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Bottom-up and top-down forces regulate spruce budworm (Lepidoptera: Tortricidae) biological performance on regenerating white spruce

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ABSTRACT

Young plantation trees are often highly vulnerable to insect herbivory in ways that are difficult to predict as underlying mechanisms linked to plant traits and natural enemy pressure interact in context-dependent ways. We compared bottom-up and top-down forces acting on spruce budworm (*Choristoneura fumiferana*) on young white spruce (*Picea glauca*) trees in plantations vs in natural regeneration under hardwood canopy. The spruce budworm is the most important outbreaking conifer defoliator in Eastern Canada, and we aim to better understand budworm herbivory on young trees, given its importance for post-outbreak forest succession. We conducted a 4-year field survey in Northwestern Québec, Canada, to compare plant phenology, budworm density, defoliation rates, predator populations, and parasitism between the two habitats. We also designed manipulative experiments with sentinel larvae to assess bottom-up and top-down forces in these habitats. The field survey showed earlier budburst phenology in plantation trees, affecting synchronization with budworm emergence from diapause. Field survey results also included slightly higher budworm density and lower larval parasitism in plantations, but no significant difference in current-year growth defoliation. The bottom-up experiment showed slightly better budworm biological performance, indicated by higher pupal mass, in plantations. The top-down experiment suggested slightly higher predation and parasitism in the natural forests. Together, our results show how mechanisms controlling insect defoliator populations are context-dependent. In plantations both bottom-up and top-down pressures on the spruce budworm appear slightly eased, leading to marginally better biological performance and higher population density of this forest pest. However, differences are so minor that no impact on defoliation is observed.

1. Introduction

Forestry plantations seek conditions to maximize tree growth, but these conditions can also be favourable to herbivorous insect pests. Indeed, habitat can influence both bottom-up (plant trait-based) and top-down (from natural enemies) forces acting on insect herbivores (Moreau et al., 2006, 2018; Vidal and Murphy, 2018) and modulate the damage they cause to plants. Changes in these forces often lead young trees in plantations to be more vulnerable to pest insects than those in natural forest understory (Comeau et al., 2009; Fischbein and Corley, 2022; Jactel and Brockerhoff, 2007).

Higher vulnerability to pest insects can arise in several ways from various plantation characteristics. The first involves direct effects of abiotic factors: the open conditions in plantations imply higher temperatures resulting in faster insect growth and development (Fischbein and Corley, 2022). Second, indirect effects through trophic relationships also influence pest-insect dynamics in different habitats (Moreau et al., 2018, 2006), and both bottom-up pressures from plant defenses and top-down pressures from natural enemies can be expected to decrease in plantations. Bottom-up pressures on insect herbivores are limited by a trade-off between plant growth and defense: fast-growing trees in open conditions often show lower resistance to insect damage, as their foliage exhibits higher nutrient content and lower chemical defenses (Züst and Agrawal, 2017). Top-down pressures from natural enemies exerting biocontrol on insect herbivores have also been observed to be lower in open environments (Rodríguez et al., 2019; Staab and Schuldt, 2020;

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Stemmelen et al., 2022).

The spruce budworm (*Choristoneura fumiferana*) is the most important defoliator in eastern North America (Aakala et al., 2023). A spruce budworm outbreak has been ongoing in Québec since 2006, with up to 10 million ha defoliated annually. Processes underlying outbreak extent, severity, and dynamics are complex and, despite abundant research, remain poorly understood; however, it is clear that both bottom-up and top-down forces are involved (Bouchard et al., 2018; Girona et al., 2023; Pureswaran et al., 2016; Regniere et al., 2019; Royama et al., 2017). The spruce budworm is an early spring feeder on coniferous trees; preferred hosts are balsam fir (*Abies balsamea* ((L.) Mill.)), and white spruce (*Picea glauca* (Moench) Voss). Larvae emerge from diapause in spring and burrow into a developing bud to feed on expanding foliage. Phenological synchronization between host tree budburst and larval emergence is critical to budworm performance (Bellemin-Noël et al., 2021; Fuentealba et al., 2017): larvae that emerge too early for buds to be available mine into less nutritious old needles, feed on staminate flowers if available (Bauce and Carisey, 1996) or disperse by ballooning (Bellemin-Noël et al., 2025). Larvae established in a bud tend to stay in place, feeding first within the bud and then on the developing shoot as it emerges. They pupate after 6 larval instars, then give rise to adults which lay eggs to start the cycle anew. While spruce budworm mostly feeds on mature trees, at high population densities understory saplings are also attacked, particularly when overstory hosts have been depleted leading to the mortality of understory saplings during extended outbreaks (Navarro et al., 2018; Nealis and Régnière, 2004). As tree age and foliage chemistry influence larval performance, with younger trees favoring early instars and older trees better supporting later stages (Bauce et al., 1994; Mattson et al., 1991), widespread defoliation of both canopy and regeneration layers can disrupt successional trajectories. Spruce budworm outbreaks last for many years, during which seed production by stressed defoliated trees is reduced (Cotton-Gagnon et al., 2018). Multiple years of defoliation lead to mortality of mature trees, at the scale of hundreds of square km during severe outbreaks, and stand regeneration generally depends on the release of pre-established understory saplings (Cotton-Gagnon et al., 2018; Lavoie et al., 2021). Understanding the conditions under which young trees suffer budworm defoliation can be essential to predicting resilience to outbreaks. Early observers reported that a mature hardwood canopy appeared to protect regeneration from defoliation relative to saplings in open areas (Craighead, 1925).

Our study builds on this early observation to compare spruce budworm performance, abundance, and defoliation between two habitats, on saplings growing under a hardwood canopy (here onwards referred to as forest) vs those in plantations, and to examine the relative roles of bottom-up and top-down pressures. The host plant we focus on in this study is white spruce, a keystone species in Canada’s boreal forest, one of the most frequently planted species in reforestation efforts, and one of the spruce budworm’s main hosts. It is a secondary succession species that often grows under faster-growing hardwood stands regenerating post-fire or other disturbance. We test the hypothesis that the open environment of plantations, while accelerating white spruce growth relative to understory regeneration, also promotes spruce budworm survival and performance, leading to higher abundance and defoliation.

In general, extensive even-age stands of preferred hosts are more vulnerable to budworm defoliation than mixed stands, but effects of stand opening on budworm damage are equivocal (Kneeshaw et al., 2021). Previous work suggests contrasting effects on spruce budworm of bottom-up pressures from sun-exposed white spruce needles: these show higher nutritional value and lower chemical defenses (Carisey and Bauce, 1997; Ranade et al., 2022), but are tougher and therefore are expected to be more resistant to feeding initiation by young larvae (Lirette and Despland, 2021). Sun-exposed white spruce trees are also expected to show earlier budburst phenology (Cartenì et al., 2023), which influences the establishment success of young spruce budworm larvae emerging from diapause in the spring (Fuentealba et al., 2018, 2017). In general, higher light levels after thinning tend to improve budworm biological performance, but also increase tree foliage production such that overall effects on tree growth and survival are context-dependent (Fuentealba and Bauce, 2012). Similarly, top-down pressures from parasitoids and predators also vary with stand diversity and openness: what data exists suggests that they could be lower in mixed stands (Cappuccino et al., 1998; MacKinnon and MacLean, 2003; Simmons et al., 1975) and in open environments (Legault and James, 2018; Marrec et al., 2018). Our study combines a four-year field survey with manipulative experiments to disentangle the relative roles of bottom-up and top-down forces acting on the spruce budworm on white spruce saplings in plantation vs forest habitats.

2. Methods

2.1. Study sites

Fieldwork was done between 2020 and 2023 in the Lac Duparquet Research and Education Forest (FERLD) in Western Quebec (48°00’0.00" N −76°00’0.00" W), where the spruce budworm outbreak was still in the early stages with rising populations but before severe defoliation damage or tree mortality (Ministère des Ressources Naturelles et des Forêts Direction de la Protection des Forêts, 2023). Within the experimental forest, we selected 10 study sites in conifer plantations and in mature aspen (*Populus tremuloides* Michx) stands with white spruce understory regeneration (forest sites).

The plantations were small stands of 2–3 m tall mixed conifers established following clear-cuts in 2006–2010, situated within a boreal mixed-wood forest matrix. Plantations are managed according to an ecosystem-based management approach (Gauthier et al., 2023; Ministère des Ressources Naturelles et de la Faune, 2008), involving brush-cutting done once, 7 years after planting, but very little other intervention. The forest sites consist of natural post-fire regeneration and are dominated by 70-year-old trembling aspen with an understory of secondary succession conifers, including balsam fir, white spruce, and black spruce (*Picea mariana* Mill) (Harvey and Leduc, 1999). Each of the 10 sites per habitat was 100–2500 m away from the nearest neighboring site. Within each site, 10 young white spruce trees, 2–3.5 meters tall, were selected at least 5 m apart. In 2020 and 2021 we surveyed 10 sites (x 10 trees per site), in 2022, 5 sites (x 5 trees per site) and in 2023, we planned to sample 8 sites (x 8 trees per site), but due to forest fires we could only conclude sampling on one site (x 8 trees) in each habitat.

2.2. Field survey overview

Between 2020 and 2023, we conducted field surveys to evaluate tree characteristics and monitor spruce budworm population density, predation, and parasitism. In 2020, fieldwork was delayed by the COVID-19 pandemic and was conducted between July 12th and August 3rd. In 2021–2023, the BioSIM phenological model (Régnière and Saint-Amant, 2013) was used to predict budworm emergence from diapause and to schedule fieldwork to coincide with spruce budburst and with maximum spruce budworm activity. BioSIM (ver. 11; Régnière et al., 2020) simulates insect development based on historical daily weather by combining site (latitude, longitude, elevation), and time-period interpolated with climate data. For all of our sites (in both habitats), we created a weather generation component using the Canada-wide daily database (1980–2019) and executed a spruce budworm development model to predict the timing of life-stage events, including peak larval diapause emergence. The output (extracted as Julian Date) provided site- and year-specific phenological estimates for ecological analysis.

2.2.1. Tree and stand attributes

We measured several stand and tree characteristics, including canopy closure, shoot elongation, foliage toughness, and bud phenology with details provided in a supplementary file (A.1 and A.2; Table S1).

Defoliation of shoots from the current year was assessed as an effect of spruce budworm feeding in August 2020 and 2021. A southeast oriented 40 cm branch was cut from the mid-crown section of each tree (x 5 trees per site, per habitat) and defoliation on current year shoots was scored using Fettes method (Sanders, 1980), which involves visually estimating the proportion of needles missing according to predetermined classes (from 0 = 0 % defoliation, all needles intact to 12 = 100 + % defoliation, no needles remaining). The defoliation scores from all shoots on a branch were aggregated to derive a branch-specific defoliation percentage. The classes were converted into midpoint percentage values (e.g., class 3 = 25 % defoliation) and scaled to the range (0, 1), ensuring each tree contributed a singular defoliation value to the overall analysis (Yataco et al., 2024).

2.2.2. *Spruce budworm density, predation, and parasitism pressure*

Budworm abundance sampling in 2020 had to be adapted due to delays caused by the COVID-19 pandemic: a 40 cm branch was collected in the field in July and brought back to the lab to count all budworm larvae. In subsequent years (2021–2023), a different method was used Spruce budworm larvae and their predators were hand-collected on mid-crown branches for 5 min. This sampling was timed using the phenological model BioSIM (Régnière and Saint-Amant, 2013) in order to coincide with the 4th – 5th instar of local spruce budworm populations: sampling was done between June 4–15 in 2021, June 1–3 in 2022, and June 1–4 in 2023. Predators were assigned to coarse taxonomic categories (spiders, ants, carabids) and released. In 2022, we added beat-sheeting on a midcrown branch for 30 strokes over 1 minute. In 2023, we sampled from only one understory and one plantation site (8 trees per site) before access to field sites was interrupted by forest fires.

The spruce budworm larvae (4 – 6 instars) collected in 2021, 2022, and 2023 were reared in the lab (each in individual containers) until fall to estimate parasitism rates.

2.3. *Bottom-up experiment*

A manipulative experiment was conducted in order to measure differences in bottom-up pressures linked to plant traits by rearing spruce budworm larvae in cages on young spruce trees in the two habitats in the absence of natural enemies.

Diapausing second instar larvae were obtained from the Great Lakes Forestry Centre Insect Production Services (Roe et al., 2018). To break diapause, insects were held at room temperature in petri dishes on agar for 24 h in order to ensure adequate hydration. At the end of this period, 15 moving larvae were chosen haphazardly and placed in sleeve cages (40 ×24 cm) on young spruce trees in the two habitats until pupation. We ensured that any wild spruce budworm larvae were not hiding in the buds of the branches where the cages were installed before the initiation of each bottom-up experiment. Cages were installed 1.5 m above the ground on branches that included at least 30 buds in order to ensure adequate nutrition for larvae to complete development. In 2021, cages were placed on 4–7 trees in each of 2 forest and 2 plantation stands on June 2nd (N = 23 cages) and brought back to the lab on June 21st. Almost all of the larvae either pupated in the cages or were in the process of pupation. They were then transferred to individual rearing containers in the lab, and pupal mass was recorded. The experiment was repeated in 2022, placing cages on 5 trees in each of 5 stands of each type on June 2nd and removing them on June 28th. Insects in the cages were counted to measure survival rate; pupae were sexed and weighed, and pupal mass was compared as an index of performance.

2.4. *Top-down experiment*

A second manipulative experiment was conducted to compare disappearance and parasitism rates in forest vs plantation habitats. Spruce budworm larvae were taken out of diapause as above and reared in the laboratory until use in experiments in the fifth instar. These larvae were fed fresh field-collected white spruce foliage with buds between bud development stage 2–6. Larvae were placed on white spruce trees in both habitats on branches 1.5 m above ground and beat-sheeting was performed before the deployment of the larvae to ensure removal of any wild budworm larvae. Branches were marked with orange flagging tape to facilitate recovery. Larvae were recovered after 72 h and the number of survivors was counted in order to estimate predation rate: larvae that disappeared were assumed to have been consumed by predators. Surviving larvae were brought back to the lab and reared to adults in order to evaluate the parasitism rate. Parasitism rate (2022) was calculated as a proportion of the larvae that had escaped predation and had been reared in the laboratory.

In 2021, two different methods were tried: in the first, larvae were placed without any protection on tree branches (1 site per habitat), and in the second a tanglefoot barrier (a sticky resin smeared upstream on the branch) was used to impede walking/non-volant predators (2 sites per habitat). In each site, 6 larvae were placed on each of 6–8 trees on June 3rd-10th. The unprotected larvae suffered very high disappearance rates (ca 80 %), implying that intense predation and/or non-predator-related loss probably hindered clear findings, such that only the Tanglefoot sites results are presented, and only this method was used in the following year. In 2022, the experiment was conducted twice: on June 6th, six larvae were placed on 5 trees in each of 5 forest and 5 plantation sites (one plantation tree was lost, for a total of 294 larvae on 49 trees); on June 28th, five larvae were placed on two trees in each of 4 sites per habitat (total of 80 larvae on 16 trees).

2.5. *Analysis*

We compared 12 different response variables from the survey and bottom-up and top-down experiments to test the effect of habitat on tree and stand attributes, shoot defoliation and spruce budworm biological performance and survival. We used generalized linear mixed models (GLMMs, *glmer*() function) and linear mixed models (LMMs, *lmer*() function), using the lme4 package (Bates et al., 2015). Habitat and year were used as fixed effects, while site was incorporated as a random effect to account for variation across our study sites.

For each response variable, we chose the respective model family according to the data's distribution. For continuous variables with normal distribution (e.g. shoot elongation, and needle toughness), we used linear and mixed models with Gaussian family. For percentage data (e.g. canopy closure, defoliation), we used beta regression, and for overdispersed count data (e.g., spruce budworm and predator abundance), we used negative binomial GLMMs, both within the glmmTMB package (Brooks et al., 2024). Survival rates were analyzed with beta-binomial GLMMs (glmmTMB package), given their nature as overdispersed proportional data. Since phenology was classified into bud stages ranging from 0 to 6, we rescaled it to a 0–1 range and then applied a beta regression including Julian date as a continuous predictor. Julian date was centered and scaled (mean = 0, SD = 1) to enhance model interpretability and convergence and reduce collinearity. For the multivariate factorial models (with multiple fixed effects, interactions, and random effects) used for SBW (2020 – 2023) and predator abundance (2021–2023), we employed bobyqa optimizer (*control = glmerControl(optimizer = "bobyqa")*) function to enhance model convergence. This optimizer is particularly effective for fitting generalized linear mixed models in cases where standard optimization techniques fail to achieve convergence (Miller, 2018). A simple Chi-square (χ^2) test was applied to assess the parasitism rate in spruce budworm individuals collected via the field survey over the four-year period across two habitats.

To facilitate model comparisons with and without the predictor of interest and to assess the significance of fixed effects, we performed likelihood ratio tests (LRTs) through *anova*() function, We also assessed the significance of fixed effects and their interactions via Wald χ^2 tests (ANOVA = type II/III) at α = 0.05 using the car package (Fox and

Weisberg, 2019). For simple group comparisons between the habitats, we provide mean values accompanied by their respective standard deviations (±). Table 1 provides details on the 12 models, including their R functions, fixed and random effects, and distribution family.

All models were checked for assumption violations (e.g., overdispersion, multicollinearity) using diagnostic tools from the performance (Lüdecke et al., 2021) and DHARMa packages (Hartig and Lohse, 2022). Model selection was guided by Akaike Information Criterion (AIC), as all analysis was performed in RStudio, and all the packages were installed in 2023 (v. 4.3.1) (R Core Team, 2023).

3. Results

3.1. *Field survey*

Canopy openness was significantly lower ($\chi^2(1) = 103.24$, $p < 0.001$) in forest sites, with a mean (± SD) of 9.32 (± 6.24)%) in forests, compared to 61.8 (± 22.4)% in plantations. These values suggest that natural forest sites usually had dense canopies, which restricted light reaching the understory, whereas plantation sites were characterized by open growth and direct sunlight exposure. Branch elongation was significantly higher in plantations compared to forests ($\chi^2(1) = 63.61$, $p < 0.001$) over the years with an average shoot elongation of 8.63 (± 2.77) cm in forests and 15.1 (± 2.47) cm in plantations. Foliar toughness was higher in plantation (2020–2022 average: 53.78 ± 2.21 g in plantation vs 49.89 ± 1.65 g in forest trees) as our model indicated year ($\chi^2(2) = 17.90$, $p < 0.001$) and habitat ($\chi^2(1) = 6.11$, $p = 0.013$) had significant effects on toughness, while their interaction was not significant ($\chi^2(2) = 5.38$, $p = 0.0675$). Defoliation levels varied significantly between years ($\chi^2(2) = 35.22$, $p < 0.001$). However, the effect of habitat was not significant ($\chi^2(1) = 2.81$, $p = 0.093$), nor was the interaction between habitat and year ($\chi^2(2) = 0.28$, $p = 0.595$). Overall mean defoliation remained less than 10 % of new foliage in all cases. A comprehensive summary of all model coefficients is available in the supplementary material (A.3, Table S2).

In 2021, bud phenology measured on the same trees over a period in May and June was more advanced in plantation than in forest habitat. Both Julian date ($\chi^2(1) = 366.11$, $p < 0.001$) and habitat ($\chi^2(1) = 24.49$, $p < 0.001$) significantly affected bud burst phenology. The absence of interaction between habitat and Julian date ($\chi^2(1) = 1.72$, $p = 0.188$) implies that the rate of phenological progression over time was consistent across both habitats. Bud development was advanced in plantations in both subsequent years (2022–2023) and our model revealed significant effects of habitat ($\chi^2(1) = 16.10$, $p < 0.001$), year ($\chi^2(1) = 77.39$, $p < 0.001$), and the interaction between habitat and year ($\chi^2(1) = 7.51$, $p = 0.006$). The BioSIM model was used to predict budworm larval emergence from diapause at our sites, and peak emergence, as well as the total duration, are plotted to estimate phenological synchronisation (Fig. 1). Field observations of later development stages concurred with BioSIM predictions, supporting confidence in the model`s performance.

The budworm larvae showed higher density in plantations, but this difference varied by year (Fig. 2; Table S2). Our model showed significant effects of habitat ($\chi^2(1) = 19.36$, $p < 0.001$) and year ($\chi^2(3) = 283.13$, $p < 0.001$) on SBW abundance and a significant interaction between habitat and year ($\chi^2(3) = 25.25$, $p < 0.001$). A similar model showed a significant effect of year on predator abundance ($\chi^2(2) = 7.15$, $p = 0.028$), while the effect of habitat ($\chi^2(1) = 2.55$, $p = 0.110$) and the interaction between habitat and year ($\chi^2(2) = 1.57$, $p = 0.455$) were not significant. Interannual differences cannot be interpreted meaningfully given differences in methodology but are included simply to control for these effects. The rate of parasitism (field-collected individuals) was significantly higher in the forest than in plantations in all four sampling periods tested (Table 2).

3.2. *Bottom-up experiment*

Overall, budworm pupae were heavier in plantations ($\chi^2(1) = 11.61$, $p < 0.001$), and there was a strong effect of sex ($\chi^2(1) = 111.34$,

Table 1

A detailed description of models used in this study. Numbers in column ‘Model’ correspond to model numbering and series in which the methods, analysis, and results are explained below. For each model we have defined the modeling framework, the R function used, the response variable, explanatory/fixed effects, random effects, whether the interaction term between fixed effects was included, and the distribution (family) of the data.

Model	Framework (*R Function*)	Response Variables	Explanatory/Fixed Effects			Random Effects	Interaction term	Distribution Family
Tree and Stand Attributes								
1.	LMMs (*glmmTMB*)	Canopy closure (%)	Habitat (Forest, Plantation)			Site	No	Beta-regression
2.	LMMs (*lmer*)	Shoot growth (cm)	Habitat (Forest, Plantation)			Site	No	Gaussian
3.	LMMs (*lmer*)	Needle toughness (gm)	Habitat (Forest, Plantation)	Year (2021, 2022)		Site	Yes	Gaussian
4.	GLMMs (*glmmTMB*)	Mean Defoliation (%)	Habitat (Forest, Plantation)	Year (2020, 2021)		Site	Yes	Beta-regression
Bud Phenology Over the years								
5.	GLMMs (*glmmTMB*)	Bud-phenology (2021)	Habitat (Forest, Plantation)	Julian date (JD)		Site	Yes	Beta-regression (logit)
6.	GLMMs (*glmmTMB*)	Bud-phenology (2022 – 2023)	Habitat (Forest, Plantation)	Year (2022, 2023)		Site	Yes	Beta-regression (logit)
Spruce budworm and Predator abundance over the years								
7.	GLMMs (*glmer.nb*)	Spruce budworm abundance (2020 – 2023)	Habitat (Forest, Plantation)	Year (2020, 2021, 2022, 2023)		Site	Yes	Negative binomial
8.	GLMMs (*glmer.nb*)	Predator abundance (2021 – 2023)	Habitat (Forest, Plantation)	Year (2021, 2022, 2023)		Site	No	Negative binomial
Bottom-up Experiment								
9.	LMMs (*lmer*)	Pupal Mass (mg)	Habitat (Forest, Plantation)	Year (2021, 2022)	Sex (Female, Male)	Site	Yes	Gaussian
10.	GLMMs (*glmmTMB*)	Survival rate	Habitat (Forest, Plantation)	Year (2021, 2022)			Yes	Beta-binomial
Top-Down Experiment								
11.	GLMMs (*glmmTMB*)	Predation rate (2021 – 2022)	Habitat (Forest, Plantation)	Year (2021, 2022)		Site	No	Binomial (logit)
12.	GLMs (*glmer*)	Parasitism rate (2022)	Habitat (Forest, Plantation)			Site	No	Binomial (logit)

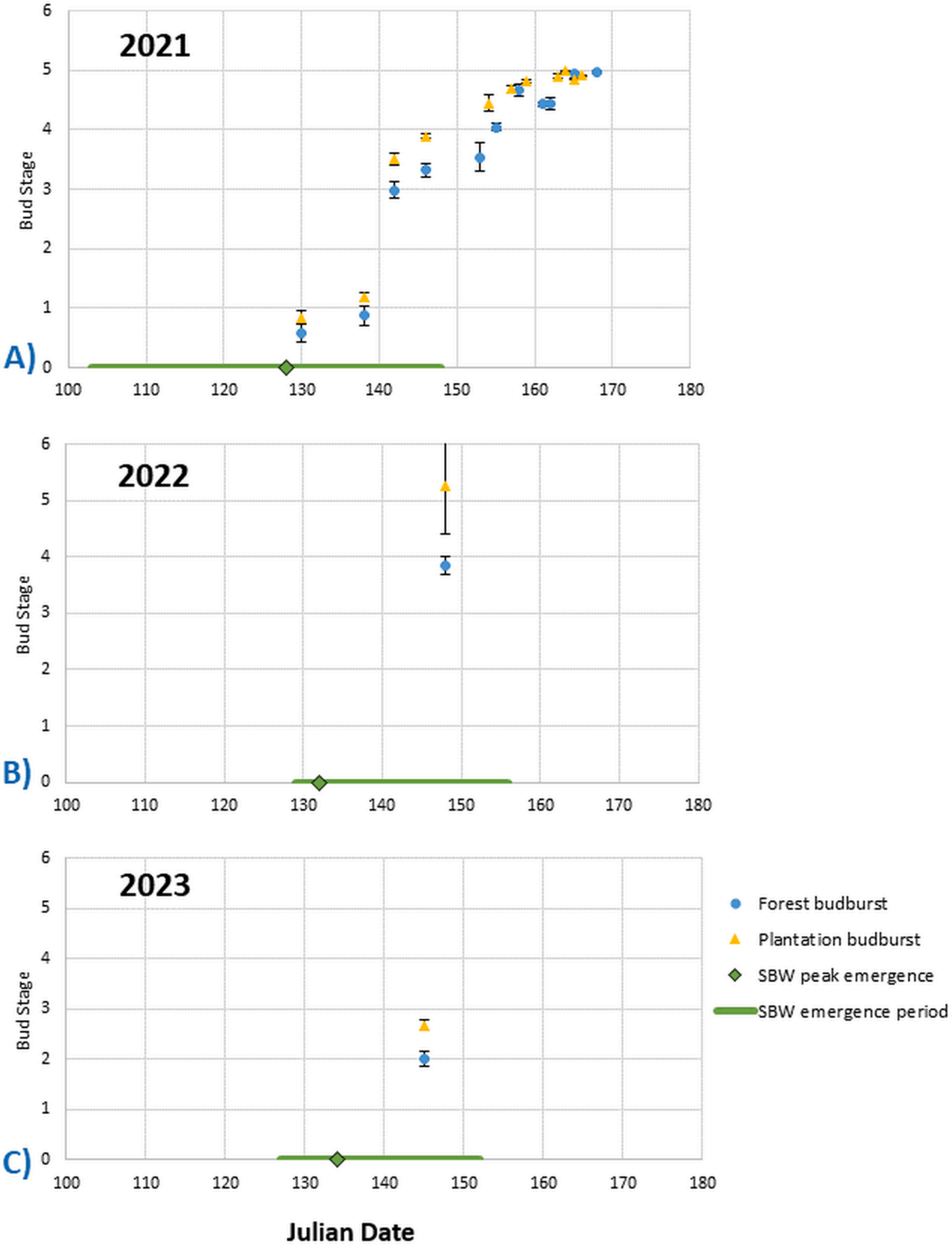

Fig. 1. Budburst phenology (bud stages as per (Dhont et al., 2010) (Dorais and Kettela, 1982), as a single value of mean ± SD on y-axis, and day of the year (DOY) on x-axis), of forest vs plantation white spruce (*Picea glauca*) saplings over 3 years of study, A) 2021 (N = 304), B) 2022 (N = 50) C) 2023 (N = 130). The model-predicted peak and total duration of spruce budworm (*Choristoneura fumiferana*) emergence is also shown. In 2021, each of the 10 studied trees per site was observed 2–4 times between May 10 and June 17. In 2022, we measured bud phenology on a subset of 5 trees per site across 5 sites per habitat, from May 28 to June 1. In 2023, we conducted measurements on May 25, using 129 trees across 8 sites per habitat.

$p < 0.001$) and year ($\chi^2(1) = 14.13$, $p < 0.001$) on pupal mass. As expected, female pupae were heavier than males (mean ± SD: 71 ± 33 mg vs 37 ± 22 mg, respectively). Insects reared on trees in plantation were overall heavier than those on forest trees (females in plantation vs forest = 73 ± 31 mg vs 69 ± 34 mg, respectively). Females were significantly heavier in the second year of the study than the first (mean ± SD: plantation = 86 ± 33 mg vs = 57 ± 19 mg, respectively; $\chi^2(1) = 56.88$, $p < 0.001$), while males showed no difference (Fig. 3). A three-way interaction between habitat, sex, and year was not significant ($\chi^2(1) = 3.65$, $p = 0.057$). There were no significant interactions between habitat and sex ($p = 0.66$) or habitat and year ($p = 0.81$).

Survival rate in the cages did not differ significantly between habitats

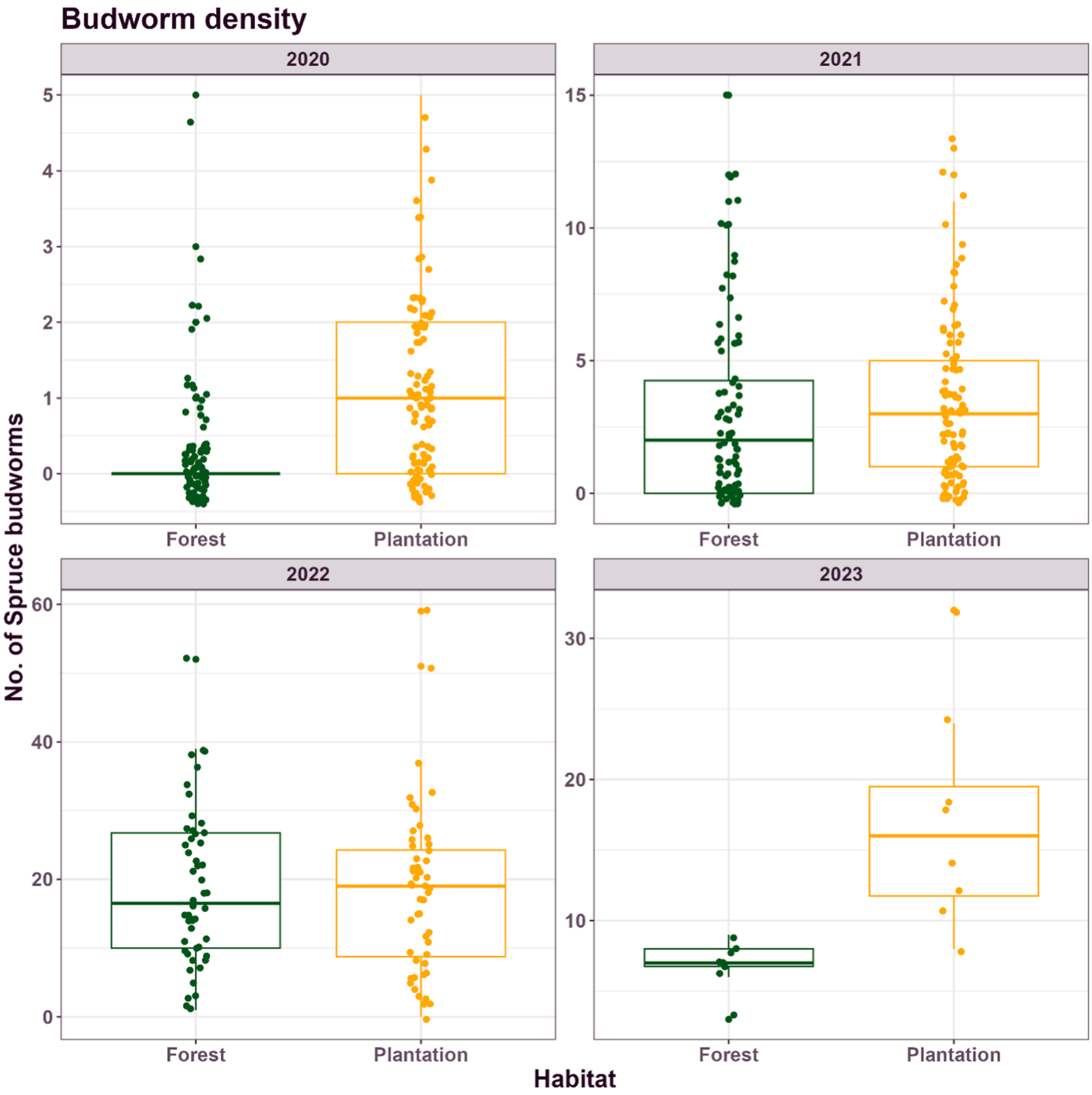

Fig. 2. Density of budworms observed per tree during a 5 min survey in each of the years of study, for both habitats (F=forest; P = plantation). Number of trees sampled varied between years: 2020 N = 189; 2021 N = 188; 2022 N = 50 and 2023 N = 16 (sampling interrupted by forest fires). Dots represent individual data points; boxes represent quartiles and midlines represent the median value.

Table 2
Spruce budworm parasitism rate from the field survey in June 2021, June 2022, July 2022, and June 2023. For each sampling period, the total number of parasitized and unparasitized larvae that were collected in each habitat is given, with the percent parasitism shown in parentheses. The chi-square comparing the proportion parasitized between habitats and its associated p-value are also shown.

Season	*Forest: parasitized vs not, %*	*Plantation: parasitized vs not, %*	χ^2	*p value*
June 2021	*9 vs 265* (3.3 %)	*1 vs 332* (0.3 %)	*6.79*	*0.009*
June 2022	*7 vs 424* (1.6 %)	*3 vs 530* (0.6 %)	*2.68*	*0.045*
July 2022	*22 vs 134* (20.2 %)	*34 vs 191*(10.3 %)	*6.51*	*0.01*
June 2023	*6 vs 55* (9.8 %)	*1 vs 137* (0.7 %)	*8.85*	*0.003*

($\chi^2(1)$ = 0.45, p = 0.505), but varied between years, ($\chi^2(1)$ = 4.67, p = 0.031). The interaction between habitat and year was not significant ($\chi^2(1)$ = 0.11, p = 0.744). Spruce budworm survival probability in plantation (2021 = mean ± SD: 43 ± 17.5 %; 2022: 26.4 ± 18.4 %) was similar to that in forest (2021 = mean ± SD: 40.6 ± 22.3 %; 2022: 24 ± 14.7 %).

3.3. Top-down experiment

The comprehensive model revealed that the disappearance rate, used as an index of predation, was significantly affected by habitat ($\chi^2(1)$ = 5.61, p = 0.018) and by year ($\chi^2(1)$ = 9.81, p = 0.002). The interaction between habitat and year was not found to be significant ($\chi^2(1)$ = 3.37, p = 0.066). In 2021, the disappearance rate was significantly higher in forest sites (mean ± SD= 16.7 ± 19.9 %) compared to plantation (3.57 ± 9.65 %). All recovered caterpillars gave rise to adults and hence no parasitism occurred during their field exposure (in 2021; Fig. 4). In 2022, the pattern persisted, with a higher disappearance rate in forest environments (37.7 ± 28.9 %) than in plantation settings (31.1 ± 23.4 %). Parasitism rate was higher in forest as well (mean

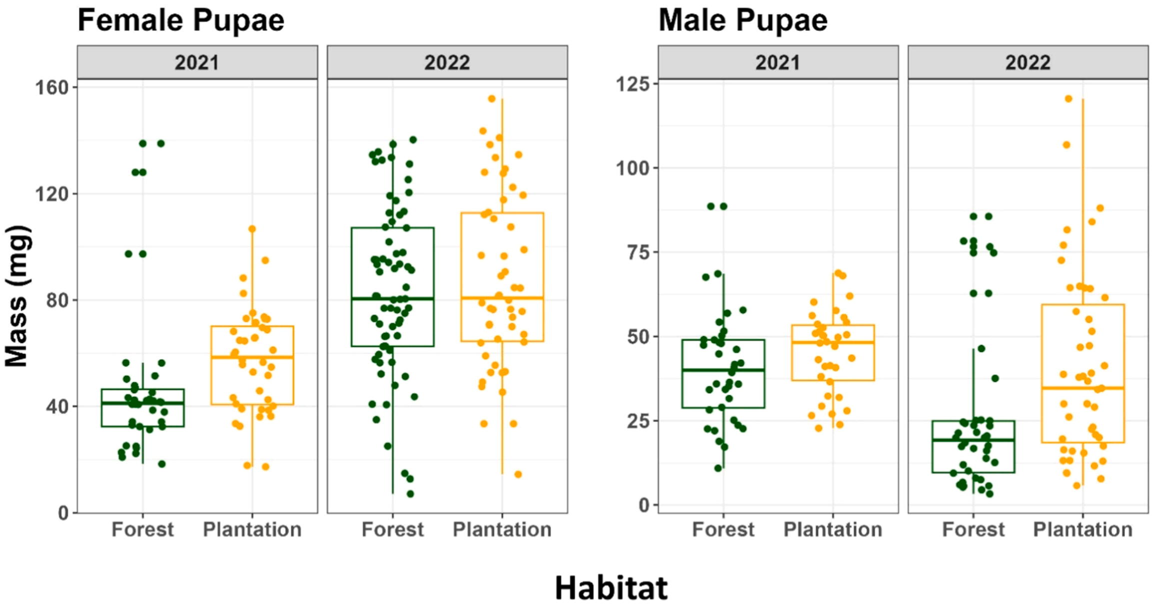

Fig. 3. Spruce budworm pupal mass (mg) on y-axis in the bottom-up experiment in forest and plantation sites (on x-axis) compared between 2021 and 2022. Dots represent individual data points; boxes represent quartiles and midlines represent the median value.

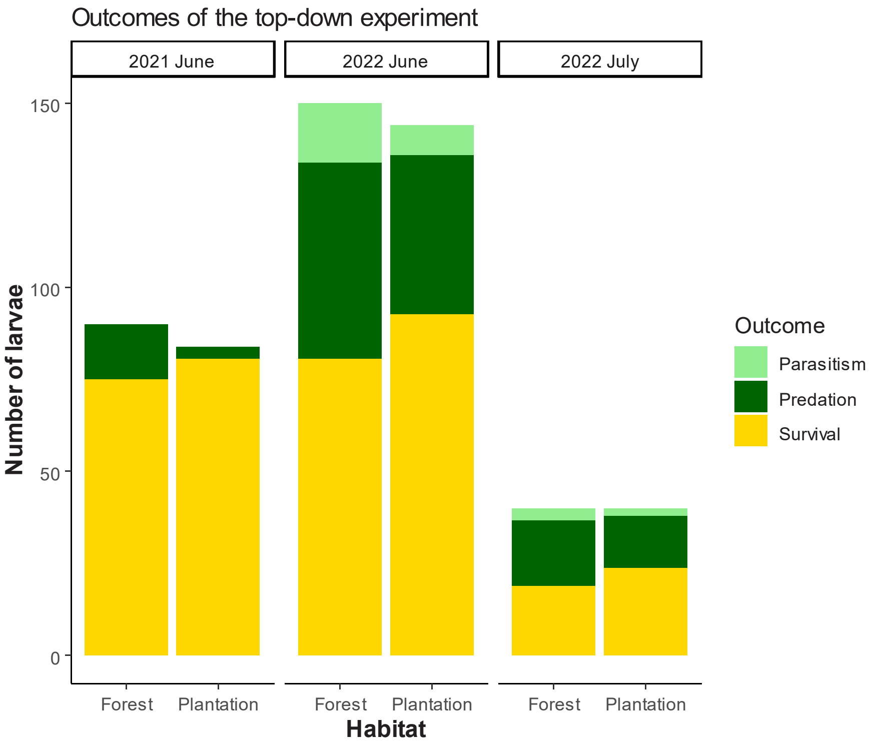

Fig. 4. Outcomes of three trials (June 2021, June 2022, and July 2022) of the top-down pressure experiment. The height of stacked bars represents the number of larvae that survived, that disappeared and are supposed to have been taken by predators, and that were parasitized. Total bar height represents the total number of larvae used in each trial. In 2021, N = 29 trees, June 2022, N = 49 trees, and July 2022, N = 16 trees; with 548 larvae in total were included in the experiment.

± SD= 21.5 % ± 30.4 %) vs in plantations (mean ± SD= 12.5 % ± 23.1 %), but the difference was not significant ($\chi^2(1) = 3.61$, p = 0.057).

4. Discussion

The field survey confirmed expected differences in canopy openness and associated tree growth. It also showed predicted higher foliar toughness and earlier budburst phenology in plantation habitats than in forest. Budworm larvae density was consistently higher in plantations across all years, and slight differences in bottom-up and top-down forces both appear to contribute to this difference. Spruce budworm exhibited better performance in plantations, as evidenced by higher pupal mass. Although no significant difference in predator density was observed between habitats, both predation and parasitism rates were slightly higher in the forest. However, these differences are slight. In general, inter-annual differences in budworm density, in pupal mass and in parasitism rate, are greater than differences between habitats. The ecological relevance of the observed differences between habitats in bottom-up and top-down forces at this early stage of the outbreak is not obvious, especially given the lack of between-habitat differences in defoliation.

The sentinel larvae experiments showed statistically significant but subtle differences in bottom-up and top-down pressures on spruce budworm populations between the two habitats. In the absence of natural enemies, the bottom-up experiment showed slightly better spruce budworm performance on plantation than on forest saplings, as indicated by higher pupal mass. Indeed, spruce budworm pupal mass is an index of food quality and is strongly correlated with fecundity in females (Quezada-García et al., 2018). Previous work has shown that spruces grown under high light open conditions have higher foliar nutrient content (especially Nitrogen) and lower defensive compounds (Carisey and Bauce, 1997; Grassi and Minotta, 2000; Ranade et al., 2022) and that sun-exposed foliage supports better spruce budworm growth and development (Carisey and Bauce, 1997). These factors could explain the higher pupal mass observed on plantation trees despite their tougher foliage. Budworm pupal mass can vary by nearly an order of magnitude (Mattson et al., 1991); in our study, the difference between habitats in pupal mass was relatively slight and was only observable in females in one of the two years of the study. It was also less than the difference between years. Thus, while these results do suggest lower bottom-up pressures on open-grown saplings, this effect is not likely to contribute much to budworm population dynamics.

The top-down experiment showed slightly higher pressure from both predators and parasitoids in the forest than in the plantation sites. A variety of arthropods, including spiders, pentatomids, carabids, elaterids, and ants have been identified as predators of late-instar spruce budworm larvae (Bowden et al., 2023), as have birds (Crawford and Jennings, 1989) and squirrels (Jennings and Crawford, 1989). Parasitism is thought to be a more important regulator of budworm populations than is predation (Royama et al., 2017). A diverse community of generalist parasitoid flies and wasps attack the spruce budworm (Eveleigh et al., 2007; Greyson-Gaito et al., 2022, 2021; Smith et al., 2011) and the combined action of these multiple agents is thought to play a critical role in the density-dependent regulation of spruce budworm outbreaks (Royama et al., 2017). It has been suggested that plant diversity increases the abundance of generalist predators and parasitoids due to a higher abundance and diversity of alternative prey species, microhabitats, and other resources such as nectar. Plant diversity could hence contribute to greater top-down control of insect herbivores; however, this hypothesis has received mixed support in the case of the budworm (Cappuccino et al., 1998; Legault and James, 2018; MacKinnon and MacLean, 2003; Simmons et al., 1975). Parasitism by various different parasitoids has been shown to correlate with forest composition (MacKinnon and MacLean, 2003; Simmons et al., 1975). Cappuccino et al. (1998), working in the same region as the present study, showed higher rates of parasitism in mixed forest than in extensive conifer stands. At the landscape scale, spruce budworm larval density decreases with forest diversity, and the rate of attack increases for one parasitoid species but not for another (Legault and James, 2018). The two spruce budworm parasitoids tested by Legault and James, (2018) responded to vegetation diversity at the scale of 3–15 km and exhibited panmixia (Legault et al., 2021) at large spatial scales, suggesting strong dispersal abilities. Only one of these species, *Apanteles fumiferanae*, was observed in the present study. This suggests that, given the small scale of our plantations, parasitoids could easily move between them and the surrounding matrix of mixed forest. The higher rate of parasitism we observed on forest saplings suggests a behavioral preference for forest settings in parasitoids rather than a difference in parasitoid population size between habitats (Gingras et al., 2002). This might not be apparent in landscape scale studies and could be a mechanism underlying stand-scale differences in spruce budworm populations.

The field survey showed slightly higher budworm density in the plantation sites in all 4 years of the study. However, this did not translate to measurable differences between the two habitats in defoliation of current-growth shoots on white spruce saplings. These results contrast with previous studies which showed higher levels of spruce budworm defoliation on black spruce regeneration in more open habitats (Sainte-Marie et al., 2015; Lavoie et al., 2019, 2021). The outbreak is still in its early stages in our study region with only mild to moderate crown defoliation recorded in mature forests (Ministère des Ressources Naturelles et des Forêts Direction de la Protection des Forêts, 2023), and previous work suggests that the difference between understory and open habitats will increase as the outbreak progresses (Nie et al., 2018).

Previous work compared defoliation in young conifers under hardwood (non-host) vs conifer (host) canopy and showed higher levels of defoliation under a conifer canopy (Nie et al., 2018). However, this difference was only apparent late in the outbreak when mature trees are heavily defoliated and larvae emerging from diapause in the canopy cannot find developing buds, balloon away from these inadequate hosts, and drift down to understory saplings (Nealis and Régnière, 2004). Earlier in the outbreak, when foliage was still available on mature trees, defoliation (and budworm abundance) on the understory was much lower and did not depend on canopy composition (Nie et al., 2018).

Other work suggests that a conifer canopy can protect young trees from defoliation relative to those in open habitats, but this effect is stronger for black spruce than balsam fir saplings. Indeed, in black spruce forests with severe defoliation, harvesting the (defoliated) mature trees increases defoliation on black spruce saplings in the understory, but not on balsam fir saplings (Cotton-Gagnon et al., 2018). Similarly, black spruce under conifer canopy exhibited lower defoliation than those in clearcuts, but balsam fir showed similar levels of damage in understory and clearcut habitats (Lavoie et al., 2019). The mechanisms underlying these results are not explained but our results suggest they could be linked to bottom-up forces that vary between host plants. Black spruce have late budburst and this is considered as a phenological defense since budworm cannot enter the closed buds (Fuentealba et al., 2018, 2017). Higher temperature advances black spruce budburst phenology making it a better host for the budworm (Bellemin-Noël et al., 2021; Pureswaran et al., 2019; Ren et al., 2020) and therefore canopy opening could improve black spruce phenological synchrony with the budworm and make it a more suitable host. Our results do point toward an improvement of synchrony between white spruce budburst and spruce budworm emergence from diapause under open conditions (Fig. 1). Potential habitat effects on budworm emergence were not tested, but these are not likely to be important, given previous research showing spruce budburst to be more affected by spring temperature than budworm emergence (Pureswaran et al., 2019). Phenological mismatches between budworm larva and host have been shown to greatly reduce early instar survival (Bouchard et al., 2018; Fuentealba et al., 2017). White spruce shows faster budburst phenology than black spruce (Cartenì et al., 2023; Ren et al., 2020) and might be expected to respond less strongly to canopy opening (Podadera et al., 2024).

Context dependence needs to be considered in interpreting ecological results (Catford et al., 2022). We showed only limited effects for bottom-up and top-down effects on white spruce which, in the context of early outbreak conditions, were associated with slight differences in budworm density and no measurable difference in defoliation. However, relative strengths of bottom-up and top-down forces can vary between host plants with different defenses during progression of a budworm outbreak (Moreau et al., 2018, 2006). Indeed, differences in budbreak phenology between host species drive differences in defoliation of adult trees (Bellemin-Noël et al., 2021; Fuentealba et al., 2017). Previous work confirms that for regeneration too, balsam fir is more vulnerable than black spruce (Cotton-Gagnon et al., 2018; Lavoie et al., 2019) and that canopy cover impacts defoliation on black spruce more than it does on balsam fir (Lavoie et al., 2019), which could be due to greater black spruce sensitivity to temperature differences (Podadera et al., 2024).

According to Stead et al. (2021), the rate of parasitism is higher on balsam fir than on black spruce, indicating potentially higher top-down pressure for spruce budworm on the former host, with different parasitoids playing varying roles at different stages of the outbreak (Royama et al., 2017). Our findings are consistent with previous work that differences between habitats in regeneration defoliation are slight early in the outbreak (Nie et al., 2018). However, as the outbreak progresses, defoliation on regeneration increases dramatically as mature trees are only sparsely foliated (or dead), and both attract fewer ovipositing moths and retain fewer larvae emerging from diapause (Nealis and Régnière, 2004; Nie et al., 2018). At the small spatial scale of our study, canopy defoliation is likely to lead to greater pressure on regeneration whether in forest or plantation habitat (Nie et al., 2018). However, as the outbreak progresses, top-down forces also increase, and it remains to be seen if this happens in the same way in our two studied habitats. Our plantations are small and in a mixed forest matrix, and parasitoid host-finding behavior is likely to drive parasitism rates in different habitats: future studies would be necessary to determine whether parasitoids exhibit reluctance to move into open plantations.

Defoliation of regeneration can have important ecosystem impacts because young trees represent the future of the forest (Subedi et al., 2023). This is particularly true as heavily defoliated trees do not produce much seed and hence most post-outbreak regeneration comes from existing young trees (Cotton-Gagnon et al., 2018). Differential defoliation can affect competition between tree species and influence forest successional trajectories (Lavoie et al., 2021); this becomes particularly complex as past defoliation events can alter the probability of future defoliation. To our knowledge, ours is the first study to follow up on Craighead's, (1925) observations and to compare budworm responses on regeneration under hardwood canopy vs open conditions. Our results do not provide strong support that bottom-up and top-down forces on the spruce budworm in early outbreak stage are meaningfully relaxed in the small mixed-species plantations we studied.

CRediT authorship contribution statement

Zahra Gozalzadeh: Data curation. **Sabina Noor:** Writing – review & editing, Writing – original draft, Investigation, Formal analysis. **Miguel Montoro Girona:** Writing – review & editing, Funding acquisition, Conceptualization, Project management. **Allison Pamela Yataco:** Data curation. **Emma Despland:** Writing – review & editing, Writing – original draft, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Code availability

Not applicable

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Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used Grammarly and Open Writefull in order to enhance English language readability and grammar. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

Declaration of Competing Interest

All the authors have asserted that they have no conflicts of interest related to the submitted manuscript. All funding sources supporting this work are disclosed in the funding section.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.122883.

Data availability

Data will be made available on request.

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