

Impact of Temperature on the Biological Performance of Eastern Spruce  
Budworm (*Choristoneura fumiferana*) on Different Hosts

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## Abstract

### Impact of Temperature on the Biological Performance of Eastern Spruce Budworm (*Choristoneura fumiferana*) on Different Hosts

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Eastern spruce budworm (*Choristoneura fumiferana*) outbreaks have long shaped boreal forests by affecting tree health and stand composition. Prior work shows that warming can shift spring timing for both insects and trees, and that even small changes in synchrony between larval feeding and newly flushed foliage can affect larval development and survival. Host trees also differ in how their buds and tissues respond to temperature, so outbreaks depend on which tree species are present and when newly flushed foliage is available.

Within this context, we examined how temperature and host plant together influence budworm performance across the intake-to-growth pathway. Larvae were reared on balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), and black spruce (*Picea mariana*) under ambient and warm conditions to see how warming might change feeding behavior and growth achieved on the three different hosts.

Warming did not affect performance in the same way for all hosts. It changes which processes limited larvae and shifted the rank order of hosts. On white spruce (*Picea glauca*), growth increased despite lower feeding because digestibility and conversion of ingested material improved. On black spruce (*Picea mariana*), growth increased mainly because larvae ate more. On balsam fir (*Abies balsamea*), conversion and growth decreased even though feeding increased. Overall, warming enlarged host differences. The results show that at ambient temperature, balsam fir has the highest growth which exceeded both spruces species. Under warming, the pattern shifts: both spruce species show increased growth, whereas balsam fir declines because its conversion efficiency is reduced.

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# 1.0 Introduction

## 1.1. Historical Dynamics of Spruce Budworm Outbreaks in Quebec

Insect outbreaks are one of the most common natural disturbances shaping boreal forest structure and function. Among these, the eastern spruce budworm (*Choristoneura fumiferana*) has produced repeated defoliation events in Quebec every 30–40 years, with large ecological and economic impacts (Boulanger & Arseneault, 2004).

*Choristoneura fumiferana* is univoltine, producing one generation per year (Pureswaran et al., 2019). Females lay egg masses averaging about 20 eggs (European Food Safety Authority (EFSA) et al., 2025), which hatch in 8–12 days depending on temperature (Wardlaw et al., 2022). Newly hatched larvae may disperse by silk threads and overwinter in diapause before resuming feeding in spring (Delisle et al., 2022), primarily on new shoots but also on older foliage under high demand. Pupation occurs in foliage and lasts 8–12 days, after which adults emerge in mid-summer, mate, and deposit eggs between July and August (Wardlaw et al., 2022).

Historical records show at least eight significant outbreaks since the early 1700s in eastern Quebec, with notable events during 1710–1724, 1752–1776, 1805–1812, 1832–1845, 1868–1882, 1914–1923, 1947–1958, and 1975–1992 (Boulanger & Arseneault, 2004). Analysis of outbreak frequency shows relatively stable intervals with an average of about 40 years, which contradicts previous assumptions of an increase in frequency in the 20th century (Boulanger & Arseneault, 2004).

Beyond host mortality, spruce budworm influences successional pathways. It primarily impacts balsam fir (*Abies balsamea*) and spruce species (*Picea spp.*), significantly affecting forest dynamics and composition (Bouchard & Pothier, 2010). In terms of relative defoliation across different hosts, based on one study, balsam fir is the most suitable host, followed by white spruce (~72% of fir defoliation), and black spruce (~28%) (Hennigar et al., 2008).

Severe outbreaks result in large scale tree mortality, leading to the development of large area of young, even-aged forest. These disturbances significantly reshape forest composition and landscape structure. The 1980s outbreak is a great example. It not only caused widespread tree death but also favored hardwood regeneration and particularly white birch (*Betula papyrifera*) in formerly conifer-dominated areas (Bouchard et al., 2006).

Looking ahead, anticipated climatic shifts will likely alter these long-standing dynamics. Climate change is expected to impact Quebec forests through rising temperatures and altered precipitation patterns. Projections for 2071–2100 suggest mean annual temperature rising to 5.5 °C alongside uneven regional shifts in precipitation (Wotherspoon et al., 2024). Consequently, longer and drier growing seasons, especially in moisture-limited ecozones may initially boost forest productivity but ultimately increase drought stress (Ameray et al., 2023). Furthermore, changing frost regimes, with changes in frequency, timing, and intensity, can disrupt plant phenology and increase the risk of frost damage, which affects tree growth and regeneration (Marquis et al., 2022).

## 1.2 Temperature-Driven Shifts in Host Budburst Phenology

Because early-instar spruce budworm larvae feed almost solely on newly expanding needles, warming-induced budburst shifts alter larval–host synchrony and thereby influence outbreak risk. Higher spring temperatures advance budburst, tightening phenological synchrony between budworm larval emergence and fresh foliage availability (Pureswaran et al., 2018). Species-specific responses to warming temperatures have been noted. Black spruce (*Picea mariana*) shows greater plasticity compared to balsam fir (*Abies balsamea*) and white spruce (*Picea glauca*). For instance, budburst is especially sensitive to the mean of night/early morning minimum temperature of May with black spruce responding more strongly than balsam fir or white spruce (Podadera et al., 2024).

### 1.3. Temperature–performance and host–phenology in eastern spruce budworm

As an ectotherm, *Choristoneura fumiferana* shows predictable thermal responses. Development time gets shorter as temperature rises, whereas survival and fecundity (metrics such as the number of eggs laid and pupal mass) respond nonlinearly (often with unimodal or threshold patterns). These nonlinear responses are best estimated with statistical model-based methods, especially near lower and upper thermal limits. The model curves reach a maximum at an optimum and fall at the extremes (Régnière, Powell, et al., 2012).

Using post-diapause *C. fumiferana* larvae reared individually on McMorran’s (1965) synthetic wheat-germ diet, Wardlaw et al. (2022) exposed insects to seven constant temperatures (5–35 °C) with short transfers to an optimal 20 °C to improve estimates near thermal limits, demonstrating successful development at both 5 °C and 35 °C and deriving stage-specific development-rate curves suitable for phenology modelling. From these data, lower stage thresholds (where the larvae cannot develop anymore) were estimated at ~3.7–4.8 °C and upper thresholds at ~36.4–38.6 °C. Development time to pupation decreased with warming, ranging from ~115 days at 5 °C to ~16 days at 25 °C (the approximate optimum) then increasing time again near the upper thermal limit. Peak development rates occurred near 30–35 °C for early instars and near 25–30 °C for later instars. When these physiological responses are incorporated in process-based spatial distribution models (including development, cold injury, and deleterious heat), predictions consistently show climatic suitability for the eastern spruce budworm to shift toward the pole and upslope under warmer climates. They also underscore the need for mechanistic drivers beyond simple correlative envelopes (Régnière, St-Amant, et al., 2012).

How these development rate responses affect population outcomes depends on host–insect phenology; the mechanisms and evidence are explained more in section 4 of the literature review.

## 1.4. Mechanisms of Bud-Insect Interaction Under Warming

Phenological defence means that when a tree has a late budburst, the larvae hatch too early before buds are available as food (Lawrence et al., 1997). Under  $\approx +2$  °C warming, spruce budworm performance on black spruce matched balsam fir, indicating weakening of black spruce's phenological defence (Bellemin-Noël et al., 2021).

A Canada-wide bud development dataset (2839 trees, 1980–2021) shows that mean minimum May temperature is the main driver of budburst timing and that black spruce advances twice as fast ( $-3.3$  days °C<sup>-1</sup>) as balsam fir or white spruce, suggesting that late-flushing black spruce and spruce budworm emergence are becoming more closely aligned in time across the boreal gradient. (Podadera et al., 2024). Following the same logic explained earlier, when researchers warmed plots by about 2 °C, buds opened sooner and larvae developed faster, though outcomes still varied by site and host. Modelling also shows that a +2 °C shift produces larger phenological overlap at northern sites yet can increase mismatch at warmer southern sites, illustrating that synchrony gains vary across regions (Portalier et al., 2022).

Where larval-host phenological synchrony is improved, second-instar spruce budworms begin feeding on developing buds earlier, shortening the early-season starvation window during which they would otherwise be forced to feed on overwintering needles (Lawrence et al., 1997). On white spruce, buds are most vulnerable from a few weeks before budbreak until shoot elongation ends. Larval survival is highest when budworm emergence occurs one to three weeks before budbreak, but it declines sharply once development extends past shoot elongation, when foliage becomes too tough for feeding (Lawrence et al., 1997). Laboratory synchrony experiments further show that early-emerging larvae placed on pre-budburst black spruce cannot mine old needles (consistent with their mechanical toughness) and suffer high early mortality, whereas counterparts on balsam fir survive by mining last year's needles; once budbreak commences, larvae on black spruce match those on balsam fir in growth and survival (Fuentelba et al., 2018). Overall the studies suggest that when the phenology of larval development is well-aligned with bud emergence in time, the caterpillars get to feed on softer tissues instead of old needles and that small shift can

greatly increase their survival on hosts that are otherwise marginal when out of phase (Fuentelba et al., 2018; Lawrence et al., 1997).

Temperature also modifies host quality. Classic feeding experiments with balsam fir collected over five springs showed that pupal biomass was 20% greater for budworms that fed on foliage formed during warm dry years, which all else equal should result in 25% higher budworm fecundity in those years (Campbell, 1989). Such quality shifts compound synchrony effects, amplifying outbreak potential when warm springs both advance host phenology and enrich needle nutrition. Behavior of first-instar larvae further couple temperature to host interaction. If the buds on the tree they are currently on are closed, young larvae are more likely to disperse to neighbouring trees via ballooning; field experiments found greater dispersal from black spruce than from balsam fir, reflecting the higher phenological risk on the former (Bellemin-Noël et al., 2025). As warming narrows the budburst gap, the incentive for risky dispersal declines as dispersal exposes larvae to desiccation, predation and failure to locate a suitable host, potentially retaining more larvae on black spruce and intensifying defoliation within stands.

Overall, evidence from experimental manipulations, long-term phenology datasets, and process-based models converges on a central theme: warmer temperatures reduce phenological barriers that historically protected late-flushing hosts (Pureswaran et al., 2019), enhances foliar quality (Tai & Carroll, 2022), reduces the rate of risky larval dispersal (Boulanger et al., 2024) and, in many boreal settings, increases spruce budworm fitness. These processes play out differently across regions: in the north, warmer conditions are aligning bud and insect timing more closely, raising the likelihood of stronger outbreaks (Tai & Carroll, 2022), whereas southern forests may experience partial offset due to increased mismatch or heat-driven stress (Boulanger et al., 2024).

## 1.5. The Nonlinear Impact of Temperature on Performance of Spruce Budworm

At the landscape scale, projections show that where warming improves synchrony of budworm developments with tree phenology, notably in the boreal north, defoliation risk increases

(Pureswaran et al., 2015). Recent modelling further shows earlier spring development and uneven regional outcomes, with strongest performance increases in cooler regions (Boulanger et al., 2024).

Importantly, the full effect of warming is determined by its interaction with host phenology. Benefits of faster growth occur only when larval emergence is synchronized with nutritious, newly flushed foliage. Improved synchrony, which warming can facilitate, allows larvae to take advantage of higher metabolic rates (Ren et al., 2020). When warming has effects on host and insect at different rates, phenological mismatch can cancel out physiological benefits, forcing feeding on tougher, more chemically defended foliage or leading to starvation (Bellemin-Noël et al., 2021; Fuentealba et al., 2017). This interaction is particularly important for previously unsuitable hosts like black spruce, which may become more susceptible as synchrony improves (Pureswaran et al., 2019).

## 1.6. The Influence of Host Species on Spruce Budworm Performance

Across the main hosts, balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), and black spruce (*Picea mariana*) and across tree ages, spruce budworm performance closely tracks foliar quality and the developmental stage of the consumed foliage. These factors drive corresponding shifts in feeding and utilization indices, including Relative Growth Rate (RGR), Relative Consumption Rate (RCR), Approximate Digestibility (AD), Efficiency of Conversion of Digested food (ECD), and Efficiency of Conversion of Ingested food (ECI). The formulas for these indices are provided in Methods §2.6.3, “Response variables and indices.”

On balsam fir, foliage stage strongly conditions performance. For early instars, young foliage on young trees promotes higher growth (RGR), higher digestibility (AD), and higher conversion of ingested food (ECI) than foliage from older trees; these outcomes are consistent with higher N:tannin ratios and elevated phosphorus early in the season (Bauce et al., 1994; Kumbaşlı et al., 2011). By contrast, at the sixth instar, performance is better on older foliage: larvae show higher RGR, higher consumption (RCR), and higher AD, but lower ECD indicating that, despite greater digestibility, the conversion of digested food to biomass is poorer and thus ECI shows no net gain relative to diets of young foliage. This switch can be explained by the fact that, during the sixth instar, foliage of young trees shows a lower N:tannin ratio and higher concentrations of bornyl acetate, terpinolene, and  $\delta$ -3-carene, which reduce larval consumption. (Bauce et al., 1994).

Field evidence matches these quality–timing effects. In New Brunswick, larval development is faster on balsam fir than on red or black spruce (Hudes & Shoemaker, 1984). Host effects also carry across generations: parents that fed on white spruce produced heavier overwintering larvae with higher winter survival, and they also produced heavier pupae; by contrast, black-spruce parents yielded smaller progeny with lower winter survival (Berthiaume et al., 2020).

Energetic budgets clarify why “better growth” does not necessarily imply “faster development.” In laboratory experiments for spruce budworm, assimilation efficiency (Assimilated/Consumed  $\approx$  AD) ranged 33.9–40.2%, gross production efficiency (Produced/Consumed  $\approx$  ECI) 9.5–13.3%, and net production efficiency (Produced/Assimilated  $\approx$  ECD) 26.1–38.8%, values low for lepidopteran defoliators and lower on balsam fir than on white spruce. Although total consumption was broadly similar across hosts, production was  $\approx$ 20% greater on white spruce, and development time was longer on spruce than on fir (Noah Koller & Leonard, 1981). Together with the foliage-stage chemistry above, these results show that AD/ECI/ECD are context-dependent, and that mass gain cannot always be predicted from development time (See Appendix J for the relationships between indices and how they affect each other.). In the field, these dynamics integrate with host plant foliar quality and phenology (e.g., faster development on fir; (Hudes & Shoemaker, 1984)) and with effects across generations (higher pupal mass and winter survival from white-spruce parents; (Berthiaume et al., 2020a)), thereby shaping outbreak potential in mixed fir–spruce landscapes.

In the typical host hierarchy, white spruce is considered intermediate, supporting successful but less than optimal development (Bauce et al., 1994; Talerico & Montgomery, 1983). Black spruce is often least suitable, a pattern linked to phenological asynchrony (budburst lagging larval emergence) and stronger chemical defenses, including higher concentrations of feeding-deterrent monoterpenes and phenolics (Berthiaume et al., 2020; Noah Koller & Leonard, 1981; Ullah et al., 2024) However, this hierarchy is not static. When phenological synchrony improves, for example, under climate warming, or when larvae use nutrient-rich tissues (e.g., staminate flowers), performance on black spruce can increase substantially, at times approaching levels on balsam fir (Bellemain-Noël et al., 2021; Blais, 1957; Fuentealba et al., 2017).

Based on evidence that warm conditions accelerate insect physiology, this study tested whether elevated temperature altered spruce budworm (*Choristoneura fumiferana*) feeding performance, quantified by RGR, RCR, AD, ECI, and ECD, on black spruce (*Picea mariana*), white spruce (*Picea glauca*), and balsam fir (*Abies balsamea*). We hypothesized that warm treatments would shift average results across all five indices, that the patterns of results within each host would be reshaped, and that host interactions would affect these responses among the three tree species. Overall, these expectations framed a clear test of how temperature-driven physiology and host identity combined to shape spruce budworm performance, providing insight to help mitigate the impacts of global warming on potential spruce budworm outbreaks in the coming years. Because of the complexity of boreal forest responses, such understanding is crucial for creating adaptive, ecosystem-based management plans.

## 2. Materials and Methods

### 2.1 Experimental Setup and Conditions:

This study examined feeding and growth by Eastern Spruce Budworm (*Choristoneura fumiferana*) on three species of coniferous trees: Black Spruce (*Picea mariana*), White Spruce (*Picea glauca*), and Balsam Fir (*Abies balsamea*). The full experiment was conducted within environmentally controlled growth chambers located at the Université du Québec à Chicoutimi (UQAC). The black spruce and white spruce saplings originated from the Laterrière nursery. The balsam firs were supplied by Productions Résinex. All trees were three years of age at the time they were introduced into the growth chambers. The spruce budworms were sourced from the Insect Production and Quarantine Laboratories at the Great Lakes Forestry Centre in Sault Ste. Marie, Ontario, Canada.

The experiment was carried out using two growth chambers (Model: Conviron CMP6050), which were operated simultaneously. One chamber was programmed to represent ambient temperature conditions, while the other chamber represented warm conditions. The ambient condition was defined using historical climate data from the Bagotville Airport weather station, based on the 30-year data (1991–2020) provided by the Government of Canada. For this program, the average maximum and minimum weekly temperatures, as well as the corresponding sunrise and sunset times, were entered and adjusted on a weekly basis to simulate seasonal progression, resulting in five

distinct temperature changes over the course of the experiment (see Appendix A for the detailed schedule). A consistent +3 °C increase was maintained in the warm chamber relative to the ambient chamber from the first day of the experiment. Humidity was maintained at 50% in both chambers. The photoperiod and light intensity (fluorescent and incandescent) followed a detailed schedule (see Appendix A) designed to mimic natural conditions, with light levels gradually increasing from a simulated sunrise to a midday peak and then decreasing toward sunset.

For this experiment, we constructed custom glass boxes with textile netting enclosures. Inside each of the two chambers, three of these boxes were placed, with each box containing a single tree species. The complete experimental setup therefore consisted of six glass boxes in total. The arrangement of species within each chamber, when viewed from the exterior, was as follows from left to right: Balsam Fir, White Spruce, and Black Spruce. Upon moving the trees from the outdoors, they were placed into their designated boxes and allowed to acclimate to the new chamber environment for one day before the experiment officially started.

A total of 63 trees of each species per each chamber were used, arranged in nine rows of seven trees each (see appendix B for the experimental design layout). Each tree was assigned a unique identification (ID) number that specified its designated chamber, species, row, and position.

Water levels in the boxes were monitored and replenished as needed to a specific level marked on the boxes to permit ad libitum consumption by the trees. The trees remained in their original plastic plug trays within these boxes. A water-soluble fertilizer (Van Iperen 20-20-20 N-P-K) was applied once at a rate of 0.25 g/L to achieve a target concentration of 50 ppm. Phenology of buds was monitored on trees located in specific rows: 2, 4, 5, 6, and 8, with the rows counted from the rearmost position in the chamber.

## 2.2 Phenology Recording

All trees were introduced into the growth chambers on Day of Year (DOY) 134 (May 13th, 2024). At the start of the experiment, the tree buds were observed to be at phenological stage one. The bud development stages were recorded for the apical bud as well as two marked lateral buds, beginning on the first day of the experiment. This monitoring was conducted for all trees in the designated phenology rows (2, 4, 5, 6, and 8) across all species and in both the ambient and warm

chambers. The phenology was recorded three times per week (on Monday, Wednesday, and Friday), and this monitoring process was continued until observed buds had reached phenological stage six.

## 2.3 Larval Introduction

Eastern Spruce Budworm larvae were obtained from the Great Lakes Forest Research Centre at the second-instar diapausing stage. Upon delivery to the lab, they were stored in cheesecloth at a temperature of  $-4^{\circ}\text{C}$  to maintain diapause. For the experiment, the cheesecloth containing the larvae was cut into small squares. Due to the very small size of the second-instar larvae and their tendency to overlap within the cheesecloth, it was not possible to determine the exact number of individuals introduced; however, we estimated that each square held approximately 5 to 8 larvae. We introduced all cheesecloth squares simultaneously within each chamber–temperature combination, pinning them near the apical bud of each host tree once the apical buds of that species had reached phenological stage six, ensuring that all larvae experienced comparable bud quality at the same developmental stage (bud stage descriptions are provided in Appendix D). The developmental stage of the larvae was monitored, and they were allowed to feed on the host trees until they reached the sixth instar (see the Appendix C for their stages). Each larva was then collected individually upon reaching this final feeding stage. The Day of Year (DOY) ranges during which larvae reached the sixth instar are shown in Table 1.

Table 1. DOY ranges for each tree species indicating when larvae reached stage 6 and were collected.

Tree Species and Temperature	DOY Range
Balsam Fir-AMBIENT	DOY 162-171
White Spruce-AMBIENT	DOY 158-171
Black Spruce-AMBIENT	DOY 161-174
Balsam Fir-WARM	DOY 162-171
White Spruce-WARM	DOY 158-171

## 2.4 Bioassay Tube Phase

Upon reaching the sixth instar, larvae were collected and transferred to custom-made bioassay tubes. These tubes were specifically designed to facilitate the collection of frass and to precisely measure larval mass gain and foliage consumption. The bioassay tubes were constructed from 50 mL Corning Falcon tubes. The cap of the Falcon tube served as a base, onto which a 2 mL Eppendorf tube was affixed using a hot glue gun. This smaller Eppendorf tube acted as a water reservoir to maintain the turgor of the foliage. Tap water (1.25 mL) was added to each Eppendorf tube, and the opening was sealed with Parafilm. A small hole was then punctured through the Parafilm using a dissecting needle for inserting the tree branch(es).

Sixth-instar larvae were collected from the trees using dissecting needles and placed in petri dishes before being weighed. Therefore, fresh new-growth shoots of sufficient length were collected. These shoots were preferably sourced from the same tree from which the larva was collected. If sufficient foliage was unavailable on the original host, shoots were taken from another tree of the same species within the same chamber, and a careful record was kept of the source tree for both the larva and the foliage. Branches were excised close to the main stem using pruning shears. Prior to assembly, the initial fresh mass of the branch(es) and the larva were measured in milligrams (mg) using an analytical balance (Mettler Toledo AX205 DeltaRange) and a weighing boat. The branch was then inserted through the Parafilm into the Eppendorf tube, and the pre-weighed larva was placed onto the shoot(s). The IDs for the larva and the foliage source tree were recorded on the Falcon tube, which was then sealed and returned to its related growth chamber for a 72-hour incubation period.

## 2.5 Post-Incubation Sample Processing

After the 72-hour incubation period had concluded, the tubes were removed from the chambers. All frass was carefully collected from the tube and branch surfaces, using brushes to move the pellets of frass into labeled glass tubes. Following this, the final fresh mass of the larva, the remaining foliage (leftover), and the produced frass were recorded using the same analytical balance. After these fresh mass measurements were completed, the larvae and frass were placed into separate, pre-labeled glass tubes, and the leftover foliage was placed into pre-labeled paper bags.

To preserve the biological integrity of the samples, they were flash-frozen in liquid nitrogen. Subsequently, all samples were transferred to a freeze-dryer (Model: Büchi Lyovapor L-200). After the freeze-drying process was complete, based on an internal protocol consisting of a 3-day drying period, the final dry mass of the larvae, the leftover foliage, and the frass was measured. An overview of the experimental workflow is shown in Figure 1, illustrating the sequence of procedures used for larval rearing on trees, feeding assays, and mass measurements.

## 2.6 Statistical Analysis

### 2.6.1. Software and packages

All analyses were performed in R 4.2.1 (RStudio) using `ggplot2` and `RColorBrewer` for data visualization, `dplyr` and `tidyr` for data wrangling, `purrr` for iterative functional operations, and `readr` for data import.

I used Anthropic Claude to assist with routine coding tasks, and I checked and finalized all code and statistical decisions myself, in line with Concordia's guidance on responsible GenAI use.

### 2.6.2. Data recorded

For each 72h feeding trial, we recorded initial and final larval fresh mass, frass mass, and remaining shoot mass. All materials (larvae, frass, needles) were oven-dried and weighed when possible. A grouping factor, `Species_Group = Species × Temperature`, was created.

To estimate initial dry mass of larvae and branches, we fitted, for each species and group, a linear regression model (intercept fixed at 0) constrained to pass through the origin as they are better fit and can capturing the variance more effectively than models with an intercept (Montgomery, 1983).

$$Dry = \beta \cdot Fresh$$

Where:

- $\beta$  is the regression coefficient of the Larvae group equation obtained from the regression analysis.

In this study, initial dry mass for both larvae and foliage was estimated indirectly from empirical measurements of fresh mass. For larvae, a calibration relating fresh mass to dry-mass was built using individuals measured for both at the end of the trial; that fitted relationship was then applied to the starting fresh mass of each larva to estimate its initial dry-mass. For foliage, we used the same approach as for larvae and the calibration was used to infer the starting dry mass of

foliage from the initial fresh mass. When a direct final dry-mass measurement was unavailable, the same calibration provided an estimate of final dry-mass from the end-of-period fresh mass.

The fitted equations for larval fresh to dry initial mass regressions and corresponding  $R^2$  values are shown in Table 2.

Table 2. Fresh-dry regression-through-origin fits

<b>Group</b>	<b>Regression (through origin)</b>	<b><math>R^2</math></b>
Balsam fir-Ambient	$y=0.1504x$	0.907
Balsam fir-Warm	$y=0.1339x$	0.817
White spruce_ Ambient	$y=0.1728x$	0.867
White spruce-Warm	$y=0.1323x$	0.829
Black spruce-Ambient	$y=0.1539x$	0.818
Black spruce-Warm	$y=0.1450x$	0.669

Branches: initial branch dry mass was imputed from  $T0\_Branch\_Mass\_mg$ :

$$\text{Initial\_Branch\_Dried\_Mass} = \beta_{\text{branch}, T0} \cdot T0\_Branch\_Mass\_mg$$

Branches: If a record lacked final dried branch mass but had final fresh branch mass, we used the fresh-to-dry branch calibration to estimate the final dried mass.

$$\text{Final\_Branch\_Dried\_Mass} = \beta_{\text{branch}, Tstop} \cdot Tstop\_Branch\_Mass\_mg$$

The fitted fresh to dry mass regressions for branch initial mass and  $R^2$  values are presented in Table 3.

Table 3. Fresh-dry regression-through-origin fits

<b>Group</b>	<b>Regression (through origin)</b>	<b><math>R^2</math></b>
Balsam fir-Ambient	$y=0.2329x$	0.962
Balsam fir-Warm	$y=0.2207x$	0.974
White spruce-Ambient	$y=0.296x$	0.939
White spruce-Warm	$y=0.2363x$	0.967
Black spruce-Ambient	$y=0.2829x$	0.941
Black spruce -Warm	$y=0.2887x$	0.958

### 2.6.3. Response variables and indices:

Indices were computed on a dry-mass basis using measured or calibrated dry values: RGR, RCR, ECI, ECD and AD following standard definitions (Tab Waldbauer, 1968).

Table 4. Feeding indices, definitions, and equations used to quantify spruce budworm larval performance.

Index (Acronym)	Full Name	Equation
<b>RGR</b>	Relative Growth Rate	$RGR = \frac{\Delta m_{\text{larva}}}{m_0 \cdot \Delta t}$
<b>RCR</b>	Relative Consumption Rate	$RCR = \frac{\text{Ingested}}{m_0 \cdot \Delta t}$
<b>AD%</b>	Approximate Digestibility	$AD = 100 \cdot \frac{\text{Ingested} - \text{Egested}}{\text{Ingested}}$
<b>ECI%</b>	Efficiency of Conversion of Ingested food	$ECI = 100 \cdot \frac{\Delta m_{\text{larva}}}{\text{Ingested}}$
<b>ECD%</b>	Efficiency of Conversion of Digested food	$ECD = 100 \cdot \frac{\Delta m_{\text{larva}}}{\text{Ingested} - \text{Egested}}$

Note: Relative Growth Rate (RGR) and Relative Consumption Rate (RCR) are expressed in  $\text{mg} \cdot \text{mg}^{-1} \cdot \text{d}^{-1}$ , while Approximate Digestibility (AD), Efficiency of Conversion of Ingested food (ECI), and Efficiency of Conversion of Digested food (ECD) are expressed as percentages (%).  $\Delta m_{\text{larva}}$  is the change in larval dry mass during the feeding period (mg),  $m_0$  is the initial larval dry mass (mg), and  $\Delta t$  is the duration of the feeding period (days). “Ingested” is the total dry mass of food consumed (mg), and “Egested” is the total dry mass of frass produced (mg).

#### 2.6.4. Data preparation and filtering:

Because AD, ECI, and ECD are proportional measures constrained between 0 and 100, and RCR and RGR are strictly positive, any negative values or values falling outside these biologically permissible ranges were removed as out-of-range observations.

##### 2.6.4.1 Outlier handling:

For index variables, outliers were identified within each Species\_Group using the interquartile range (IQR) rule, where values below  $Q1 - 1.5 \times IQR$  or above  $Q3 + 1.5 \times IQR$  were excluded.

Here,  $Q1$  (the first quartile) and  $Q3$  (the third quartile) represent the 25th and 75th percentiles of the data, respectively, and the IQR is their difference ( $IQR = Q3 - Q1$ ) (Mcgill et al., 1978).

#### 2.6.5. Hypothesis testing:

We evaluated the effects of host species, temperature treatment, and their interaction on larval nutritional indices using generalized linear models. RGR and RCR were modeled using Gamma GLMs with a log link, while AD, ECI, and ECD were modeled using Beta GLMs with a logit link. The fixed-effects structure for all models was:

**Response~Species×Temperature**

To translate model coefficients into ecologically interpretable results, we calculated estimated marginal means (marginal effects) for each species–temperature combination. These provided response-scale predictions and 95% confidence intervals, which allowed us to compare warm vs ambient conditions within species and to test species differences under each temperature treatment. Full marginals mean tables and confidence intervals are provided in the Appendix G.

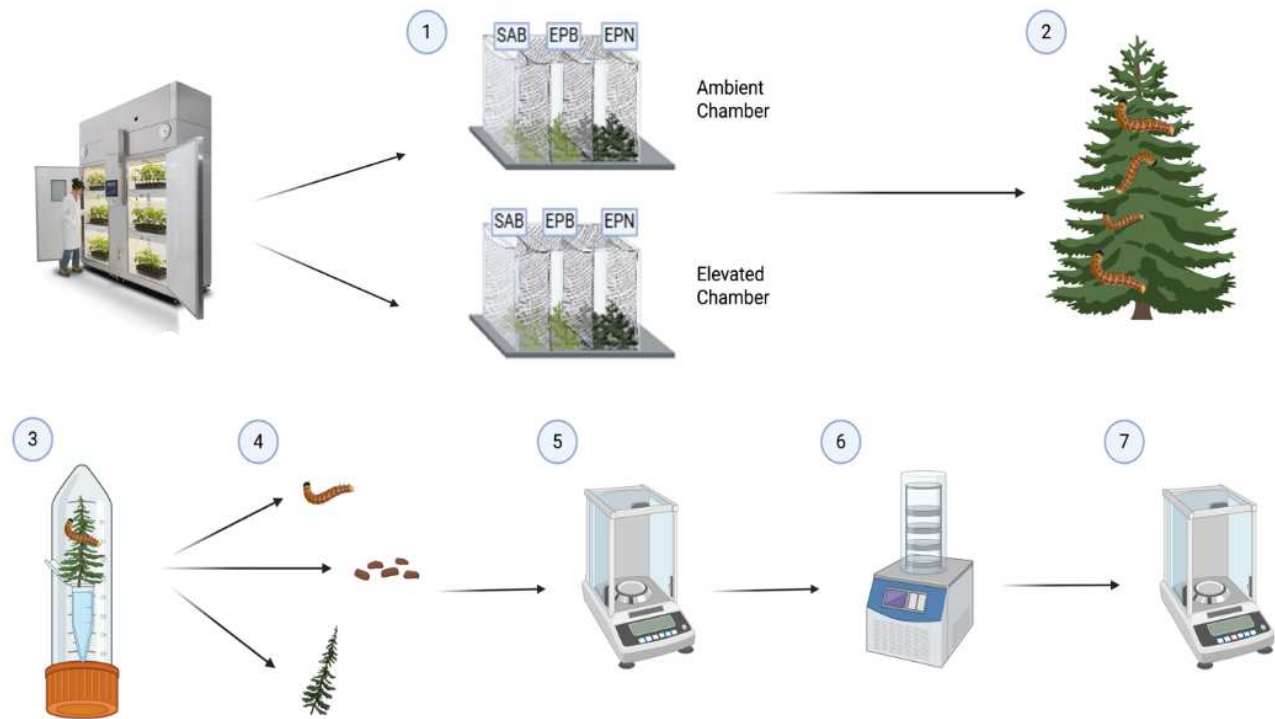


Figure 1. Experimental workflow illustrating the spruce budworm feeding assay. (1) Chamber setup with three host tree species under controlled conditions; (2) larval inoculation onto host branches; (3) incubation of individual larvae with branch segments in ventilated tubes; (4) sample collection of larvae, frass, and remaining foliage; (5) fresh mass measurement after blotting; (6) freeze-drying (lyophilization); and (7) dry mass measurement for final mass determination.

### 3. Results:

Group means for the predicted initial and final dry mass of larvae, the dry mass of consumption based on the dry weight of branches and the dry mass of frass are summarized in Table 5. Values are presented as means  $\pm$  standard deviations (SD) for each Species and Temperature group. All masses are expressed in milligrams (mg); consumption and dry frass are reported in dry mass. In the following tables and figures, SAB refers to balsam fir, EPB to white spruce, and EPN to black spruce.

Table 5. Descriptive statistics (N, mean  $\pm$  SD) for larval dry mass variables by species and temperature treatment.

Variable	Species	Ambient (N)	Ambient (Mean $\pm$ SD)	Warm (N)	Warm (Mean $\pm$ SD)
Predicted Initial Larva	SAB	51	5.03 $\pm$ 2.35	56	6.62 $\pm$ 3.83
	EPB	54	5.39 $\pm$ 2.92	51	6.07 $\pm$ 4.18
	EPN	52	5.22 $\pm$ 2.99	53	4.03 $\pm$ 2.24
Final Larva Dry Mass	SAB	51	9.00 $\pm$ 3.92	56	8.79 $\pm$ 4.11
	EPB	54	8.04 $\pm$ 3.64	51	8.76 $\pm$ 4.45
	EPN	52	7.83 $\pm$ 3.98	53	7.34 $\pm$ 2.82
Feces Dry Mass	SAB	51	28.07 $\pm$ 15.22	56	32.29 $\pm$ 17.79
	EPB	54	37.59 $\pm$ 20.35	51	30.82 $\pm$ 20.83
	EPN	52	29.99 $\pm$ 15.43	53	28.35 $\pm$ 14.18
Dry Consumption Weight	SAB	51	32.62 $\pm$ 23.84	56	49.80 $\pm$ 28.64
	EPB	54	40.95 $\pm$ 20.44	51	60.87 $\pm$ 30.07
	EPN	52	47.81 $\pm$ 21.13	53	48.12 $\pm$ 21.51

### 3.1 Indices Results

#### 3.1.1. Relative Growth Rate (RGR)

At ambient temperature, larvae on balsam fir had higher RGR than on white spruce, whereas black spruce did not differ from white spruce. Warming increased RGR on both spruces, as indicated by a positive warm-chamber effect for the white spruce baseline and a non-significant  $EPN \times \text{Warm}$ , but strongly reduced RGR on balsam fir, reflected in a large negative  $SAB \times \text{Warm}$  (Table 6). Marginal means from the Gamma GLM (on the response scale) confirmed these patterns: RGR on white spruce and black spruce increased by  $\sim 36\%$  and  $\sim 27\%$  under warming (from  $\sim 0.18$  to  $0.25$  and from  $\sim 0.19$  to  $0.24$ , respectively), whereas RGR on balsam fir decreased by  $\sim 23\%$  (from  $\sim 0.23$  to  $0.17$ ). As a result, the host ranking reversed under warm conditions, with both spruces supporting higher RGR than balsam fir (See appendix H for marginal means + 95% CIs).

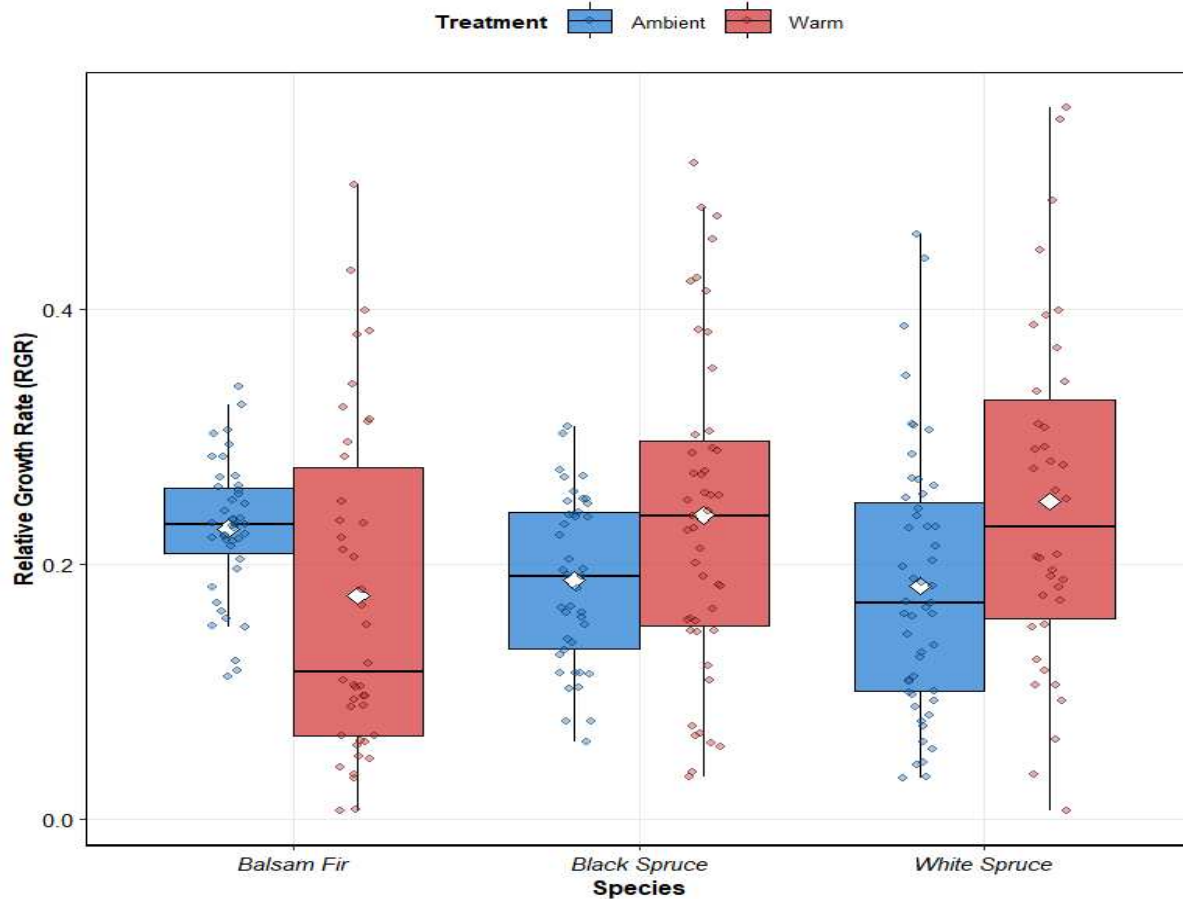


Figure 2. Relative Growth Rate (RGR) ( $\text{mg} \cdot \text{mg}^{-1} \cdot \text{d}^{-1}$ ) of spruce budworm larvae feeding on white spruce (EPB), black spruce (EPN), and balsam fir (SAB) under ambient (A) and warm (W) temperatures. White diamonds represent mean values; boxes indicate interquartile ranges.

Table 6. GLM output for RGR

<i>Parameter</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>z value</i>	<i>p-value</i>
<i>(Intercept)</i>	-1.700	0.073	-23.290	< 0.001***
<i>Species: EPN</i>	0.024	0.109	0.222	0.825
<i>Species: SAB</i>	0.220	0.108	2.037	0.043*
<i>Chamber: Warm (vs Amb.)</i>	0.311	0.112	2.784	0.006**
<i>EPN × Warm</i>	-0.070	0.157	-0.443	0.658
<i>SAB × Warm</i>	-0.574	0.159	-3.612	< 0.001***

Notes: RGR units are  $\text{mg} \cdot \text{mg}^{-1} \cdot \text{d}^{-1}$ , Formula:  $\text{RGR} \sim \text{Species} * \text{Chamber}$ , family = Gamma (log link). Reference levels: Species = EPB; Chamber = Ambient. AIC = -422.185; Dispersion  $\phi = 0.356$ . \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ .

### 3.1.2. Relative Consumption Rate (RCR)

Relative consumption rate (RCR) showed a clear Species  $\times$  Chamber interaction (Table 7). At ambient temperature, larvae on balsam fir had lower RCR than on white spruce, whereas black spruce did not differ from white spruce. Warming reduced RCR on white spruce but increased it

on both black spruce and balsam fir. Marginal means indicated that warming decreased RCR on white spruce by about 24% (from ~2.67 to ~2.03), but increased RCR by ~18% on black spruce (from ~2.51 to ~2.96) and by ~29% on balsam fir (from ~1.75 to ~2.26). Thus, warming reduced consumption on white spruce while stimulating higher consumption on both black spruce and balsam fir, with the highest feeding rates occurring on black spruce under warm conditions.

Table 7. GLM output for RCR

<i>Parameter</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>z value</i>	<i>p-value</i>
<i>(Intercept)</i>	0.983	0.069	14.249	< 0.001***
<i>Species: EPN</i>	-0.063	0.099	-0.634	0.527
<i>Species: SAB</i>	-0.422	0.099	-4.267	< 0.001***
<i>Chamber: Warm (vs Amb.)</i>	-0.273	0.104	-2.613	0.009**
<i>EPN × Warm</i>	0.438	0.145	3.028	0.003**
<i>SAB × Warm</i>	0.527	0.144	3.662	< 0.001***

Notes. RCR units:  $mg \cdot mg^{-1} \cdot d^{-1}$ , Formula:  $RCR \sim \text{Species} * \text{Chamber}$ , family = Gamma (log link). Reference levels: Species = EPB; Chamber = Ambient. AIC = 1008.644; Dispersion  $\phi = 0.403$ . \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ .

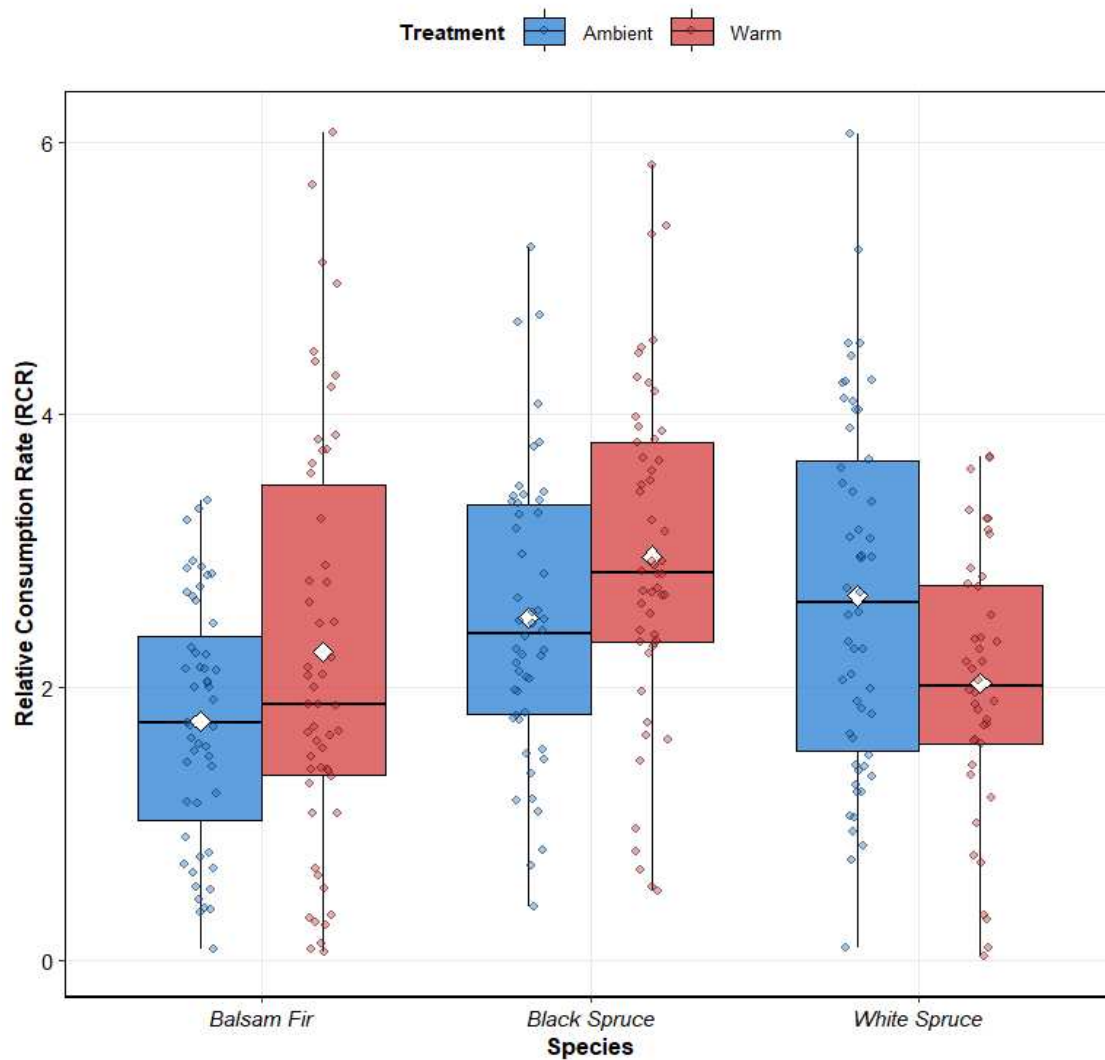


Figure 3. Relative Consumption Rate (RCR) ( $\text{mg} \cdot \text{mg}^{-1} \cdot \text{d}^{-1}$ )

### 3.1.3. Efficiency of Conversion of Ingested Food (ECI)

Efficiency of conversion of ingested food (ECI) also responded to warming in a host-dependent way (Table 8). Under ambient conditions, larvae on balsam fir had higher ECI than on white spruce, whereas black spruce was like white spruce. Warming slightly increased ECI on white spruce, had little effect on black spruce, and strongly reduced ECI on balsam fir. Marginal means showed that ECI on white spruce increased modestly under warming (from  $\sim 16.3$  to  $\sim 16.8$ ), remained essentially unchanged on black spruce ( $\sim 16.6$  to  $\sim 16.5$ ), and declined markedly

on balsam fir (from ~17.8 to ~16.3). Overall, warming improved ECI on white spruce, produced no gain on black spruce, and substantially reduced ECI on balsam fir, eroding balsam fir's advantage over the spruces.

Table 8. GLM output for ECI (%)

<i>Parameter</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>z value</i>	<i>p-value</i>
<i>(Intercept)</i>	-1.221	0.116	-10.548	< 0.001***
<i>Species: EPN</i>	0.217	0.165	1.317	0.188
<i>Species: SAB</i>	1.003	0.160	6.260	< 0.001***
<i>Chamber: Warm (vs Amb.)</i>	0.369	0.170	2.167	0.030*
<i>EPN × Warm</i>	-0.451	0.239	-1.886	0.059
<i>SAB × Warm</i>	-1.379	0.241	-5.722	< 0.001***

Notes. Formula:  $ECI \sim Species * Chamber$ , family = Beta (logit link). Reference levels: Species = EPB; Chamber = Ambient. AIC = -237.453; Pseudo- $R^2 = 0.154$ . \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ .

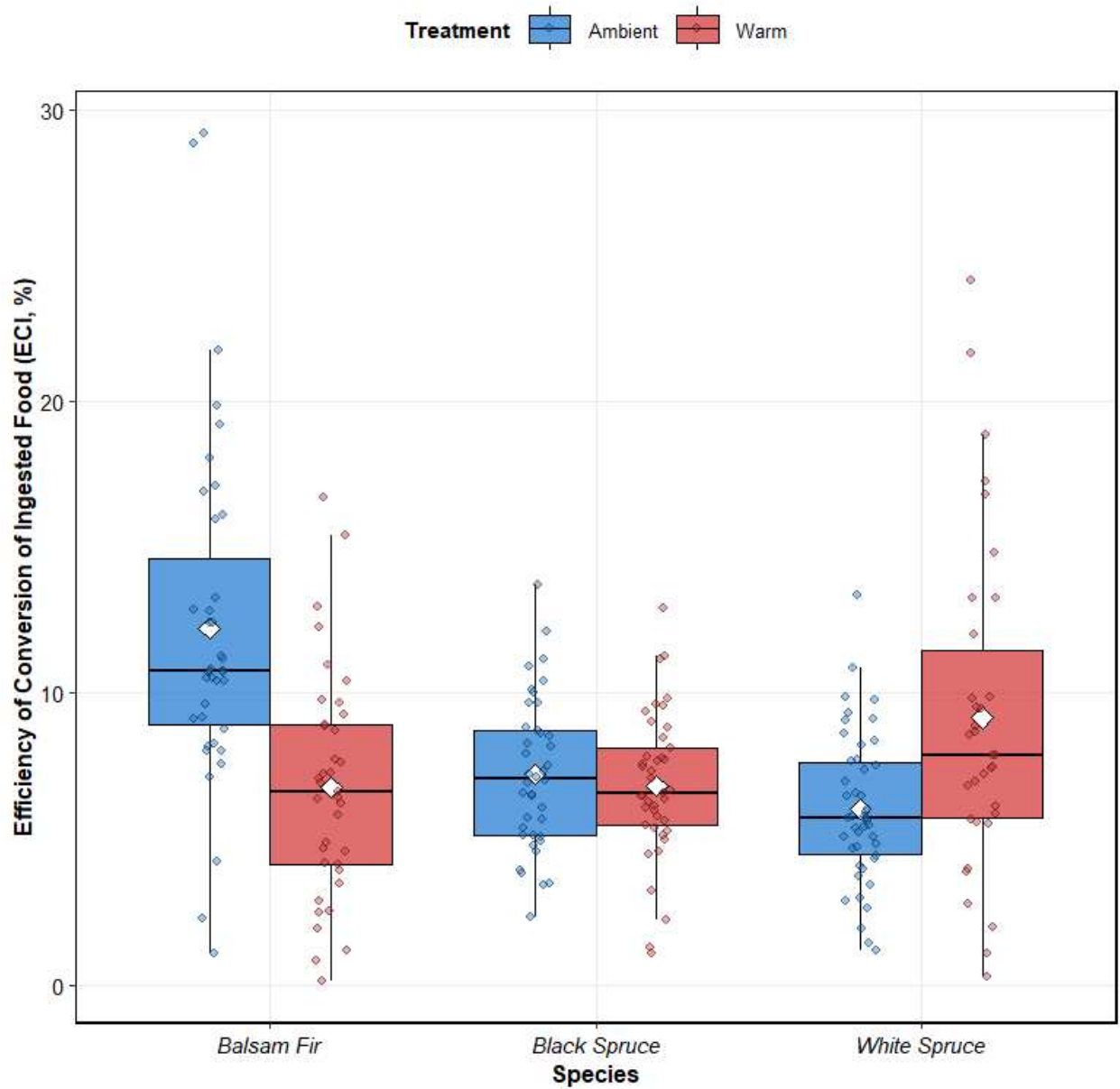


Figure 4. Efficiency of Conversion of Ingested Food (ECI) (%)

### 3.1.4. Approximate Digestibility (AD)

Approximate digestibility (AD) increased with warming across all hosts but with stronger effects on some species than others (Table 9). At ambient temperature, larvae on black spruce had higher AD than on white spruce, whereas balsam fir was like white spruce. Warming increased AD on all three hosts, with the largest gains on white spruce. Marginal means showed that AD increased

by about 4.2 units on white spruce (from ~50.7 to ~54.9), by ~1.8 units on black spruce (from ~53.1 to ~54.8), and by ~1.2 units on balsam fir (from ~51.8 to ~53.0). Thus, warming made foliage more digestible on all hosts, particularly on white spruce.

Table 9. GLM output for AD (%)

<i>Parameter</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>z value</i>	<i>p-value</i>
<i>(Intercept)</i>	-0.891	0.140	-6.377	< 0.001***
<i>Species: EPN</i>	0.486	0.192	2.533	0.011*
<i>Species: SAB</i>	0.236	0.204	1.159	0.246
<i>Chamber: Warm (vs Amb.)</i>	0.850	0.208	4.076	< 0.001***
<i>EPN × Warm</i>	-0.503	0.280	-1.800	0.072
<i>SAB × Warm</i>	-0.614	0.291	-2.110	0.035*

*Notes. Formula: AD ~ Species \* Chamber, family = Beta (logit link). Reference levels: Species = EPB; Chamber = Ambient. AIC = -74.878; Pseudo-R<sup>2</sup> = 0.089. \*p < 0.05, \*\*p < 0.01, \*\*\*p < 0.001.*

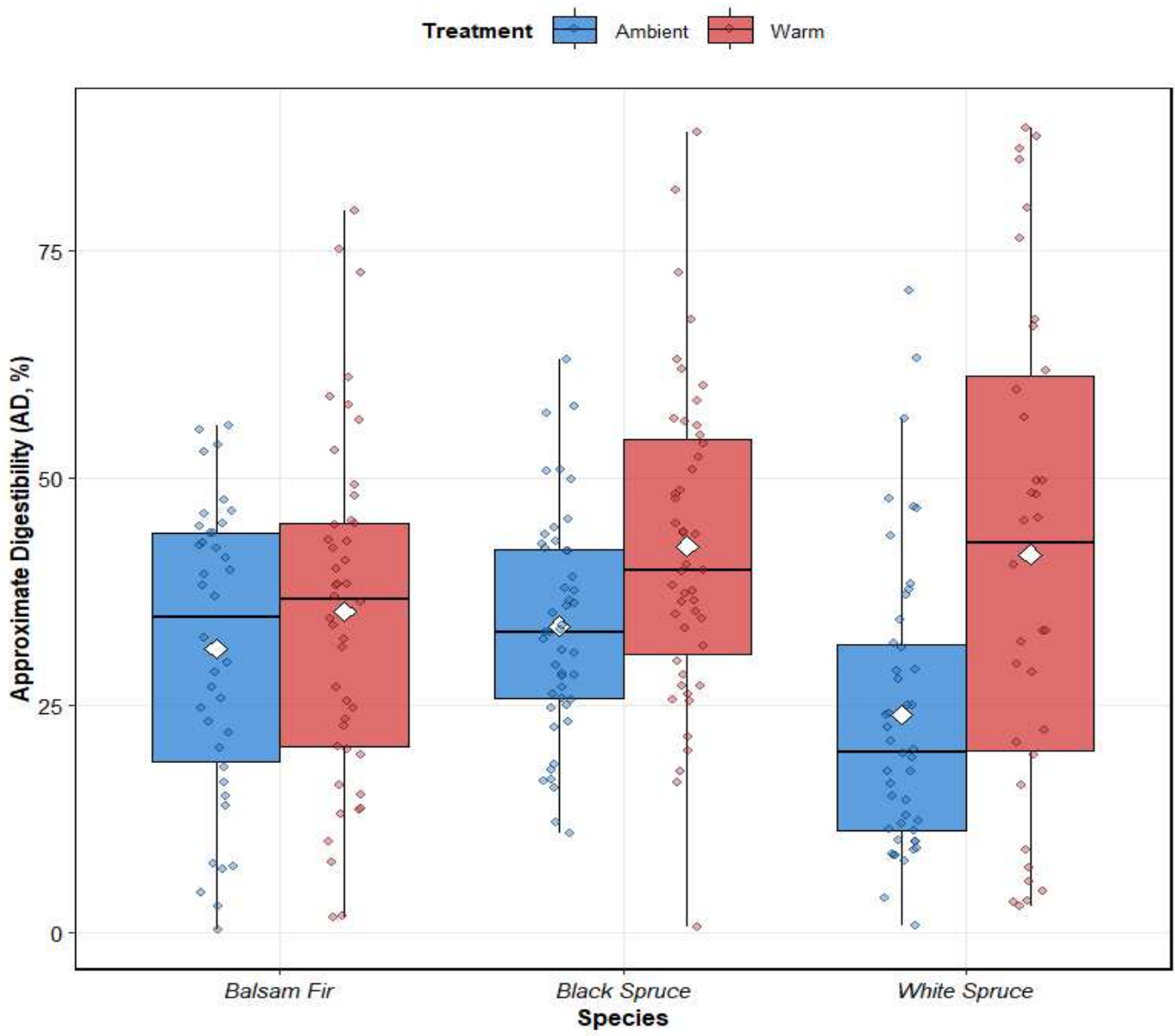


Figure 5. Approximate Digestibility (AD) (%)

### 3.1.5. Efficiency of Conversion of Digested Food (ECD)

Efficiency of conversion of digested food (ECD) tended to be higher on balsam fir under ambient conditions and declined with warming across all hosts (Table 10). Under ambient temperature, larvae on balsam fir showed slightly higher ECD than on white spruce, whereas black spruce was similar to white spruce. Warming reduced ECD on all three hosts, with no strong differences among species in the magnitude of decline. Marginal means showed that ECD fell from ~52.5 to ~49.5 on white spruce, from ~51.8 to ~50.3 on black spruce, and from ~54.5 to ~50.6 on balsam fir. Overall, warming reduced the efficiency with which digested food was converted into growth on all three hosts and removed the modest advantage of balsam fir observed under ambient conditions.

Table 10. GLM output for ECD (%)

<i>Parameter</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>z value</i>	<i>p-value</i>
<i>(Intercept)</i>	-0.673	0.138	-4.890	< 0.001***
<i>Species: EPN</i>	-0.148	0.195	-0.761	0.447
<i>Species: SAB</i>	0.400	0.208	1.923	0.055
<i>Chamber: Warm (vs Amb.)</i>	-0.694	0.255	-2.723	0.006**
<i>EPN × Warm</i>	0.362	0.325	1.114	0.265
<i>SAB × Warm</i>	-0.121	0.339	-0.357	0.721

Notes. Formula:  $ECD \sim \text{Species} * \text{Chamber}$ , family = Beta (logit link). Reference levels: Species = EPB; Chamber = Ambient. Pseudo-R<sup>2</sup> = 0.120; AIC = -130.138. \*p < 0.05, \*\*p < 0.01, \*\*\*p < 0.001.

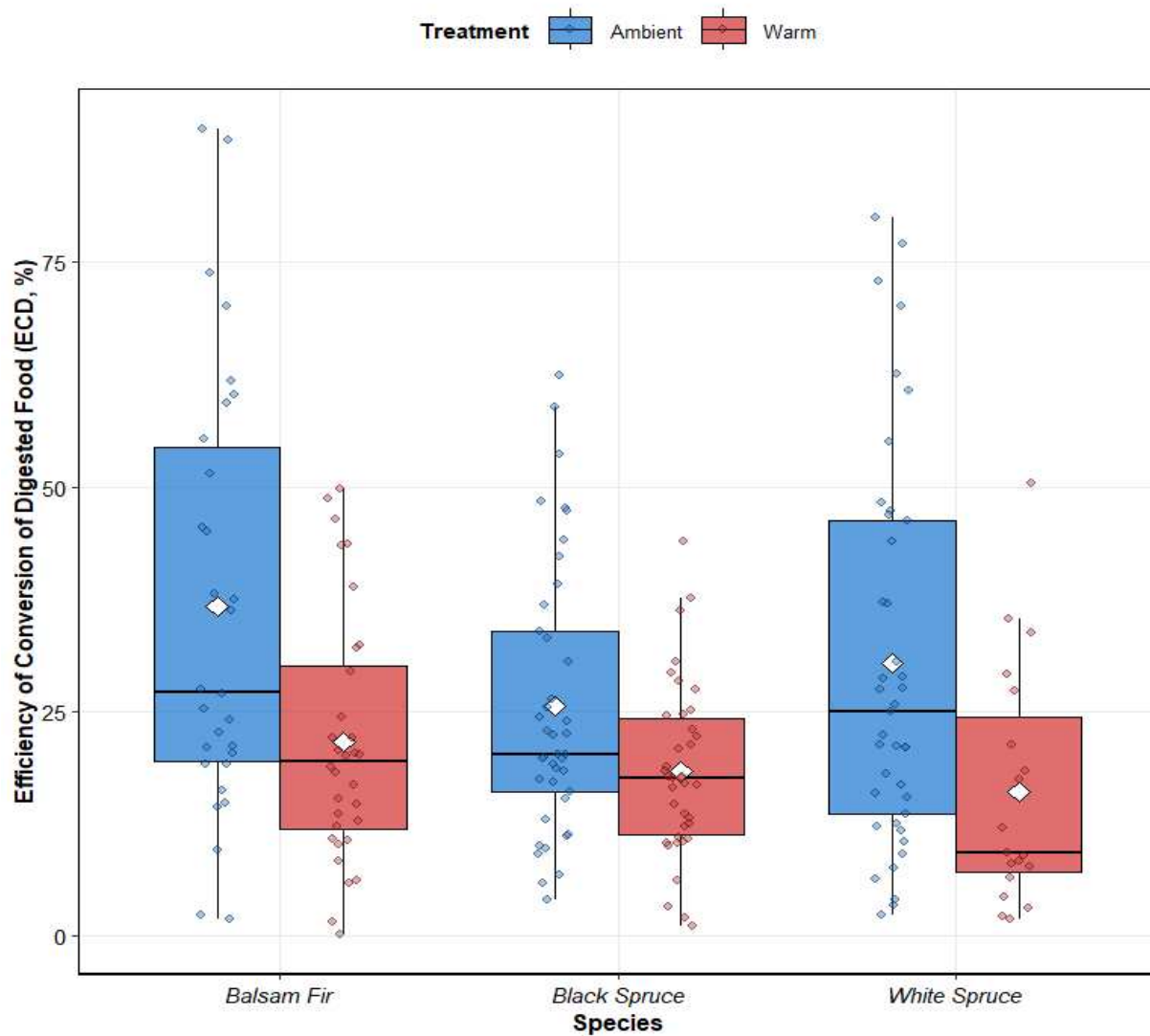


Figure 6. Efficiency of Conversion of Digested Food (ECD) (%)

## 4. Discussion

This experiment showed that a +3 °C warming does not affect spruce budworm performance in the same way on all hosts. Instead, warming changes where the main limitation is along the feeding pathway from intake, through digestion, to conversion into growth. Under ambient conditions, larvae grew fastest on balsam fir and more slowly on white and black spruce, which matches the classical view that balsam fir is a high-quality host, and the spruces are less favourable

(Bauce et al., 1994; Hudes & Shoemaker, 1984). Under warm conditions, this ranking reversed: RGR increased on both spruces but decreased on balsam fir.

The nutritional indices help explain why this reversal occurred. On white spruce, warming lowered Relative RCR but increased AD and the ECI, while RGR went up. Larvae therefore ate less foliage but took more from each unit eaten and converted more of that assimilated material into biomass. This is an “efficiency” response: higher temperature appears to improve digestive and post-digestive processes enough that growth rises even when intake falls (Lazarević et al., 2023). In energetic terms, metabolic costs did not rise so much that they cancelled out the gains in digestion and conversion.

On black spruce, warming also increased RGR, but through a different combination of indices. RCR increased, AD changed only slightly, and ECI remained roughly stable. Here, larvae compensated for higher thermal demand mainly by eating more rather than by becoming markedly more efficient. This fits the idea of compensatory feeding, where herbivores respond to challenging diets or higher costs by increasing throughput (Waldbauer, 1968). Black spruce has stronger chemical defences than the other hosts (Ullah et al., 2024), so a rate-based response is plausible: larvae cope with a difficult host under warm conditions by increasing intake just enough, along with a small gain in AD, to raise growth.

Balsam fir showed the opposite pattern. Warming increased RCR and slightly increased AD, but both ECI and the ECD decreased, and RGR declined. Larvae therefore ate more and digested somewhat more but converted a smaller share of that digested food into body mass. This suggests that post-digestive processes became limiting: more of the assimilated energy was spent on maintenance, activity, or heat-related respiration rather than growth (Gillooly et al., 2001). Across all three hosts, ECD declined with warming, consistent with an overall increase in respiration costs, but balsam fir was the host where this decline was least offset by changes in intake and digestibility. As a result, the host that looked best at ambient temperature lost its advantage under warming.

Taken together, these patterns show that the effect of warming on growth depends on how three things interact: how much larvae eat (RCR), how much they digest (AD), and how efficiently they turn digested food into tissue (ECI and ECD). On white spruce, higher efficiency overcame lower intake; on black spruce, higher intake compensated for only modest efficiency gains; on balsam fir, a drop in conversion efficiency outweighed higher intake and digestibility. This explains why RGR moved in different directions on the three hosts even though the same +3 °C warming treatment was applied.

Comparative studies show that temperature drives complex shifts in feeding and growth indices. For instance, *Manduca sexta* larvae significantly increase Relative Consumption Rate (RCR) with rising temperatures to fuel metabolic demands, although Relative Growth Rate declines as escalating respiration costs outweigh intake gains (Kingsolver & Woods, 1997). Similarly, research on *Spodoptera exigua* demonstrates that while warmer conditions accelerate feeding, they often reduce conversion efficiency, specifically lipid storage, due to these energetic trade-offs (Lee & Roh, 2010). This study also shows that warming alters the balance between intake and conversion rather than uniformly enhancing performance, suggesting that physiological constraints determine the limitations of growth.

These contrasting responses suggest that the position of larvae relative to their thermal optimum differs by host species. While the improved performance on spruce indicates that ambient temperatures were sub-optimal and warming moved larvae closer to their peak efficiency, the decline on balsam fir implies that the warm treatment likely exceeded the thermal optimum. This demonstrates that improved fitness at higher temperatures depends on whether the thermal shift maintains the insect within its optimal metabolic range or pushes it into physiological stress.

These results also complement earlier work on spruce budworm and climate. Many studies focus on temperature effects on development rates and on phenological synchrony between larvae and host trees (Régnière et al., 2012; Pureswaran et al., 2015). In this experiment, larvae were introduced when buds of each species had reached the same phenological stage, so differences between ambient and warm treatments mainly reflect physiological responses, not timing. The results therefore show that even once larvae are feeding on suitable foliage, warming can still shift

which host supports better growth by changing how food is used inside the insect. This adds a physiological layer to phenology-based projections of future outbreak risk.

Finally, the index-based approach used here helps link individual-level physiology to larger-scale patterns. Small changes in the indices can matter for growth and fecundity in spruce budworm. By explicitly breaking RGR into intake, digestion, and conversion, this study provides parameters and mechanisms that can be used to refine process-based models of spruce budworm under climate change (Régnière et al., 2012; Pureswaran et al., 2015).

## 4.1. Limitations

The experimental design included only two temperature levels, which limits our ability to determine the precise thermal optimum or identify the point at which digestion and conversion begin to decline. Because the indices used combine multiple physiological processes, they reflect overall performance shifts rather than isolating the mechanisms underlying those changes. Consequently, the findings apply specifically to the temperature range tested. It is also important to note that the outlier-removal technique employed was chosen as the most appropriate method for excluding extreme values caused by measurement errors. These outliers were few and atypical.

## 4.2. Practical and Experimental Implications

These results have both practical and experimental implications. Under warm temperatures, spruce budworm growth increases on black spruce come mainly from increased intake rather than better conversion. Balsam fir, by contrast, shows a conversion deficit that more food does not fix. Controlled feeding experiments can separate efficiency-driven growth (white-spruce-like) from increased-intake responses (black-spruce-like), while focused experiments can address conversion failures (balsam-fir-like). Ecologically, these results highlight that temperature alone cannot predict outbreak potential: host identity and phenological synchrony determine whether warming enhances or suppresses budworm success, meaning that forest vulnerability will depend on local host composition and timing rather than uniform warming effects. In practical terms, this framework can

help forest managers anticipate which tree species may become more susceptible under climate change and design host-specific monitoring programs. Integrating these physiological indices into regional outbreak models could improve risk predictions and support early warning systems across mixed fir–spruce forests.

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## 6. Appendix

### Appendix A. Temperature Programming of the Ambient and Warm Chamber Over the Course of Experiment

The warm chamber's temperature program was derived directly from the ambient schedule. Minimum and maximum temperatures, along with sunrise and sunset times (as described in the main text), were obtained from the Government of Canada dataset. We entered the weekly average minimum and maximum temperatures, and all intermediate time points were then calculated by preserving the same relative differences used in the ambient program. For example, if the ambient temperature at midnight was 10 °C and the increase from midnight to sunrise was 7.5 °C, this difference was applied consistently across all weeks. The same method was used for all other time-of-day transitions. For checking the full schedule, please check the link in Appendix J.

	Variable	Value
To modify	Min	10
	Max	25
	Sunrise	4:45:00 AM
	Sunset	8:47:00 PM
Auto generated	Noon (Hour)	12:00:00 PM
	Midnight (Hour)	12:00:00 AM
	Half-interval between noon and sunrise (Hour)	3:37:30 AM
	Half-interval between noon and sunset (Hour)	4:23:30 AM
	Temperature range sunrise–sunset	7.5
	Half of the temperature range sunrise–sunset	3.75

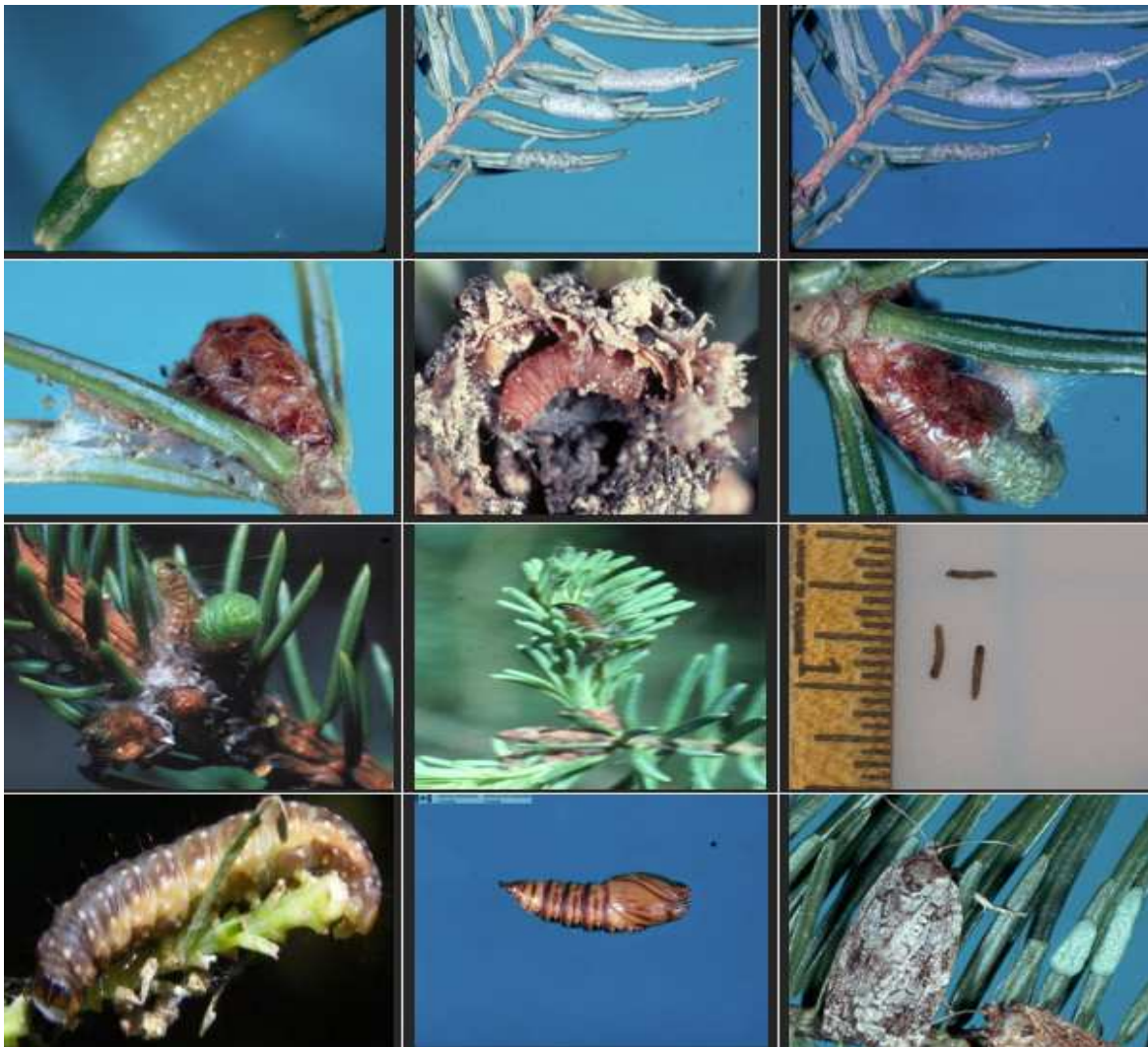
Program for Ambient Chamber					
Row	Hour	Temperature (°C)	Humidity (%)	Florescent	Globe
1	4:45:00 AM	17.5	50	1	1
2	8:22:30 AM	21.3	50	2	2
3	12:00:00 PM	25	50	4	4
4	4:23:30 PM	21.3	50	2	2
5	8:47:00 PM	17.5	50	0	0
6	12:00:00 AM	10	50	0	0
Program for Warm Chamber					
Row	Hour	Temperature (°C)	Humidity (%)	Florescent	Globe
1	4:45:00 AM	20.5	50	1	1
2	8:22:30 AM	24.3	50	2	2
3	12:00:00 PM	28	50	4	4
4	4:23:30 PM	24.3	50	2	2
5	8:47:00 PM	20.5	50	0	0
6	12:00:00 AM	13	50	0	0

## Appendix B. Structure of the Growth Chambers

This figure shows the layout of the growth chambers and the arrangement of the three tree species. The designated phenology rows indicate the rows where bud development stages were monitored and recorded.

Ambient Temperatur																					
TN-SAB-11	TN-SAB-12	TN-SAB-13	TN-SAB-14	TN-SAB-15	TN-SAB-16	TN-SAB-17	TN-EPB-164	TN-EPB-165	TN-EPB-166	TN-EPB-167	TN-EPB-168	TN-EPB-169	TN-EPB-170	TN-EPN-1-027	TN-EPN-1-028	TN-EPN-1-029	TN-EPN-1-030	TN-EPN-1-031	TN-EPN-1-032	TN-EPN-1-033	
TN-SAB-2-8	TN-SAB-2-9	TN-SAB-2-10	TN-SAB-2-11	TN-SAB-2-12	TN-SAB-2-13	TN-SAB-2-14	TN-EPB-2-71	TN-EPB-2-72	TN-EPB-2-73	TN-EPB-2-74	TN-EPB-2-75	TN-EPB-2-76	TN-EPB-2-77	TN-EPN-2-047	TN-EPN-2-048	TN-EPN-2-049	TN-EPN-2-050	TN-EPN-2-051	TN-EPN-2-052	TN-EPN-2-053	Phenology row
TN-SAB-3-5	TN-SAB-3-6	TN-SAB-3-7	TN-SAB-3-8	TN-SAB-3-9	TN-SAB-3-10	TN-SAB-3-11	TN-EPB-3-78	TN-EPB-3-79	TN-EPB-3-80	TN-EPB-3-81	TN-EPB-3-82	TN-EPB-3-83	TN-EPB-3-84	TN-EPN-3-147	TN-EPN-3-148	TN-EPN-3-149	TN-EPN-3-150	TN-EPN-3-151	TN-EPN-3-152	TN-EPN-3-153	
TN-SAB-4-22	TN-SAB-4-23	TN-SAB-4-24	TN-SAB-4-25	TN-SAB-4-26	TN-SAB-4-27	TN-SAB-4-28	TN-EPB-4-85	TN-EPB-4-86	TN-EPB-4-87	TN-EPB-4-88	TN-EPB-4-89	TN-EPB-4-90	TN-EPB-4-91	TN-EPN-4-147	TN-EPN-4-148	TN-EPN-4-149	TN-EPN-4-150	TN-EPN-4-151	TN-EPN-4-152	TN-EPN-4-153	Phenology row
TN-SAB-5-29	TN-SAB-5-30	TN-SAB-5-31	TN-SAB-5-32	TN-SAB-5-33	TN-SAB-5-34	TN-SAB-5-35	TN-EPB-5-92	TN-EPB-5-93	TN-EPB-5-94	TN-EPB-5-95	TN-EPB-5-96	TN-EPB-5-97	TN-EPB-5-98	TN-EPN-5-157	TN-EPN-5-158	TN-EPN-5-159	TN-EPN-5-160	TN-EPN-5-161	TN-EPN-5-162	TN-EPN-5-163	Phenology row
TN-SAB-6-36	TN-SAB-6-37	TN-SAB-6-38	TN-SAB-6-39	TN-SAB-6-40	TN-SAB-6-41	TN-SAB-6-42	TN-EPB-6-99	TN-EPB-6-100	TN-EPB-6-101	TN-EPB-6-102	TN-EPB-6-103	TN-EPB-6-104	TN-EPB-6-105	TN-EPN-6-167	TN-EPN-6-168	TN-EPN-6-169	TN-EPN-6-170	TN-EPN-6-171	TN-EPN-6-172	TN-EPN-6-173	
TN-SAB-7-43	TN-SAB-7-44	TN-SAB-7-45	TN-SAB-7-46	TN-SAB-7-47	TN-SAB-7-48	TN-SAB-7-49	TN-EPB-7-106	TN-EPB-7-107	TN-EPB-7-108	TN-EPB-7-109	TN-EPB-7-110	TN-EPB-7-111	TN-EPB-7-112	TN-EPN-7-167	TN-EPN-7-168	TN-EPN-7-169	TN-EPN-7-170	TN-EPN-7-171	TN-EPN-7-172	TN-EPN-7-173	Phenology row
TN-SAB-8-50	TN-SAB-8-51	TN-SAB-8-52	TN-SAB-8-53	TN-SAB-8-54	TN-SAB-8-55	TN-SAB-8-56	TN-EPB-8-113	TN-EPB-8-114	TN-EPB-8-115	TN-EPB-8-116	TN-EPB-8-117	TN-EPB-8-118	TN-EPB-8-119	TN-EPN-8-177	TN-EPN-8-178	TN-EPN-8-179	TN-EPN-8-180	TN-EPN-8-181	TN-EPN-8-182	TN-EPN-8-183	Phenology row
TN-SAB-9-57	TN-SAB-9-58	TN-SAB-9-59	TN-SAB-9-60	TN-SAB-9-61	TN-SAB-9-62	TN-SAB-9-63	TN-EPB-9-120	TN-EPB-9-121	TN-EPB-9-122	TN-EPB-9-123	TN-EPB-9-124	TN-EPB-9-125	TN-EPB-9-126	TN-EPN-9-187	TN-EPN-9-188	TN-EPN-9-189	TN-EPN-9-190	TN-EPN-9-191	TN-EPN-9-192	TN-EPN-9-193	
Warmer Temperature (+3 °C)																					
TE-SAB-1-00	TE-SAB-1-01	TE-SAB-1-02	TE-SAB-1-03	TE-SAB-1-04	TE-SAB-1-05	TE-SAB-1-06	TE-EPB-1-253	TE-EPB-1-254	TE-EPB-1-255	TE-EPB-1-256	TE-EPB-1-257	TE-EPB-1-258	TE-EPB-1-259	TE-EPN-1-316	TE-EPN-1-317	TE-EPN-1-318	TE-EPN-1-319	TE-EPN-1-320	TE-EPN-1-321	TE-EPN-1-322	
TE-SAB-2-07	TE-SAB-2-08	TE-SAB-2-09	TE-SAB-2-10	TE-SAB-2-11	TE-SAB-2-12	TE-SAB-2-13	TE-EPB-2-260	TE-EPB-2-261	TE-EPB-2-262	TE-EPB-2-263	TE-EPB-2-264	TE-EPB-2-265	TE-EPB-2-266	TE-EPN-2-323	TE-EPN-2-324	TE-EPN-2-325	TE-EPN-2-326	TE-EPN-2-327	TE-EPN-2-328	TE-EPN-2-329	Phenology row
TE-SAB-3-20	TE-SAB-3-21	TE-SAB-3-22	TE-SAB-3-23	TE-SAB-3-24	TE-SAB-3-25	TE-SAB-3-26	TE-EPB-3-267	TE-EPB-3-268	TE-EPB-3-269	TE-EPB-3-270	TE-EPB-3-271	TE-EPB-3-272	TE-EPB-3-273	TE-EPN-3-330	TE-EPN-3-331	TE-EPN-3-332	TE-EPN-3-333	TE-EPN-3-334	TE-EPN-3-335	TE-EPN-3-336	
TE-SAB-4-21	TE-SAB-4-22	TE-SAB-4-23	TE-SAB-4-24	TE-SAB-4-25	TE-SAB-4-26	TE-SAB-4-27	TE-EPB-4-274	TE-EPB-4-275	TE-EPB-4-276	TE-EPB-4-277	TE-EPB-4-278	TE-EPB-4-279	TE-EPB-4-280	TE-EPN-4-337	TE-EPN-4-338	TE-EPN-4-339	TE-EPN-4-340	TE-EPN-4-341	TE-EPN-4-342	TE-EPN-4-343	Phenology row
TE-SAB-5-28	TE-SAB-5-29	TE-SAB-5-30	TE-SAB-5-31	TE-SAB-5-32	TE-SAB-5-33	TE-SAB-5-34	TE-EPB-5-281	TE-EPB-5-282	TE-EPB-5-283	TE-EPB-5-284	TE-EPB-5-285	TE-EPB-5-286	TE-EPB-5-287	TE-EPN-5-344	TE-EPN-5-345	TE-EPN-5-346	TE-EPN-5-347	TE-EPN-5-348	TE-EPN-5-349	TE-EPN-5-350	Phenology row
TE-SAB-6-22	TE-SAB-6-23	TE-SAB-6-24	TE-SAB-6-25	TE-SAB-6-26	TE-SAB-6-27	TE-SAB-6-28	TE-EPB-6-288	TE-EPB-6-289	TE-EPB-6-290	TE-EPB-6-291	TE-EPB-6-292	TE-EPB-6-293	TE-EPB-6-294	TE-EPN-6-351	TE-EPN-6-352	TE-EPN-6-353	TE-EPN-6-354	TE-EPN-6-355	TE-EPN-6-356	TE-EPN-6-357	
TE-SAB-7-23	TE-SAB-7-24	TE-SAB-7-25	TE-SAB-7-26	TE-SAB-7-27	TE-SAB-7-28	TE-SAB-7-29	TE-EPB-7-295	TE-EPB-7-296	TE-EPB-7-297	TE-EPB-7-298	TE-EPB-7-299	TE-EPB-7-300	TE-EPB-7-301	TE-EPN-7-358	TE-EPN-7-359	TE-EPN-7-360	TE-EPN-7-361	TE-EPN-7-362	TE-EPN-7-363	TE-EPN-7-364	Phenology row
TE-SAB-8-23	TE-SAB-8-24	TE-SAB-8-25	TE-SAB-8-26	TE-SAB-8-27	TE-SAB-8-28	TE-SAB-8-29	TE-EPB-8-302	TE-EPB-8-303	TE-EPB-8-304	TE-EPB-8-305	TE-EPB-8-306	TE-EPB-8-307	TE-EPB-8-308	TE-EPN-8-365	TE-EPN-8-366	TE-EPN-8-367	TE-EPN-8-368	TE-EPN-8-369	TE-EPN-8-370	TE-EPN-8-371	Phenology row
TE-SAB-9-24	TE-SAB-9-25	TE-SAB-9-26	TE-SAB-9-27	TE-SAB-9-28	TE-SAB-9-29	TE-SAB-9-30	TE-EPB-9-309	TE-EPB-9-310	TE-EPB-9-311	TE-EPB-9-312	TE-EPB-9-313	TE-EPB-9-314	TE-EPB-9-315	TE-EPN-9-372	TE-EPN-9-373	TE-EPN-9-374	TE-EPN-9-375	TE-EPN-9-376	TE-EPN-9-377	TE-EPN-9-378	

## Appendix C. Life stages of *Choristoneura fumiferana*



Life stages of *Choristoneura fumiferana* (Eastern spruce budworm)

1- *Choristoneura fumiferana* egg mass

2,3- Blackheaded *Choristoneura fumiferana* eggs and hatching 1st instar larvae

4- 2nd instar *Choristoneura fumiferana* mining needle

5-2nd Instar *Choristoneura fumiferana* overwintering in old flower bract

6-3rd instar *Choristoneura fumiferana* developing shoot

7-Moulting 3rd instar *Choristoneura fumiferana*

8-4th Instar *Choristoneura fumiferana* on expanding balsam fir shoot

9-5th Instar *Choristoneura fumiferana*










10-*Choristoneura fumiferana* on eaten Balsam Fir shoot



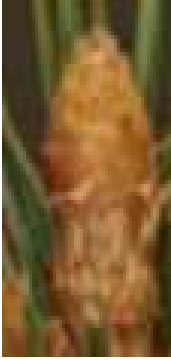








11-*Choristoneura fumiferana* female pupa

12-*Choristoneura fumiferana* adults and egg masses

Source: Natural Resources Canada, n.d

Appendix D. Bud Development Stages in Black Spruce (*Picea mariana*), Balsam Fir (*Abies balsamea*), and White Spruce (*Picea glauca*)

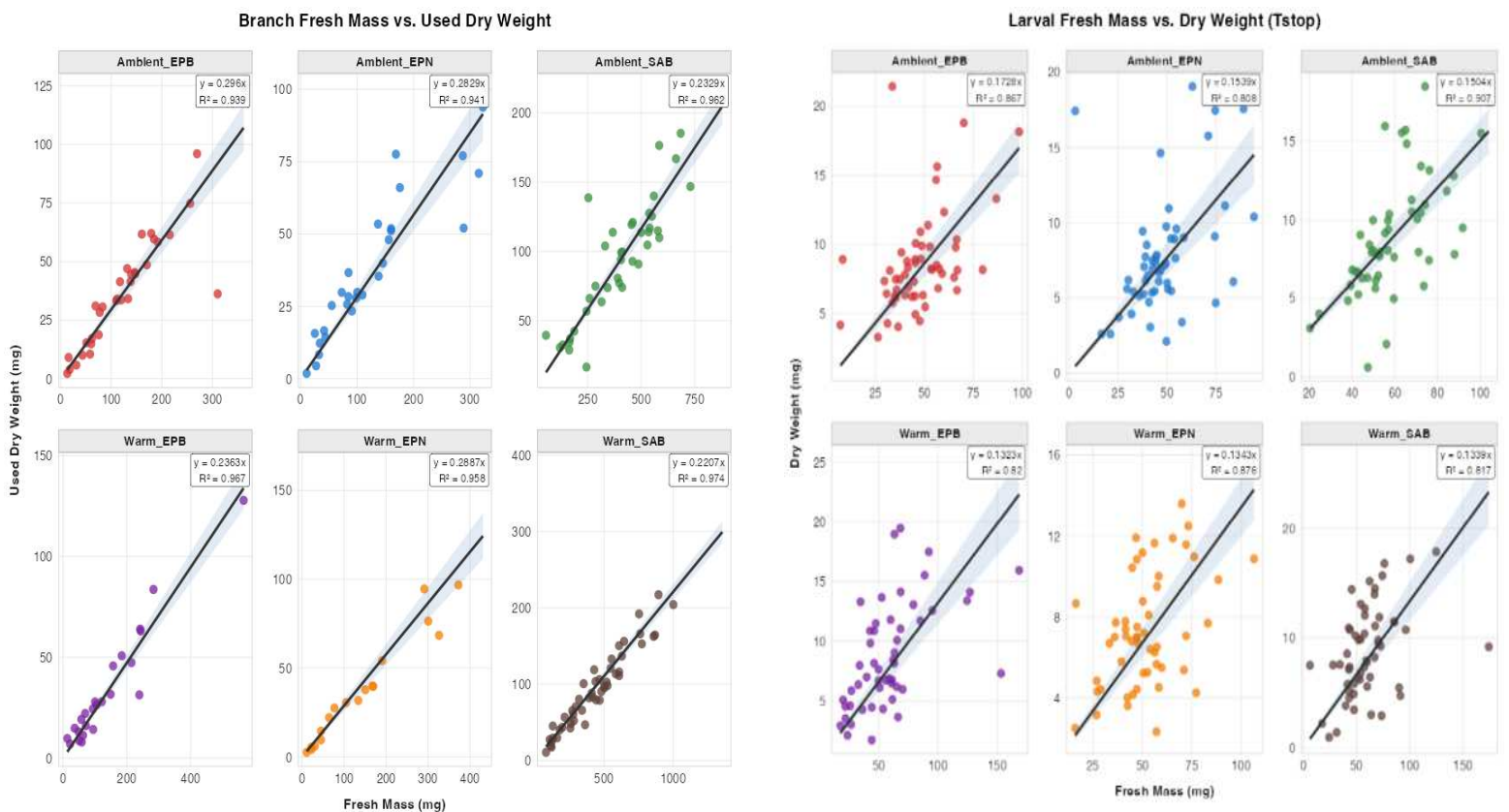
Stage	Description	Black spruce	Balsam fir	White spruce
0	Bud closed and dormant.			
1	Bud scales swelling; tips loosen slightly.			
2	Bud elongating: scales start to separate.			

3	Scales translucent; inner green tissue visible.			
4	Scales rupture; needles tightly packed.			
5	Needles elongate, still bunched.			
6	Needles fully expanded and spreading.			

Development stages of the spring bud phenology of Black spruce ((Numainville & Desponts, 2004) , Balsam fir(McCarthy, P.C, 2013) , and White spruce(Dhont, 2010).

## Appendix E. Scatter plots for larvae Final Fresh: Dry mass and Branch Fresh Mass: Dry mass

In the following scatter plots, Branch Fresh Mass refers to the final fresh mass of branches measured at the end of the 72-hour trial, and Used Dry Weight represents the final dry mass of those branches after drying. In the second scatter plot, Tstop denotes the time point at which the 72-hour trial ended. In addition, the fresh mass on the X-axis corresponds to the larval fresh weights measured at the end of the 72-hour bioassay-tube phase.



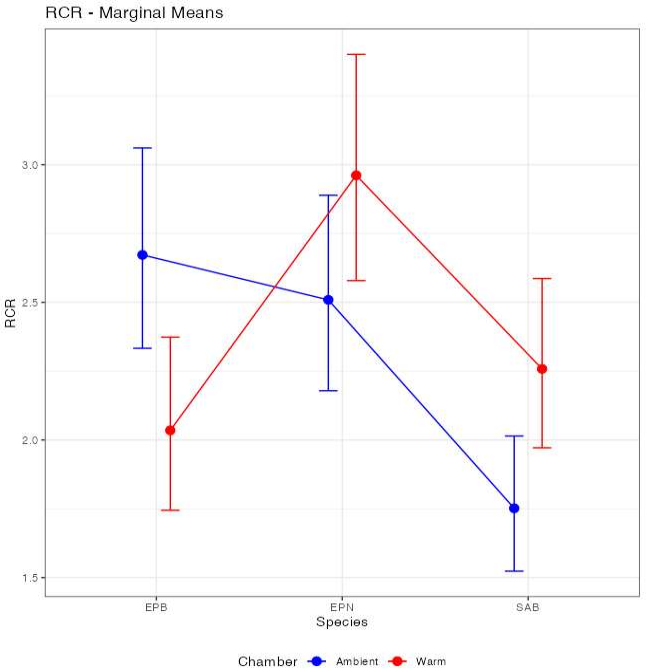
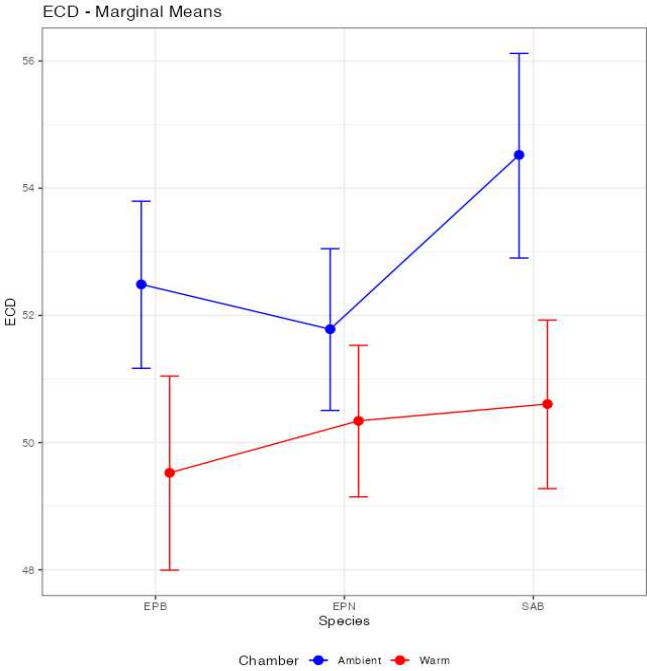
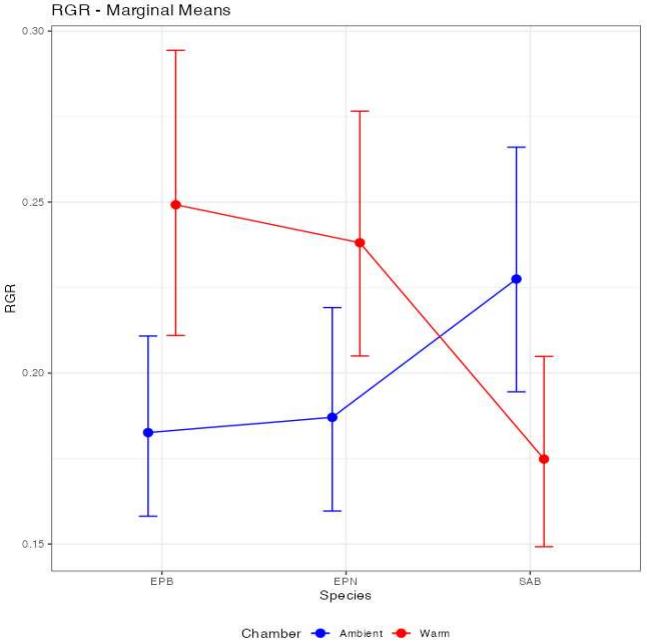
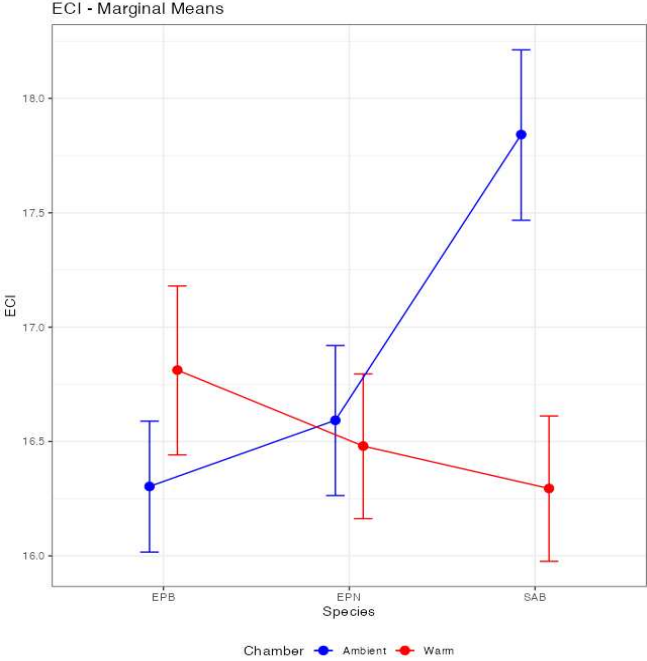
## Appendix F. Dataset Structure Overview

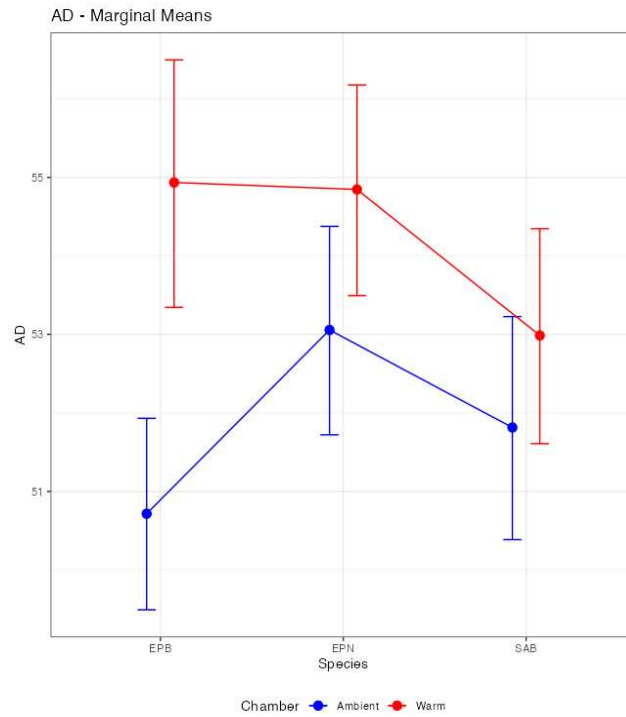
This appendix presents screenshots illustrating the structure and organization of the dataset used in the analysis.

Chamber	Species	ID	Year	DOY	ID_Tree_Larv	ID_Tree_Shoc
Ambient	SAB		1	2024	162	6
Ambient	SAB		2	2024	165	58
Ambient	SAB		4	2024	163	59
Ambient	SAB		9	2024	164	23
Ambient	SAB		14	2024	164	18
Ambient	SAB		17	2024	164	9
Ambient	SAB		21	2024	166	43
Ambient	SAB		22	2024	164	10
Ambient	SAB		24	2024	166	12

Quantity_Ana	Analyse_Bran	T0_Larva_Ma	T0_Larva_Init	Quantity_T0	T0_Bran	T0_DOY
1	281.7	24.9	3.64785	1	665.3	162
1	939.21	50.05	7.332325	1	780.05	165
1	515.21	22.26	3.26109	1	503.1	163
1	547	50.84	7.44806	1	454.8	164
1	576.96	8.9	1.30385	1	591.36	164
1	567.62	23.61	3.458865	1	577.93	164
1	449.87	23.95	3.508675	1	551.79	166
1	518.75	27.41	4.015565	1	697.32	164
1	630.75	37.35	5.471775	1	593.36	166

# Appendix G. The marginal effects for each temperature, species interaction





Note: RGR and RCR are expressed in  $\text{mg} \cdot \text{mg}^{-1} \cdot \text{d}^{-1}$ , and AD, ECI, and ECD are expressed as percentages (%).

## Appendix H. Marginal means + 95% Cs

a) Estimated marginal means and 95% confidence intervals for Relative Growth Rate (RGR) ( $\text{mg} \cdot \text{mg}^{-1} \cdot \text{d}^{-1}$ ).

Species	Chamber	Mean	Lower 95% CI	Upper 95% CI
EPB	Ambient	0.1826	0.1581	0.2108
EPN	Ambient	0.1870	0.1596	0.2192
SAB	Ambient	0.2275	0.1945	0.2661
EPB	Warm	0.2492	0.2110	0.2944
EPN	Warm	0.2381	0.2050	0.2766
SAB	Warm	0.1748	0.1492	0.2059

b) Estimated marginal means and 95% confidence intervals for Relative Consumption Rate (RGR) ( $\text{mg} \cdot \text{mg}^{-1} \cdot \text{d}^{-1}$ ).

Species	Chamber	Mean	Lower 95% CI	Upper 95% CI
EPB	Ambient	2.6723	2.3331	3.0609
EPN	Ambient	2.5090	2.1788	2.8892
SAB	Ambient	1.7516	1.5233	2.0143
EPB	Warm	2.0348	1.7445	2.3734
EPN	Warm	2.9614	2.5788	3.4008
SAB	Warm	2.2581	1.9714	2.5864

c) Estimated marginal means and 95% confidence intervals for Approximate Digestibility (AD) (%).

<b>Species</b>	<b>Chamber</b>	<b>Mean</b>	<b>Lower 95% CI</b>	<b>Upper 95% CI</b>
EPB	Ambient	16.30	16.02	16.59
EPN	Ambient	16.59	16.26	16.92
SAB	Ambient	17.84	17.47	18.21
EPB	Warm	16.81	16.44	17.18
EPN	Warm	16.48	16.16	16.80
SAB	Warm	16.29	15.98	16.61

d) Estimated marginal means and 95% confidence intervals for Efficiency of Conversion of Ingested food (ECI) (%).

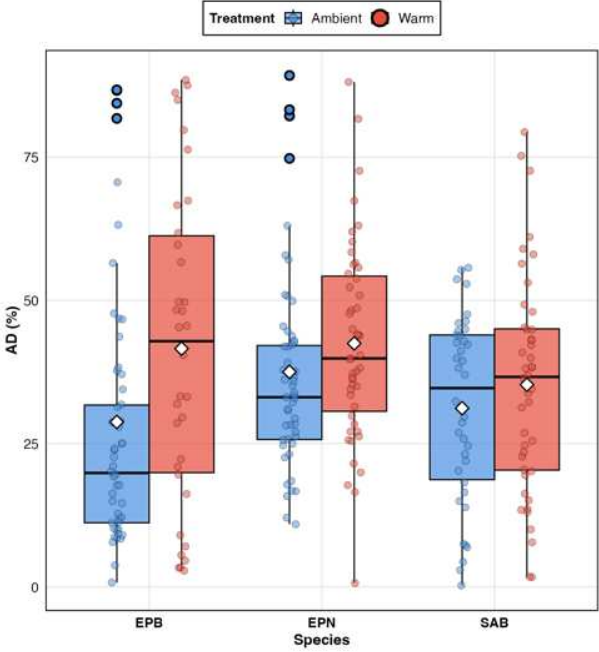
<b>Species</b>	<b>Chamber</b>	<b>Mean</b>	<b>Lower 95% CI</b>	<b>Upper 95% CI</b>
EPB	Ambient	50.72	49.49	51.93
EPN	Ambient	53.06	51.72	54.38
SAB	Ambient	51.81	50.39	53.23
EPB	Warm	54.94	53.34	56.50
EPN	Warm	54.85	53.49	56.18
SAB	Warm	52.99	51.61	54.35

e) Estimated marginal means and 95% confidence intervals for Efficiency of Conversion of Digested food (ECD) (%).

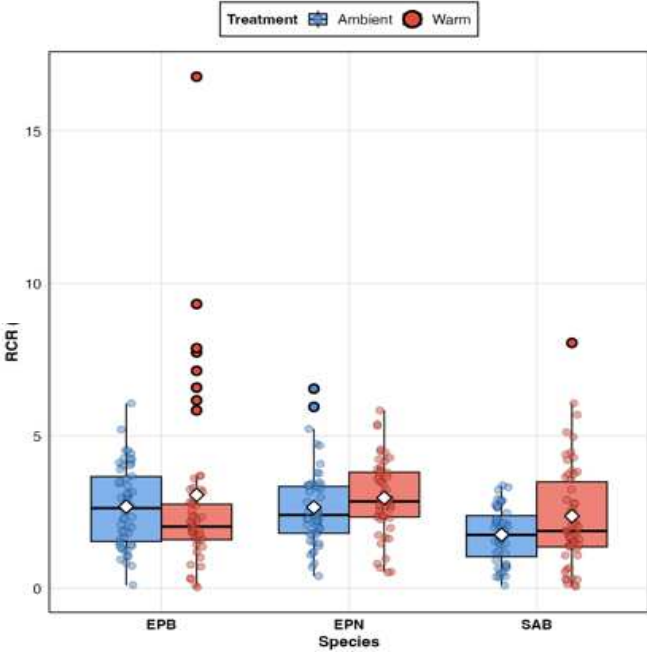
<b>Species</b>	<b>Chamber</b>	<b>Mean</b>	<b>Lower 95% CI</b>	<b>Upper 95% CI</b>
EPB	Ambient	52.49	51.17	53.79
EPN	Ambient	51.78	50.51	53.05
SAB	Ambient	54.52	52.90	56.12
EPB	Warm	49.53	47.99	51.05
EPN	Warm	50.34	49.15	51.53
SAB	Warm	50.61	49.28	51.93

# Appendix I. Indices with outliers highlighted

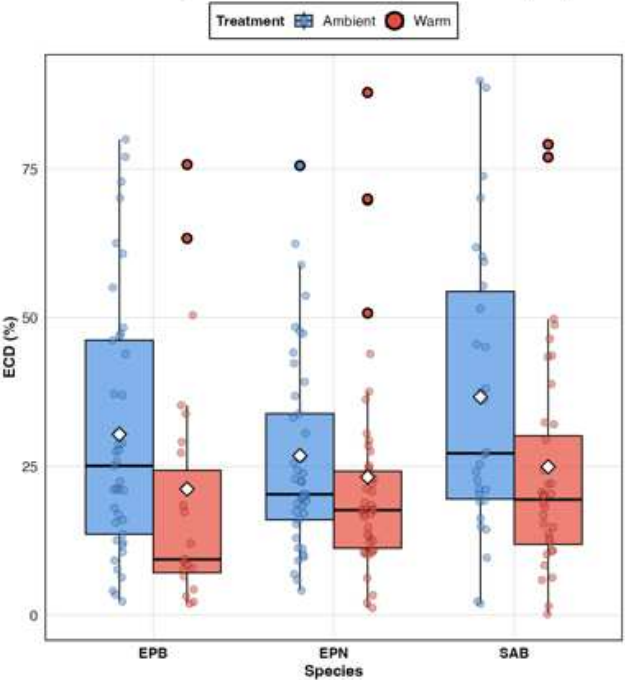
Approximate Digestibility (AD)



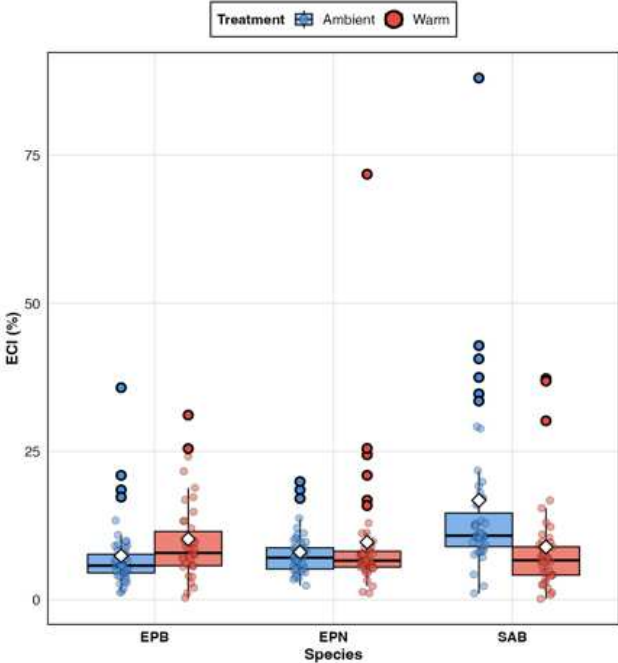
Relative Consumption Rate (RCR)

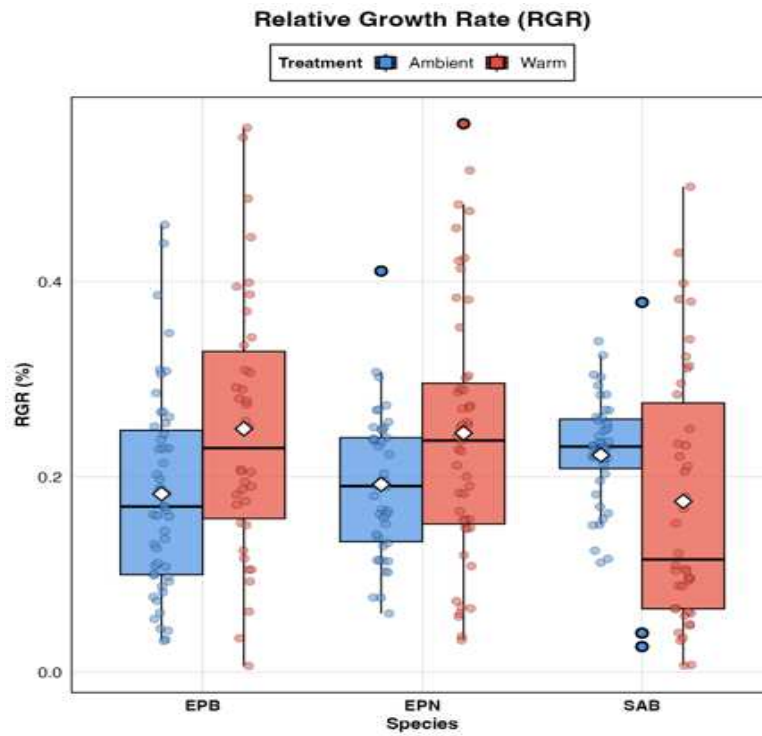


Efficiency of Conversion of Digested Food (ECD)



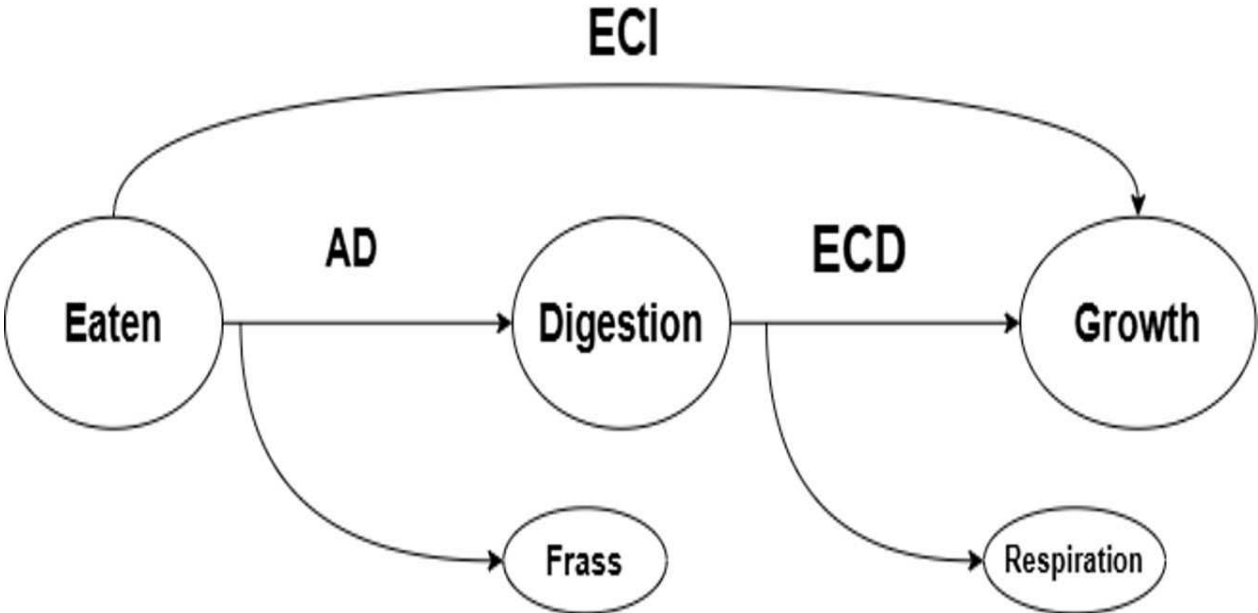
Efficiency of Conversion of Ingested Food (ECI)





Note: RGR and RCR are expressed in  $\text{mg} \cdot \text{mg}^{-1} \cdot \text{d}^{-1}$ , and AD, ECI, and ECD are expressed as percentages (%).

# Appendix J. Interrelationships Among Nutritional Indices



*Courtesy of Dr. Emma Despland*

# Appendix K. Link to the Dataset and Code

The dataset, experimental photos, and analysis code are openly accessible through the following link.

[https://github.com/ErfanBari/SBW\\_Experiment](https://github.com/ErfanBari/SBW_Experiment)