

Bottom-up and top-down forces regulate spruce budworm biological performance on white spruce regeneration

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Research Article

Keywords: bottom-up, defoliation, plantation, spruce budworm, top-down, understory, white spruce

Posted Date: January 9th, 2025

DOI: <https://doi.org/10.21203/rs.3.rs-5656061/v1>

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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. Recognized as the most important outbreaking conifers defoliator in Eastern Canada, we aim to better understand how its herbivory on young trees can affect 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 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, which improves synchronization with a model (BioSIM) predicted timing of budworm emergence from diapause. The field survey showed higher budworm density and lower larval parasitism in plantations, but no significant difference in current-year growth defoliation during the initial outbreak phase. The bottom-up experiment showed slightly better budworm biological performance, indicated by higher pupal mass, in plantations. The top-down experiment showed greater predator and parasitoid pressure in the understory. Together, our results show how mechanisms controlling insect defoliator populations are context-dependent. In plantations both bottom-up and top-down forces on the spruce budworm are relaxed in these open habitats, leading to better biological performance and higher population density of this forest pest.

Introduction

The relationship between an herbivorous insect and its host plant depends on surrounding plant community composition (Agrawal et al 2006). 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 & Murphy, 2018) and modulate the damage they cause to plants. A case in point are forestry plantations: these provide conditions to maximize tree growth, conditions which tend to also be favourable to insect herbivores. Thus, trees in plantations are often more vulnerable to pest insects than those in natural forest understory regeneration (Jactel and Brockerhoff 2007; Comeau et al. 2009; Fischbein and Corley 2022), threatening regeneration success. We test the hypothesis that conditions in plantations alter bottom-up and top-down pressures on an outbreaking forest pest, the Eastern spruce budworm (*Choristoneura fumiferana*) to increase damage to young planted white spruce (*Picea glauca*). Findings will provide insights into how to best manage insect pests in a world where forests are increasingly in decline, and plantations contribute substantially to regeneration (Girona et al, 2023).

Higher vulnerability to pest insects can arise in several ways from various characteristics of tree plantations. The first involves direct effects of abiotic factors: the open conditions in plantations imply higher temperatures resulting in faster insect growth and development. Second, indirect effects through trophic relationships also influence pest-insect dynamics in different habitats (Moreau et al. 2006, 2018)

and both bottom-up pressures from plant defenses and top-down pressures from natural enemies can be predicted to decrease in plantations as described. Bottom-up pressures on insect herbivores are limited by a trade-off between plant growth and defense: fast-growing trees in open conditions tend to 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; Stemmelen et al. 2022). This study examines the degree to which each of these pressures explains patterns of spruce budworm damage in natural or planted regeneration in the eastern boreal forest of Canada.

The spruce budworm 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 (Pureswaran et al. 2016; Royama et al. 2017; Bouchard et al. 2018; Regniere et al. 2019; Girona et al. 2023). The spruce budworm is an early spring feeder on coniferous trees; preferred hosts are balsam fir (*Abies balsamea* ((L.) Mill.)), and white spruce. 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 (Fuentealba et al. 2017; Bellemin-Noël et al. 2021): larvae that emerge too early for buds to be available either mine into less nutritious old needles or disperse by ballooning. Larvae established in a bud tend to stay in place, feeding on the developing shoot. They pupate after 6 larval instars, then give rise to adults which lay eggs to start the cycle anew.

At the stand level, plant community composition modulates budworm population density, and while these variations might not affect outbreak progress, they have important effects on local defoliation and hence tree mortality risk. Previous work shows that damage suffered by individual trees depends on the species of surrounding trees (Bognounou et al. 2017; Debaly et al. 2022): defoliation is higher in forests dominated by the preferred host plant balsam fir, and decreases with content of secondary black spruce (*Picea mariana* ((Mill.) Britton, Sterns & Poggenburg)) hosts or non-host hardwoods (Sainte-Marie et al. 2015; Subedi et al. 2023). We build on this work to examine defoliation on saplings and test whether it depends on understory vs plantation habitat.

Indeed, while spruce budworm mostly feed on mature trees, at high population densities, understory saplings are also attacked (Nealis and Régnière 2004; Navarro et al. 2018). Defoliation of saplings can critically impact forest regeneration after the outbreak crashes. 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). Understanding the conditions under which young trees suffer budworm defoliation can be essential to predicting resilience to outbreaks.

Earlier observers reported that a mature hardwood canopy appeared to protect regeneration from defoliation relative to saplings in open areas (Craighead 1925). More recent work has shown that defoliation on understory saplings is higher under canopy of host conifers than non-host hardwoods (Nie et al. 2018) and higher under-preferred than secondary conifer hosts (Cotton-Gagnon et al., 2018; Lavoie et al., 2021). Defoliation on saplings is higher in clearcuts than in undisturbed understory (Lavoie et al. 2019) or in strip cuts (Lavoie et al., 2021).

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 predict that the open environment of plantations, while accelerating white spruce growth relative to understory regeneration, also promotes spruce budworm survival and performance.

Previous work suggests contrasting effects in terms of bottom-up pressures from sun-exposed white spruce leaves: these show higher nutritional value and lower chemical defenses (Carisey and Bause 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. 2017, 2018). In addition, top-down pressures from parasitoids and predators play an important role in regulating budworm population cycles (Pureswaran et al. 2016; Royama et al. 2017) but have only recently been related to stand composition: what data exists suggests that they could be lower in open environments (Marrec et al. 2018; Legault and James 2018). This 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 open vs understory conditions.

Methods

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 stands with white spruce understory regeneration.

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 (Ministère des Ressources naturelles et de la Faune 2008;

Gauthier et al. 2023), 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 (*Populus tremuloides* (Michx)) with an understory of secondary succession conifers, including balsam fir, white and black spruce (Harvey and Leduc 1999). Each of the 10 sites per habitat was 100 to 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.

Field Survey Overview

From 2020 to 2023, we conducted comprehensive field surveys to assess tree and stand characteristics representing bottom-up pressures and to monitor spruce budworm (SBW) population density, predation, and parasitism pressure. 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 & 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. Differences between environmental factors such as soil and air temperature and humidity were evaluated in a previous study by Yataco et al. (2024) and were not included in this study.

Tree and stand attributes

We measured several stand and tree characteristics, including canopy closure, shoot elongation, foliage toughness, and bud phenology as follows

- a) Canopy closure at each study tree (N = 100 in each habitat) was evaluated with a densiometer (model C: manufactured by Forest Densiometers, Rapid City, USA) to confirm the expected difference in sun exposure between forest and plantation trees (done in 2020 only).
- b) On each tree, shoot elongation was measured on a mid-crown branch 1.5 m (southeast oriented) from the ground for 2017–2020 to confirm the expected higher growth rate of plantation saplings.
- c) The toughness of mature foliage was assessed on 10 current-year needles on a subset of 4 trees per site in 2020 and 2021, and 5 trees per site in 2022, using a penetrometer following Lirette and Despland (2021).
- d) We assessed bud phenology according to the scale of (Dorais and Kettela 1982; Dhont et al. 2010) (Table S1; supplementary file). Buds become available to the budworm for feeding at stage 2 (Desbiens, 2006). We assessed budburst phenology on one apical and two lateral shoots on each of 10 mid-crown branches per tree, pooling these 30 buds to obtain one value per tree. 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.
- e) Defoliation of shoots from the current year was assessed as an effect of spruce budworm feeding in

August 2020 and 2021 (along with other insect herbivory patterns were quantified in a previous study by Yataco et al. (2024)). 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) was used.

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 it back to the lab to count all budworm larvae. This method was abandoned in subsequent years for two reasons: (a) the young trees were too small for repeated branch collection and b) this method proved ineffective for collecting predators.

In 2021, the abundance of spruce budworm larvae and their predators was observed in the field, using hand-collecting on mid-crown branches for 5 min, between June 4–15. This sampling was timed using the phenological model BioSIM (Régnière & Saint-Amant, 2013) in order to coincide with the 4th -5th instar of local spruce budworm populations. Predators were assigned to coarse taxonomic categories (spiders, ants, carabids) and released.

Similar techniques were used in 2022 to measure budworm and predator abundance from 1–3 June (following BioSIM predictions). We hand-collected as in the previous year and added beat-sheeting for 30 strokes over 1 minute. While hand-collecting was more efficient for collecting spruce budworms from the entire tree and generally yielded higher abundance, beat-sheeting (conducted on one branch of 75 cm to 1 m) was effective for collecting both predators and spruce budworms. Although we did not directly compare abundance values between the two techniques, the combined methods aimed to enhance the comprehensiveness of our data collection.

In 2023, we used the same methods as in 2022 and sampled budworm and predator abundance 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 collected in 2021, 2022, and 2023 were reared in the lab (individually) until fall to estimate parasitism rates.

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 x 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.

Top-down Experiment

A second manipulative experiment was conducted to compare predation and parasitism rates in understory 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.

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 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 mortality rates (ca 80%) such that only the Tanglefoot 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 (total of 300 larvae on 50 trees); on June 28th, six larvae were placed on two trees in each of 4 sites per habitat (total of 96 larvae on 16 trees).

Analysis

All analysis was performed in RStudio (v. 4.3.1) (R Core Team 2023). The data were organized and summarized using the “dplyr” package (Wickham et al. 2023). Generalized linear model approaches were used to compare values between forest and plantation habitats, using the appropriate link function depending on data distribution. Site was included as a random factor in mixed models, using the glmer and lmer functions from the “lme4” package (Bates et al. 2015). For simpler approach, we used the glm

and `lm` functions from the “stats” package (R Core Team 2023). When warranted by differences in sampling timing or technique, data for different years were analyzed separately.

We developed individual models for all our response variables and detailed descriptions of these models are assembled in a supplementary file (Table S2). Canopy closure was recorded as a percentage and analyzed with beta regression (`betareg` package, (Cribari-Neto and Zeileis 2010) in the “`glmmTMB`” package (Brooks et al. 2024) for linear mixed-effect models, with site as a random effect and habitat as the only fixed effect. Shoot elongation was averaged for 2017–2020 and analyzed with a mixed model with habitat * year as fixed effects. For needle toughness, the same trees were not measured each year and a mixed model was not appropriate. Instead, we used a linear model to assess the effects of year and habitat on toughness.

We missed the 2020 bud phenology dates due to COVID-19 restrictions. In 2021 phenology was recorded repeatedly on the same trees and. Julian date (JD) was included in the model as a fixed effect. Budworm emergence from diapause in the region was predicted with the BioSIM phenological model (Régnière et al. 2014) and related to the timing of tree budburst in order to evaluate herbivore-host phenological synchrony, an important predictor of spruce budworm performance (Fuentelba et al. 2017). For 2022–2023, a simple linear model was used to compare phenology between habitats for each year.

Percent defoliation was analyzed with beta regression. Each sampled branch's defoliation was converted to the midpoint of predetermined defoliation classes to calculate a mean value per site, habitat, and year. Mean defoliation per site was then used as the response variable in the model following Nie et al. (2018), with habitat and year included as fixed factors.

For each year, the abundance of budworm larvae and predators observed per tree was compared between habitats using a generalized linear model (`glm`) based on a quasipoisson distribution. Parasitism rate of budworm larvae collected during the field survey was compared between habitats with a simple chi-square analysis since the number of larvae varied substantially between trees, making them inappropriate to use as units of replication in a linear model.

In the bottom-up experiment, budworm survival rate is compared between habitats and years with a factorial generalized mixed model (binomial link function), and pupal mass is analyzed with a factorial mixed model including habitat, sex and year as fixed factors. In the top-down experiment, predation and parasitism rates are compared between the two habitats * season (time of the year) using binomial generalized mixed models.

Model assumptions were tested using residual plots generated with the DHARMA package (Hartig and Lohse 2022). A likelihood ratio test was performed via the `lrtest` function in “`lmtest`” package (Hothorn et al. 2022) to select between simple and mixed models. The best-suited model was chosen based on the AIC function, prioritizing models with at least 2 lower AIC scores.

Results

Field survey

Canopy closure was higher in forest understory sites (2020 data: $61.8 \pm 2.24\%$ in natural forest vs $9.32 \pm 0.66\%$ in the plantation; LMM coefficient = 2.59, $p < 0.0001^{***}$) and branch elongation was higher in plantation trees (2017–2020 average: 8.63 ± 0.29 cm in forest vs 15.1 ± 0.24 cm in the plantation; LMM coefficient = 6.34, $p < 0.0001^{***}$). 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; LM coefficient = 10.30, $p = 0.019$). For comparison with other studies (Sanson et al. 2001; Onoda et al. 2011), this corresponds to approximately 0.53 ± 0.02 N in plantation trees and 0.49 ± 0.02 N in forest trees, using the conversion factor (1 g = 0.0098 N). While we report foliar toughness in grams as per the convention used in Lirette & Despland, (2021), we provide the equivalent values in Newtons for clarity. A comprehensive summary of all model coefficients is available in the supplementary material (Appendix C, Table S3).

In 2021, bud phenology measured on the same trees over a period in May and June was slightly more advanced in open than in understory habitats, but not significantly so (LMM estimate = 1.88, $p = 0.076$). Measurements made on a single date showed more advanced bud phenology in plantation both in 2022 (LM 2022: 1.398, $p < 0.0001^{***}$) and in 2023 (LM 2023: 0.655, $p < 0.0001^{***}$) (Fig. 1). The BioSIM model was used to predict budworm larval emergence from diapause at our sites, and peak, as well as the total duration of emergence (Fig. 1).

For late summer defoliation of current-year shoots, the model showed a significant effect of year ($p < 0.0001$), indicating a substantial decrease in defoliation from 2020 (mean $\pm$ SD: Forest = $7.25\% \pm 9.59\%$; Plantation = $5.15 \pm 4.90\%$) to 2021 (mean $\pm$ SD: Forest = $0.642\% \pm 1.74\%$; Plantation = $0.828\% \pm 3.61\%$), while neither habitat nor the interaction between habitat and year was statistically significant (Table S3). Overall mean defoliation remained less than 10% of new foliage in all cases.

The budworm larvae showed higher density in plantations in each of the years tested (Fig. 2, Table S3). However, comparison between years is not meaningful due to variations in methods and in the timing of sampling. A similar model showed no difference in the density of predators between habitats (mean $\pm$ SD: Forest 2021 = 2.39 ± 2.79 ; 2022 = 3.96 ± 2.071 ; 2023 = 3.0 ± 2.26 ; and in Plantation 2021 = 3.23 ± 3.51 ; 2022 = 4.20 ± 2.94 ; 2023 = 1.37 ± 1.30) in any sampling periods tested.

Bottom-up experiment

As expected, females were heavier than males (mean $\pm$ SD: 71 ± 33 mg for females vs 37 ± 22 mg for males; LMM coefficient: -0.004; $p = 0.047$). Insects reared on trees in plantation were overall heavier than those on understory trees (females in plantation = 73 ± 31 mg vs forest 69 ± 34 mg; LMM coefficient: 0.0158; $p = 0.038$). An interaction term showed that females were significantly heavier in the second year of the study (mean $\pm$ SD: plantation (2022) = 86 ± 33 mg vs in 2021 = 57 ± 19 mg; LMM coefficient - 0.053, $p < 0.0001^{***}$), while males showed no difference between years (Fig. 3).

Survival rate in the cages did not differ significantly between habitats (coefficient = 0.061, $p = 0.785$) but decreased between years (coefficient: -0.899, $p < 0.0001^{***}$).

Top-down experiment

In 2021, we only considered the caterpillars protected by Tanglefoot; predation rate was significantly higher in forest understory than in plantation sites (mean $\pm$ SD: $16.7 \pm 19.9\%$ in forest vs $3.57 \pm 9.65\%$ in plantations; coefficient = 1.676, $p = 0.010$). All recovered caterpillars gave rise to adults and hence no parasitism occurred during their field exposure.

In 2022, predation rate was slightly higher in forest understory than in plantation sites in both June and July, but not significantly so. Parasitism rate was calculated as a proportion of the larvae that had escaped predation and had been reared in the laboratory. Results showed higher parasitism rates in forest sites in both June and July but did not quite attain statistical significance (coefficient: 0.867, $p = 0.061$). Adding together consumed and parasitized larvae and testing against the number that survived to adulthood showed an overall higher mortality rate in forest than in plantation sites ($42.9 \pm 26.2\%$ in forest vs $34.5 \pm 22.6\%$ in plantations; overall mortality was also higher in July than in June ($44.5 \pm 26.9\%$ vs $36.9 \pm 23.9\%$; coefficient: -1.00764, $p = 0.030$).

Discussion

The field survey confirmed expected differences in canopy openness and associated tree growth. It also showed predicted lower foliar toughness and earlier budburst phenology in plantation habitats. 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 difference in predator density was observed between habitats, both predation and parasitism rates were higher in the forest understory.

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 (Lavoie et al., 2019, 2021; Sainte-Marie et al., 2015). 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).

The sentinel larvae experiments showed significant 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 understory

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 & Bauce, 1997; Grassi & Minotta, 2000; Ranade et al., 2022) and that sun-exposed foliage supports better spruce budworm growth and development (Carisey & 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; in comparison, the increase in pupal mass on plantation trees observed in our experiment was relatively slight (Mattson et al. 1991) and was only observable in females in one of the two years of the study. 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). Higher predation rates in the forest understory could contribute to protecting young natural regeneration spruce trees. 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; Smith et al. 2011; Greyson-Gaito et al. 2021, 2022) 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 vegetational 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 (Legault and James 2018). On 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 understory saplings suggests a behavioral preference for forest understories in parasitoids rather than a difference in 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.

Previous work compared defoliation in young conifers under hardwood (non-host) vs conifer (host) canopy and unsurprisingly showed higher levels of defoliation under a conifer canopy (Nie et al. 2018).

However, this difference was only apparent late in the outbreak cycle 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. Earlier in the outbreak cycle, 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). However, perhaps counterintuitively, other work suggests that even a conifer canopy can protect young trees from defoliation relative to those in open habitats, but that 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 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 (Fuatealba et al. 2017, 2018). Higher temperature advances black spruce budburst phenology making it a better host for the budworm (Pureswaran et al. 2019; Ren et al. 2020; Bellemin-Noël et al. 2021) and therefore canopy opening could improve black spruce phenology and make it a more suitable host. Our results do suggest an improvement of synchrony between white spruce budburst and spruce budworm emergence from diapause under open conditions (Fig. 1) (Podadera et al. 2024). Phenological mismatches between budworm larva and host have been shown to greatly reduce early instar survival (Fuatealba et al. 2017; Bouchard et al. 2018). White spruce shows faster budburst phenology than black spruce (Ren et al. 2020; Cartenì et al. 2023) and might be expected to respond less strongly to canopy opening.

Context dependence needs to be considered in interpreting ecological results (Catford et al. 2022). We showed only slight effects for bottom-up and top-down effects on white spruce that, in the context of early outbreak conditions, led to 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 and between points in budworm-parasitoid population cycles (Moreau et al. 2006, 2018). Indeed, differences in budbreak phenology between host species drive differences in defoliation of adult trees (Fuatealba et al. 2017; Bellemin-Noël et al. 2021). 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. 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 distinct roles at various stages (Royama et al., 2017). However, while differences in top-down pressure between host species may not be consistent (Seehausen et al. 2013) these pressures can vary as an outbreak progresses and different parasitoids play distinct roles (Royama et al. 2017). Our findings are consistent with previous work that differences between habitats in regeneration defoliation are slight early in the outbreak cycle (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 (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 understory or open 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 understory and open 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.

Finally, our results confirm that white spruce trees in open habitat plantations exhibit higher growth rates than under forest canopies. This increased vigour protects them against mortality: balsam fir saplings in understory die with 50% defoliation but can survive 75% in open conditions (Nie et al. 2018). The relative success of open vs under-canopy white spruce regeneration is thus a tradeoff between levels of insect herbivore populations and resilience to foliage loss (Nie et al. 2018); we show that multiple factors including budburst phenology, foliar quality, and predation and parasitism rates are involved in determining regeneration resilience to budworm outbreaks.

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). 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, and we identify bottom-up and top-down forces that are relaxed in plantations. Notably, we report a novel mechanism: advanced phenology in open conditions can improve synchrony with budworm emergence from diapause and make open-canopy regeneration trees more suitable hosts.

Declarations

ED and MG conceived the ideas and designed the methodology; SN, ZG, and APY collected the data; ED and SN analyzed the data and wrote the initial draft of the manuscript. Other authors provided editorial comments, and all authors contributed critically to the draft and gave final approval for publication.

Acknowledgments

Thanks to Elyse Moisan, Natalie Dupont, Beatrice Boulet-Couture, Georgia Drummond, Sebastian Caucci, Marie-Eve Jarry, Rosalie Deblois and Alin Buruiana for help with fieldwork. This study was funded by an MFFP grant and an NSERC Alliance grant ALLRP 560575-20, as well as Concordia undergraduate research awards to ME Jarry and A Buruiana, and an NSERC USRA to N Dupont.

Funding: This study was funded by Ministère des Forêts, de la Faune et des Parcs (MFFP) and the Natural Sciences and Engineering Research Council of Canada (NSERC) Alliance grant ALLRP 560575-20, as well as Concordia undergraduate research awards to ME Jarry and A Buruiana, and an NSERC USRA to N Dupont.

Conflicts of interest/Competing interests: 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.

Ethics approval: Not applicable

Consent to participate: Not applicable

Consent for publication: Not applicable

Availability of data and material: Data generated through this study can be made available upon request to the corresponding author.

Code availability: Not applicable

Authors' contributions: ED and MMG conceived the ideas and designed the methodology; SN, ZG, and APY collected the data; ED and SN analyzed the data and wrote the first draft of the manuscript. Other authors provided editorial comments, and all authors contributed critically to the draft and gave final approval for publication.

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Appendix

Appendix A is not available with this version

Figures

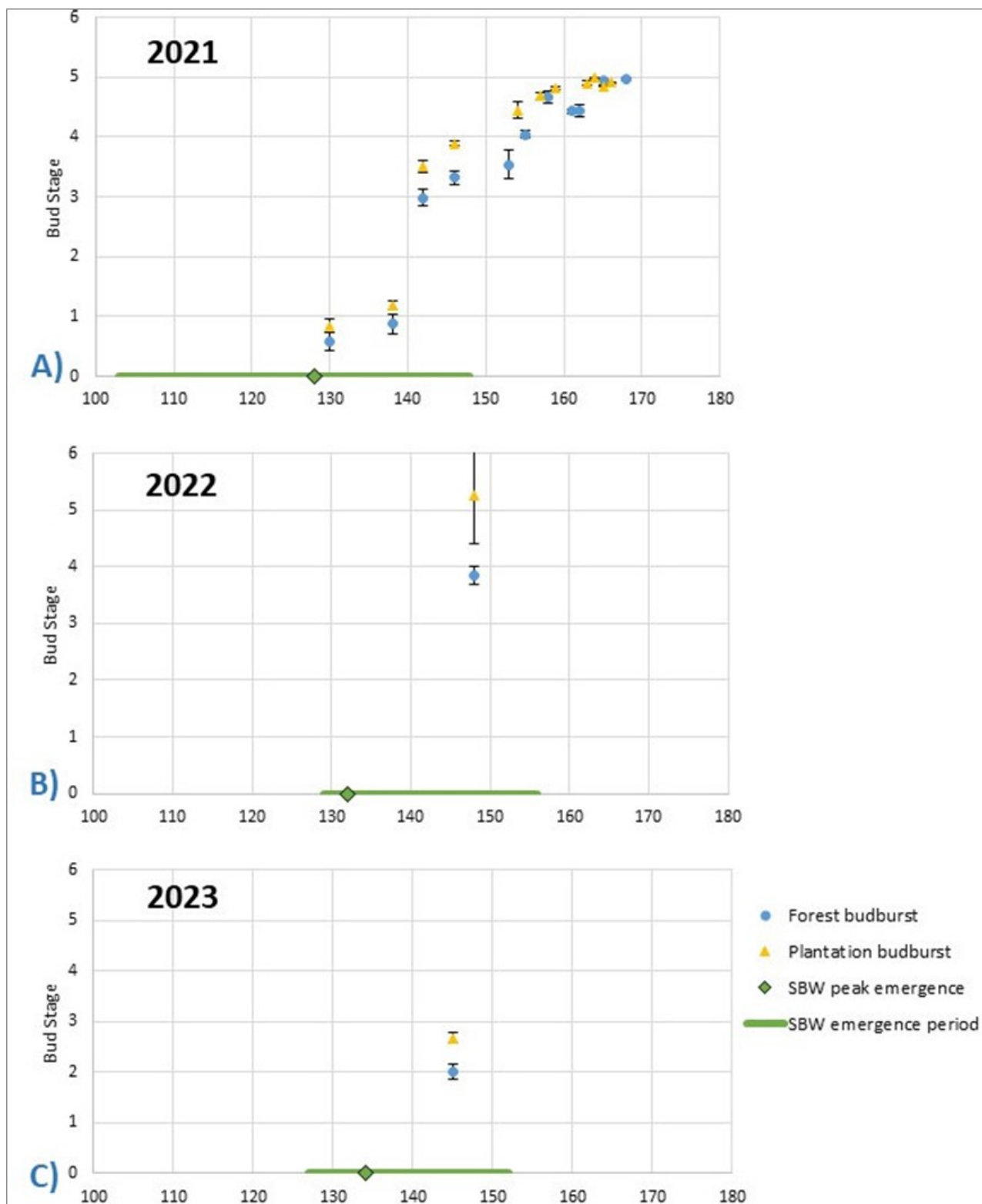


Figure 1

Legend not included with this version

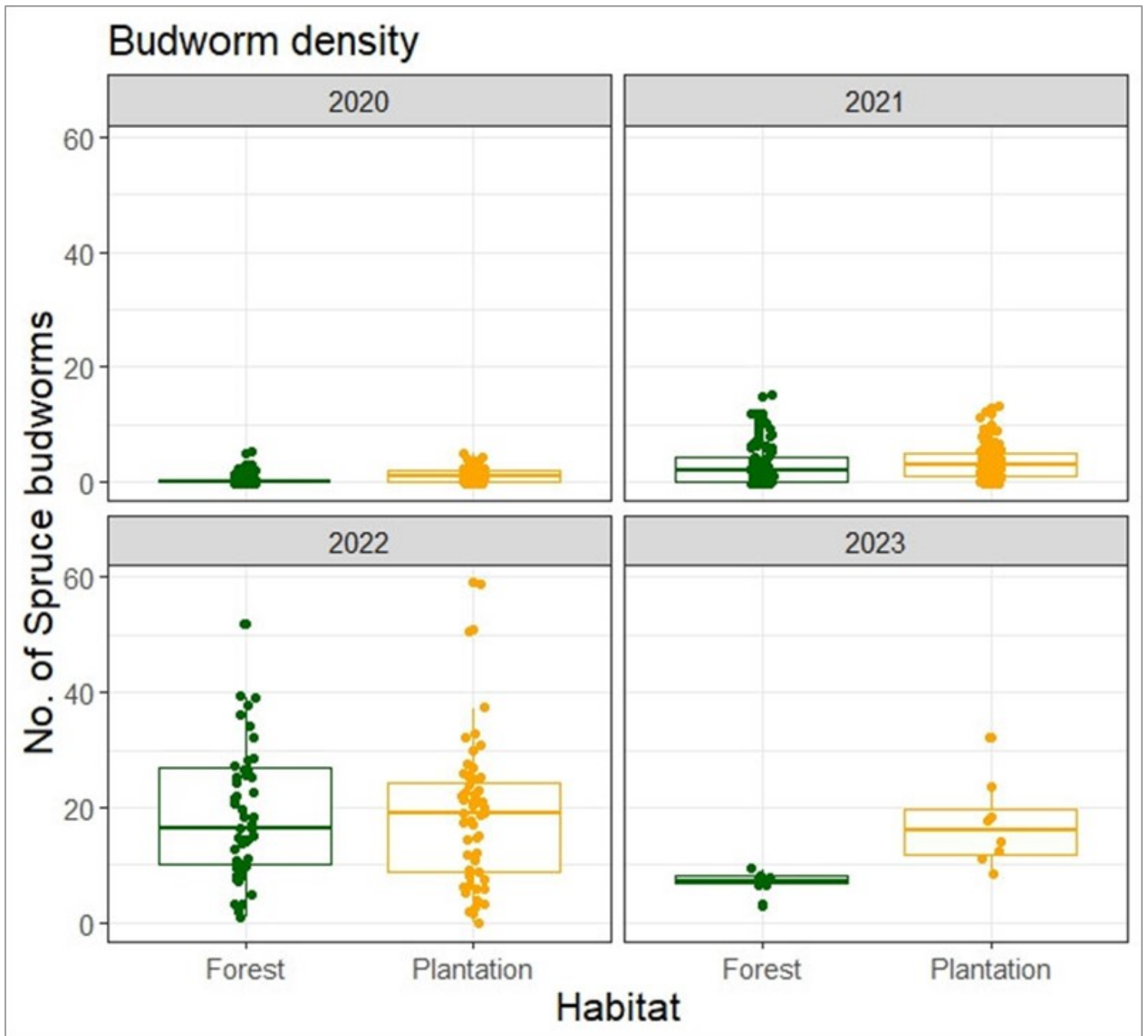


Figure 2

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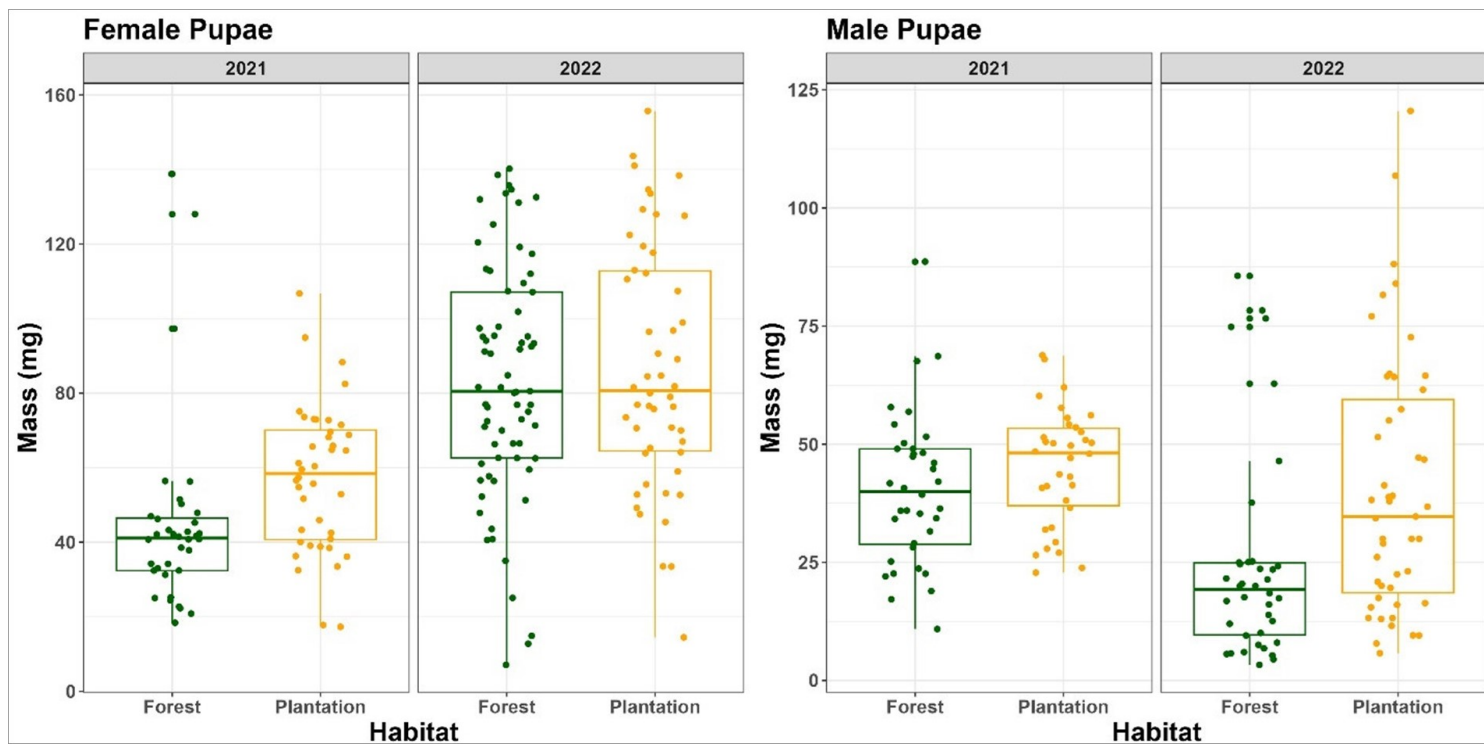


Figure 3

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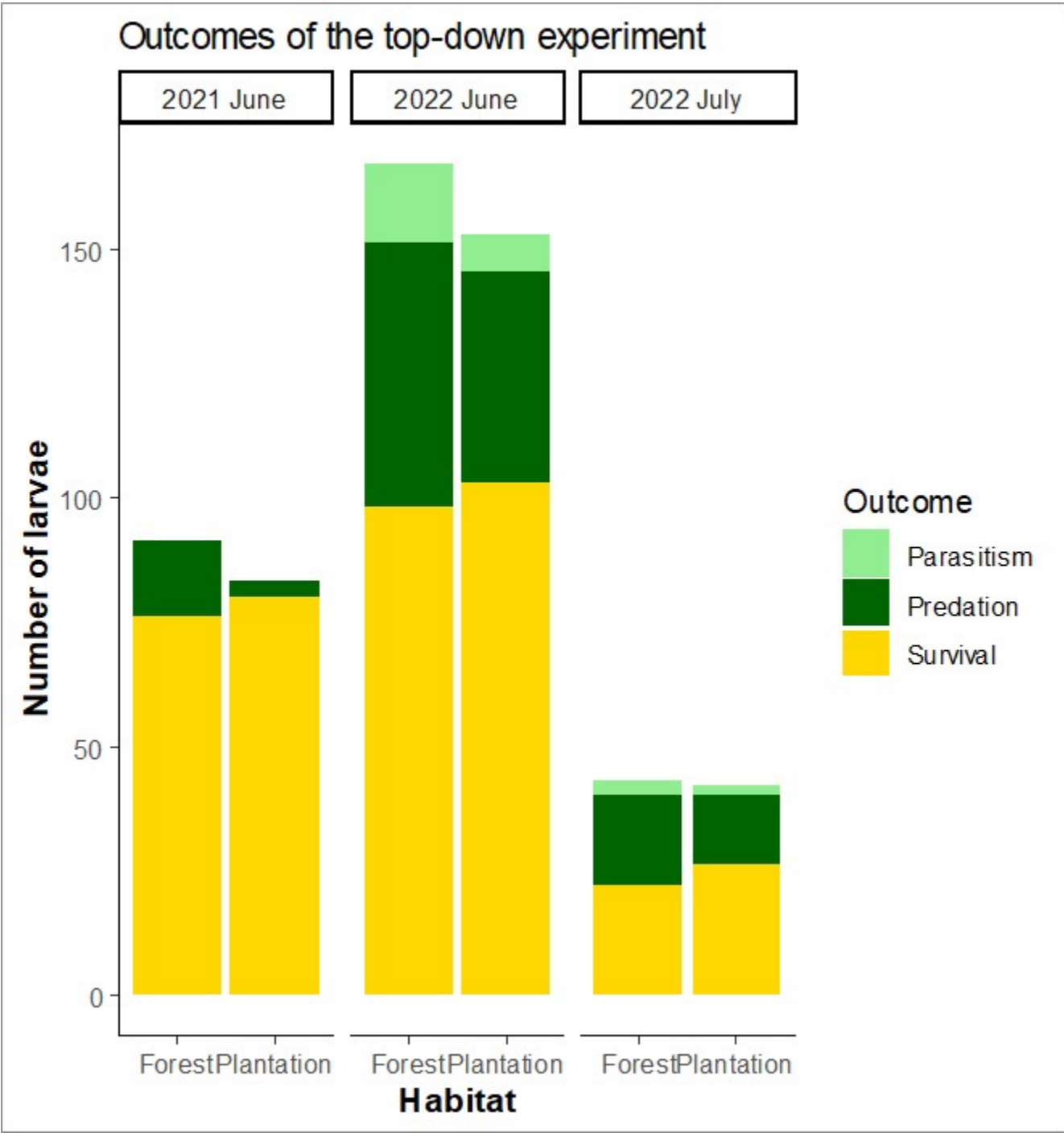


Figure 4

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