusion on balsam fir forests. Black arrows denote statistically significant relationships (see Table 2 for details) with *** <0.001, ** <0.01, * <0.05. Values on black arrows are standardized coefficient estimates. Note that standardized coefficient estimates are not provided for categorical variables budworm disturbance and moose exclusion—see Table 2 for raw coefficient estimates for each level of these categorical variables. Grey arrows denote non-significant relationships. Values in parentheses of the boxes are marginal and conditional R^2 of each model response variable. Note that budworm disturbance is measured using canopy openness (i.e. closed, partial, open) created by budworm

plots because seed rain can cover a large area (i.e. control + enclosure) and we did not expect any direct effects of moose on seed production after 18 years of moose exclusion. Moss or bryophyte cover is critical to the establishment and development of balsam fir advanced regeneration and therefore, to test prediction (b) we used % bryophyte cover in 1×1 m quadrats as our measure of seedbed quality. To test prediction (c), we recorded the density (individuals/ m^2) of live balsam fir seedlings in the 2×2 m quadrats and the height (cm) of each seedling measured from the tree base, at ground level, to the tip of the apical branch in 5×5 m quadrats. To test prediction d) we recorded the density (individuals/ m^2) of live balsam fir saplings and the height (cm) of each sapling measured from the tree base, at ground level, to the tip of the apical branch, in the 5×5 m quadrats. Following previous work, we defined a seedling as <30 cm in height and a sapling as 30–200 cm in height (Gosse et al., 2011; Table A1).

2.4 | Statistical analysis

2.4.1 | Structural equation model of spruce budworm and moose herbivory in balsam fir forests

We fit a piecewise structural equation model (SEM; Lefcheck, 2016; Shipley, 2000, 2009) to test our a priori predictions relating spruce budworm and moose herbivory to balsam fir life stages (Figure 1B). The SEM included six linear mixed models with balsam fir adult density, seedling height, seedling density, sapling height, sapling density and bryophyte cover as the responses. Note that in our analysis budworm disturbance, moose exclusion and balsam fir adult density are measured at the resolution of the plot and all other variables are measured at the subplot or quadrat (see Table A1). We did not include seed density in the SEM because seed density data were only

collected in control plots (see below). We included site as a random intercept in all models to account for spatial autocorrelation in the paired enclosure–control plots. The two primary predictor variables were spruce budworm disturbance gap openness (categorical variable with three levels; closed, partially open and open), and moose exclusion (categorical variable with two levels; moose exclusion and control). Predictions (a–d; Figure 1) outline the expected paths linking these two variables to the six response variables. In addition to these main effect paths, we included paths to control for the basic ecology of balsam fir forest regeneration. Specifically, we predicted a positive effect of balsam fir adult density and bryophyte cover on seedling density and height. Also, we predicted a positive effect of seedling density and height on sapling density and height respectively (Franks, 1990; Gosse et al., 2011; McLaren & Janke, 1996). We used Shipley's test of directed separation (i.e. d-sep test) to evaluate that there are no missing relationships without paths in our model (i.e. test of conditional independence). This test revealed three paths that did not meet the assumption of conditional independence. These paths were spruce budworm disturbance openness, balsam fir seedling and sapling height, and balsam fir seedling height and sapling density. We added these three additional paths to our initial model because despite not having included them in our a priori predictions, they are consistent with our understanding of balsam fir forest ecology. Specifically, we expect balsam fir seedlings and saplings to grow taller in more open canopied environments and we expect that taller balsam fir seedlings may lead to higher seedling survival and increased densities of balsam fir saplings (Franks, 1990). We evaluated the fit of this final SEM by comparing the Fisher C value against a chi-square distribution (Lefcheck, 2016; Shipley, 2009). We visually assessed the residuals of each individual linear mixed model in our SEM, and we report the marginal and conditional R^2 of each model as well as the standardized and raw coefficient estimates. We

also conducted Tukey's HSD multiple comparisons to assess if there were differences in the mean responses to budworm disturbance and moose exclusion. We used R v. 3.6.1 (R Core Team, 2019) for all analyses and the packages *LME* (Pinheiro et al., 2017) for the linear mixed models, package *PSEM* (Lefcheck, 2016) for the SEM, and package *MULTCOMP* (Hothorn et al., 2020) for the Tukey's HSD analyses. All data and R code are available online (Leroux et al., 2021).

2.4.2 | Effects of spruce budworm on balsam fir seed density

Because balsam fir seed data were only collected in control plots, we did not include these data in the SEM. Instead, to test the effect of spruce budworm on seed density, we fit a linear model with budworm disturbance openness as the predictor and seed density as the response. We conducted Tukey's HSD multiple comparisons to assess if there were differences in the mean seed density across budworm disturbance levels.

3 | RESULTS

3.1 | Structural equation model of spruce budworm and moose herbivory in balsam fir forests

The SEM model provided a good fit to the data (Fisher's $C = 22.22_{df=24}$, $p = 0.57$) and included nine statistically significant

($p < 0.05$) paths (Table 2; Figure 2). We found strong support for an effect of spruce budworm disturbance openness on balsam fir adult density. Specifically, open canopy sites had balsam fir adult densities that were on average 0.6% and 3% of the densities in closed and partially open canopy sites respectively (Figure 3). We found no support for an indirect effect of budworm disturbance via adult density on seedbed quality, measured as bryophyte cover (Table 2). We found strong support for an effect of spruce budworm disturbance openness on balsam fir seedling and sapling height (Table 2). Specifically, counter to our prediction, balsam fir seedling height was lower in budworm disturbed sites with open canopies relative to sites with partial or closed canopies (Figure 4). Consistent with our prediction, however, sapling height was higher in budworm disturbed sites with open or partially open canopies relative to sites with closed canopies (Table 2; Figure 5). The SEM

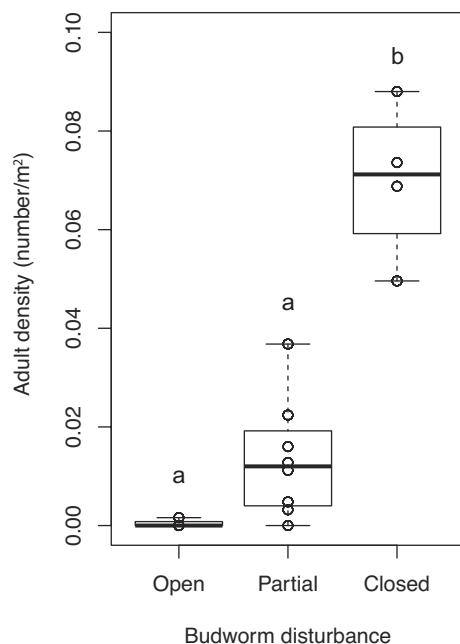


FIGURE 3 Balsam fir adult density across a gradient of canopy openings created by spruce budworm disturbance (see Table 1). Each point is raw data from an exclusion or control plot. Letters above the boxes indicate groups identified by Tukey's HSD multiple comparison analysis

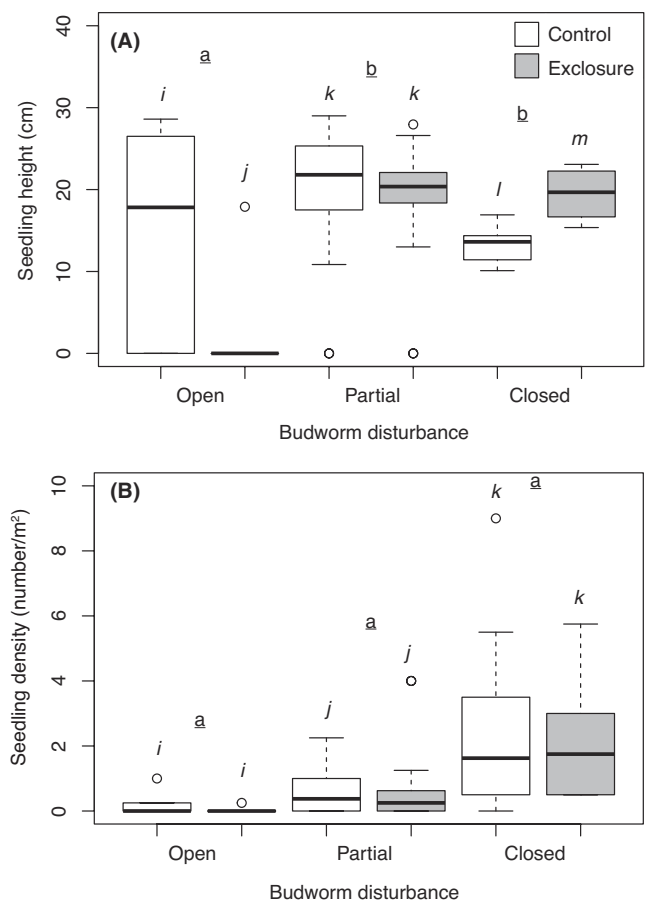


FIGURE 4 Balsam fir seedling height (A) and density (B) across a gradient of canopy openings created by spruce budworm disturbance in moose exclusion and control plots (see Table 1). Data are raw data from each subplot in each exclusion and control plot. The line is the median value and the whiskers are the upper and lower quartiles for each group. Dots represent outlier observations in each boxplot. Letters above the boxes indicate groups identified by Tukey's HSD multiple comparison analysis. We conducted two levels of comparisons; across budworm disturbance levels (letters a and b), and exclusion–control within each budworm disturbance level (letters i–m)

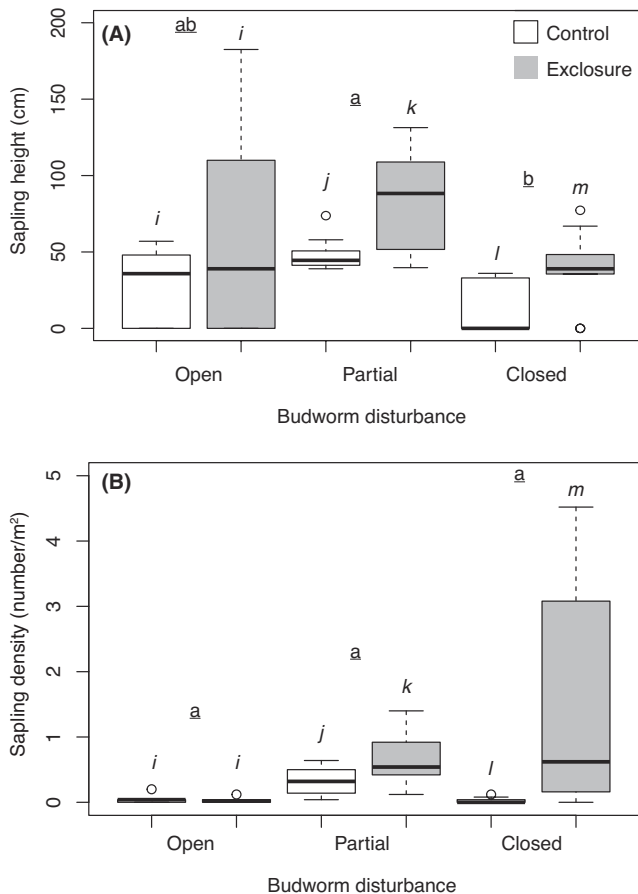


FIGURE 5 Balsam fir sapling height (A) and density (B) across a gradient of canopy openings created by spruce budworm disturbance in moose exclosure and control plots (see Table 1). Data are raw data from each subplot in each exclosure and control plot. The line is the median value and the whiskers are the upper and lower quartiles for each group. Dots represent outlier observations in each boxplot. Letters above the boxes indicate groups identified by Tukey's HSD multiple comparison analysis. We conducted two levels of comparisons; across budworm disturbance levels (letters a and b), and exclosure–control within each budworm disturbance level (letters *i–m*)

revealed that balsam fir adult density was a good predictor of seedling density (standardized regression coefficient $\beta = 0.53$). Also, seedling density was a good predictor of sapling density ($\beta = 0.43$, Table 2). Taken together, these two results suggest cascading effects of spruce budworm disturbance openness on seedling and sapling density mediated through adult density (Table 2). The SEM demonstrated support for a positive effect of bryophyte cover on balsam fir seedling density, but no support for an effect on seedling height (Table 2). We observed a strong effect of moose on balsam fir sapling height and density. Specifically, fir saplings were more than 2× taller and were denser in moose exclosures than control plots (Table 2). Moose effects are most pronounced in sites with spruce budworm disturbed partially open or undisturbed closed canopied sites relative to spruce budworm disturbed open canopied sites (Figure 5).

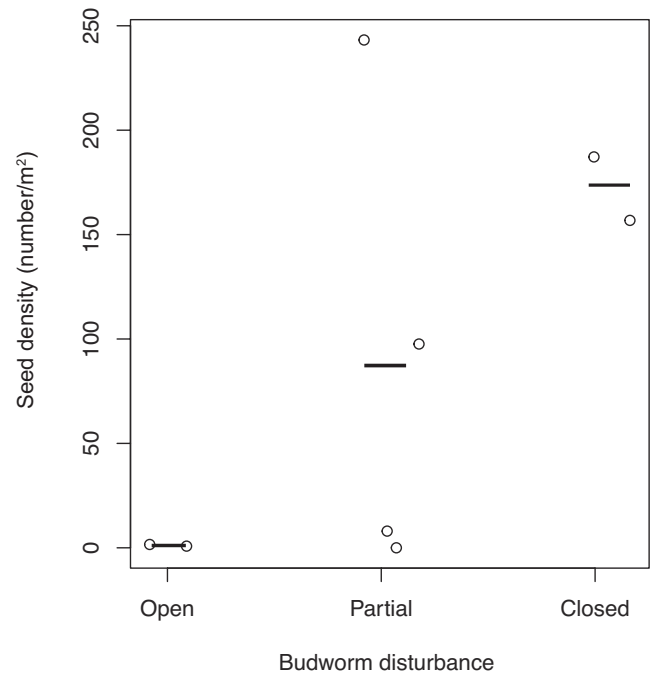


FIGURE 6 Balsam fir seed density across a gradient of canopy openings created by spruce budworm disturbance (see Table 1). Seed data were only collected in control plots so each point represents raw data from a control plot. Points are jittered for clarity and horizontal lines are mean seed density per disturbance category

3.2 | Effects of spruce budworm on balsam fir seed density

On average, seed density was lowest in spruce budworm disturbed sites with open, followed by partially open, and closed canopy sites (Figure 6). The linear model revealed that spruce budworm disturbance openness explained a sizable amount of variation in seed density ($R^2 = 0.43$) but the model was not statistically significant ($F_{2,5} = 1.88$, $p = 0.25$).

4 | DISCUSSION

Ungulate herbivores can have significant impacts on forest ecosystems as demonstrated from research across many biomes (see reviews in Bernes et al., 2018; Côté et al., 2014; Forbes et al., 2019). Ungulate impacts may be amplified in areas with human (Hidding et al., 2013; Speed et al., 2014), or natural (Conway & Johnstone, 2017; Nuttle et al., 2013, 2014) disturbances, yet there are few studies looking at the cumulative or interactive impacts of ungulates and other natural disturbances on forest ecosystems. Results from our 18-year experiment in a balsam fir dominant boreal forest demonstrate that spruce budworm and moose herbivory act in tandem to influence all components of balsam fir life history including adults, seeds, seedlings and saplings. Our analysis revealed that spruce budworm disturbance has strong direct

impacts on adult density, and weaker effects on seed density, and seedling and sapling height. Moose herbivory, however, has strong direct effects on sapling height and density. Overall, our long-term experiment demonstrates that the cumulative effects of spruce budworm and moose herbivory can lead to slower regeneration of balsam fir dominant boreal ecosystems.

The relative and cumulative effects of spruce budworm disturbance and moose browsing affected all components of balsam fir recruitment (Figure 2; Table 2). A lack of sufficient seed rain may inhibit regeneration of seedlings to saplings and saplings to adults. Slowed regeneration at these life stages can prevent seed rain and indirectly shift the vegetation community and seedbed to low quality impairing recruitment (Charron & Hermanutz, 2016; Gosse et al., 2011; McInnes et al., 1992; McLaren & Janke, 1996). Spruce budworm disturbance is a natural process in eastern North American boreal forests (Royama et al., 2005), shaping balsam fir's life-history strategy of advanced regeneration without a persistent seed bank. Budworm herbivory responds to and is responsible for landscape-level spatial heterogeneity in forest stand composition and age (Bouchard & Auger, 2014; Zhao et al., 2014). Despite our moose treatment being relatively long term compared to other wild ungulate exclusion studies (Forbes et al., 2019, meta-analysis reports median length of wild ungulate exclosure studies as 6 years), our study is still not long enough to detect moose impacts on balsam fir adult and seed production due to the legacy of severe overbrowsing by moose prior to the start of the experiment. However, as expected, we observed a strong direct effect of spruce budworm disturbance on balsam fir adult density and weaker effects on fir seed density, which is likely due to the lack of adult cone-producing trees in heavily disturbed sites (Figures 3 and 6). As expected, we observed a direct negative impact of moose browsing on balsam fir sapling height and density. We surmise that this impact may impede growth and survival of fir to the adult stage which is consistent with empirical evidence from Brandner et al. (1990)'s study on Isle Royale, USA. Specifically, budworm disturbance appears to modulate the speed of the balsam fir regeneration cycle (Smith et al., 2010), and in particular how quickly balsam fir reaches the sapling stage. Once in the sapling stage, our study provides evidence that moose herbivory may create an additional disturbance that prevents the transition of balsam fir saplings to adults, and is a force acting on the opposite end of balsam fir life history to spruce budworm. Continued monitoring of our experiment and other long-term experiments that span at least one full regeneration cycle (~20–30 years for fir to transition from seedling to adult) will allow us to test this prediction. Our experiment suggests that spruce budworm or moose disturbance can impact different life stages of balsam fir; however, the combination of moose and budworm herbivory may slow natural regeneration of balsam fir dominant boreal forests.

Previous evidence shows that human disturbances and ungulate herbivory can lead to ecosystem shifts (Hidding et al., 2013; McInnes et al., 1992). Similar to previous ungulate-disturbance studies (Nuttall et al., 2013, 2014; Royo et al., 2010), we observed

some evidence of an ecosystem shift triggered by an initial natural disturbance followed by ungulate herbivory. Specifically, the negative effects of moose on the height and density of balsam fir saplings were greatest in sites with partial canopy openings created by budworm and these data suggest that fir may not follow a natural pattern of regeneration to the canopy-dominant species in this ecosystem. It is notable, however, that we did not detect strong effects of moose on sapling height or density and effects of moose were opposite than expected on seedling height in open canopy sites. We speculate that this pattern is a result of moose legacy effects where significant moose disturbance occurred prior to fences being erected (mid-1990s). Evidence in support of this is the generally low average seedling and sapling height and density in exclosure and control plots at these sites (Figures 4 and 5). An alternative but less supported explanation (see Ellis & Leroux, 2017; Kolstad et al., 2018), is that abiotic factors not measured in this study (e.g. soil temperature) could be additional mechanisms driving seedling and sapling dynamics. Previous research on Isle Royale, USA demonstrates that regularly browsed fir sapling can persist in stunted form for decades (McLaren & Peterson, 1994). Importantly, even after 18 years of moose exclusion, we do not observe significant balsam fir regeneration in intense budworm disturbance sites, suggesting that active restoration may be required for ecosystem recovery (Charron & Hermanutz, 2016). Evidence from other systems suggests that changes in forest community composition triggered by moose may be long term and constitute an alternative state (Rotter & Robertus, 2015). Specifically, Rotter and Robertus (2015) demonstrate that once established, white spruce *Picea glauca* and grass *Poa* sp. may compete with each other and both may inhibit the establishment and regeneration of balsam fir forests on Isle Royale, USA. What is less appreciated from classic studies of moose effects on ecosystems (e.g. Danell et al., 1991; McInnes et al., 1992) is the role of other initial disturbances (e.g. fire, insects, forestry) in mediating moose effects. Our study suggests a greater focus on the cumulative and interactive effects of multiple disturbances in order to understand ungulate--ecosystem feedbacks. Long-term experiments are key to detect disturbance and ungulate-mediated changes in forest composition over time and to evaluate management effectiveness (Ellis & Leroux, 2017; Rotter & Robertus, 2015; Speed et al., 2014).

Accounting for abiotic conditions and primary productivity (Andriuzzi & Wall, 2017; Speed et al., 2014) may help predict the intensity of ungulate impacts on ecosystems, with impacts of ungulates, for example, on the abundance of other consumers, mediated by site productivity (Daskin & Pringle, 2016). Consequently, we may expect large impacts of moose herbivory on forest dynamics in our maritime boreal forest study system characterized by low primary productivity and a short growing season (Ellis & Leroux, 2017; Gosse et al., 2011). As the next round of budworm outbreaks is taking place in Eastern North America we see a unique opportunity to establish experimental plots that will allow ecologists to test our findings by explicitly tracking: (a) individual and combined impacts of budworm and moose herbivory on forest communities and (b) potential feedbacks between budworm and moose herbivory on

herbivory dynamics. Previous research has shown that moose herbivory can impact insect herbivores (Bernes et al., 2018; Teichman et al., 2013) but this work has not explored the potential links between moose herbivory and insect outbreak dynamics. Future research in this direction could help improve our ability to predict long-term dynamics of boreal forests and its foundation species. Ungulate browsing can be a major disturbance in forests (Forbes et al., 2019; Nuttle et al., 2013) and there is a need to incorporate herbivore impacts into general models of forest dynamics (de Jager et al., 2017), especially in the face of climate change. We have demonstrated how a long-term experiment can help uncover cumulative effects between insect disturbance and moose herbivory on diverse life stages of a canopy forming tree species. These results can contribute to the development of a general theory to predict ungulate-ecosystem feedbacks across biomes. Specifically, ungulate-ecosystem feedbacks may be modulated by other herbivores or disturbance gradients and these effects may help explain the broad context dependency observed in zoogeochemical studies (Schmitz et al., 2018).

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AUTHORS' CONTRIBUTIONS

L.H., J.F., S.J.L. and L.C. designed the study. L.H., J.F., L.C. and S.J.L. collected and synthesized the data. L.C., S.J.L., L.H. and J.F. analyzed the data. S.J.L., L.C., L.H. and J.F. interpreted results and wrote the manuscript.

DATA AVAILABILITY STATEMENT

All data and R code are available from the figshare at <https://doi.org/10.6084/m9.figshare.12791090.v3> (Leroux et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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