

1 **Title: A temperature-driven model of phenological mismatch**
2 **provides insights into the potential impacts of climate change on**
3 **consumer-resource interactions**

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Abstract

1. Anthropogenic climate change is increasingly affecting species phenology. Because trophic interactions often occur at specific phenological stages, changes in one species' phenology may affect others through phenological mismatch. In the case of a consumer and a resource that both exhibit a seasonal resting period, the synchrony of the end of their respective resting period is fundamental for the persistence of their interaction. Since the consumer and its resource may react differently to a change in temperature regime, the synchrony between them will likely be altered.
2. The goal of this study is to investigate the potential effects of climate change of species synchrony.
3. We propose a general theoretical model that determines the duration of the resting period according to temperature, and its effects on the mismatch between phenological stages of two interacting species. We illustrate our approach using the spruce budworm – balsam fir system in eastern Canada.
4. We found that an increase in temperature would usually advance the end of the resting period. However, the effects of a warm or cold spell during the resting period would strongly vary according to the time and the duration of the spell. Depending on the way each species reacts to the same temperature shift, the mismatch between the consumer and its resource may increase or decrease. The spruce budworm – balsam fir model predicts that an increase in temperature may increase the mismatch between the insect and the tree in southern sites, but may increase the synchrony in northern sites.
5. This type of modelling approach is of prime importance to investigate potential effects of climate change on consumer – resource systems.

Keywords:

Balsam fir, consumer, climate change, phenology, resource, spruce budworm

1. Introduction

Anthropogenic climate change has increasingly disrupted ecological interactions for the past century (Pachauri et al., 2014). This trend is expected to continue and amplify as interacting species are likely to respond differently to similar environmental changes and selective pressures (Parmesan, 2006). Trophic interactions between consumers and resources, which are fundamental to the functioning of ecosystems, may be affected by climate change through: (1) direct changes in life history traits (e.g., fecundity, mortality) of consumer and/or resource (Bale et al., 2002), (2) changes in abundance of consumer and/or resource due to cascading effects from other trophic levels (e.g., changes in the consumer's predators) (Both, ~~van Asch~~, et al., 2009), and (3) differential shifts in the phenology of consumer and/or resource leading to phenological mismatch (Kharouba et al., 2018).

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The concept of phenological mismatch has evolved since its inception in the early 1990s and is still debated today (e.g., Singer & Parmesan, 2020's response to Kharouba & Wolkovich, 2020). In its stricter, original form, it states that the recruitment of a consumer is highest if the most energy expensive part of its life cycle is in synchrony with the peak availability of its resource (Cushing, 1990). The concept was later extended to the case where the phenologies of consumer and resource varied (Visser & Holleman, 2001), but still assumed that maximum fitness of the consumer is achieved at phenological synchrony. However, recent observations

suggest that, in some systems, phenological mismatch is the historical baseline (Singer & Parmesan, 2010). Historical mismatch can result from trade-offs between fecundity and mortality (Singer & Parmesan, 2010), mutualistic interactions (Forrest & Thomson, 2012) or intraspecific competition (Iwasa et al., 1983). Relaxing the assumption of baseline synchrony complicates predictions of potential climate change impacts. Indeed, if synchrony is the baseline, any differential change will be detrimental to the consumer's fitness. If the baseline is a mismatch, a change that decreases asynchrony will likely be beneficial to the consumer (but see Régnière & Nealis, 2018) while the opposite might exacerbate the detrimental effect of asynchrony to the point of extinction of the consumer (Singer & Parmesan, 2010).

Many organisms have advanced their phenology in recent decades (Post et al., 2001; Parmesan & Yohe, 2003), particularly the timing of spring events at mid-high latitudes (Parmesan, 2006; Cohen et al., 2018). In a meta-analysis of 27 pairs of interacting species, Kharouba et al. (2018) found that phenology advanced by an average of 4 days/decade across species since the early 1980s. Interacting species have advanced their phenology by similar magnitudes, resulting in relatively small (6.1 days/decade) but significant increases in mismatch. The observed mismatch had no consistent direction as 31 interactions shifted closer while 23 shifted further apart. The clearest examples of climate-driven mismatch have been reported for insect herbivores at high altitudes or latitudes (Renner & Zohner, 2018), where many organisms rely on a seasonal resting period because temperatures affecting physiological processes tend to be below species optima for most of the year. After a seasonal arrest in development that can last for several months, synchrony between the emergence of phytophagous insects from diapause and the end of their host plants dormancy, is critical to the consumer's fitness (Van Asch & Visser, 2007). Spring defoliators have evolved to exploit foliage at its annual optimal nutritional

qualities, i.e., high concentration in nutrient and water and low concentrations in fibre and secondary metabolites (Mattson & Scriber, 1987). This strategy requires a precise phenological match between the consumer and its resource because the quality of foliage declines quickly with foliar expansion. If the consumer emerges too early, it may encounter a long initial period with no food or poor food quality. If it emerges too late, the speed at which the nutritional quality of the foliage degrades may outpace the consumer's capacity to adjust physiologically, thus negatively impacting its fitness.

The seasonal resting phase of many organisms is divided into two successive stages called endodormancy and ecodormancy in perennial woody plants, and diapause and quiescence in insects (Chuine & Régnière, 2017). Development and metabolism are generally inhibited by internal factors (e.g., depletion of energy reserves, hormones) in the first stage and by external factors (e.g., temperature, photoperiod) in the second. In our study system, the consumer and its resource show a seasonal resting period during part of the year (e.g., during winter). For both, we assume that the first stage is accomplished early in the winter before the return of favourable conditions, a common case in temperate and colder climates, and that temperature is the main driver that triggers the end of the second stage and therefore the resting period. We will refer to the second stage of the seasonal resting period simply as the "resting period".

Science is currently unable to predict the direction or the magnitude of phenological mismatch between consumer and resource induced by climate change and the associated risks that it poses to species (Samplonius et al., 2021). While patterns of change in phenological synchrony are observed at an increasing rate because of climate change (Kharouba et al. 2018), they have been difficult to explain mechanistically. Different mechanisms can lead to a phenological mismatch between a consumer and its resource. Different species can respond to

different climatic factors or to the same factor but in a different way. Species can also face different constraints in phenological plasticity (Both & Visser, 2001) or have different costs associated with phenological response (Gienapp & Visser, 2006).

The aim of this study is to investigate potential effects of climate change on the phenological synchrony between a consumer and its resource when both species respond to the same climatic factor (i.e., temperature). The interaction occurs at the end of both species' resting periods, which is often the case for insect herbivores in mid-high latitudes. We begin with the general theoretical aspects that determine the duration of the resting period according to temperature, and their effects on synchrony / mismatch between phenological stages of the two species. Then we use a major insect pest of the Canadian boreal forest, the spruce budworm (SBW), and its main host, balsam fir, as a case study. We investigate the phenological synchrony between budworm's emergence from winter diapause and balsam fir's budburst across a gradient of latitudes and a number of different future climates.

2. The general model

We begin with a unified description of the mechanisms that determine the duration of the resting period of a consumer and its resource in terms of accumulation of ambient temperature. Then, we develop the main theoretical results at the single species level and for two interacting species.

2.1 Theoretical development

Throughout the resting period, an organism accumulates units of some quantity. The instantaneous rate of accumulation depends on ambient temperature. The resting period ends when a certain level of the quantity has accumulated. For trees, this quantity can be heat, for

example in degree-day models (Colombo, 1998) or more recent nonlinear models (Chuine, 2000; Desbiens, 2007). For insects, the quantity can be the proportion of the corresponding life-cycle stage that they have completed (also referred to as physiological stage) (Cobbold & Powell, 2011; Régnière, ~~St-Amant, & Duval~~ ^{et al}, 2012). Since the development rate is temperature dependent, this quantity ultimately measures accumulated heat. This concept of an accumulating quantity is “still the most important assumption in plant and animal phenology modelling” (Chuine & Régnière, 2017).

We denote time by t in days and temperature by $x = x(t)$ in degrees Celsius. The instantaneous rate of accumulation is some nonnegative, increasing function of temperature, denoted by $R = R(x)$. While developmental rates may decrease when temperatures exceed an upper threshold (Amarasekare & Coutinho, 2014), such temperatures do not generally arise during the winter resting period in mid-high latitudes. The resting period begins at time t_0 and ends at time t^* when the accumulated quantity reaches the threshold level F . The fundamental equation that connects all these quantities and determines the end of the resting period is

$$\int_{t_0}^{t^*} R(x(t))dt = F. \quad \text{Eq. 1}$$

A typical example for the accumulation rate function is

$$R(x) = \frac{1}{1 + \exp(b(x-c))}, \quad \text{Eq. 2}$$

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with parameters $b < 0$ and c (Chuine, 2000; Rebaudo & Rabhi, 2018). We illustrate the rate function in Eq. 2 as well as the condition in Eq. 1 for two different species and two simplistic temperature time series in Figure 1. As temperature patterns during the resting period change

because of climate change, the end time of the resting period of a species may shift. When temperatures increase, accumulation occurs faster and the phenology advances, i.e., the end time is earlier (Fig. 1D).

We are particularly interested in the case where the two species are a consumer and its resource. Their rate accumulation functions generally differ even in the same temperature regime (compare solid and dashed curves in Fig. 1C), which typically leads to different end times of the resting period (Fig. 1D). In view of our intended application, we also refer to the consumer as the insect and to the resource as the tree. We denote ~~these~~ **the corresponding end times** by t_e^* (emergence time) for the consumer (insect) and by t_b^* (budburst time) for the resource (its host tree). We call the difference in end times the *mismatch* between the two species (i.e., $mismatch = t_e^* - t_b^*$). When the end times of the resting period of two species respond differently to climate change, then the mismatch between the two species will change. This is the fundamental quantity that we study here (Fig. 1D).

2.2 Theoretical results

Model equation (Eq. 1) can in general not be solved explicitly for the end time, t^* , at least not for realistic temperature time series $x(t)$. Instead, we derive a general approximation formula for how t^* changes when future temperature time series ($x_2(t)$) deviate from historical expectation ($x_1(t)$) by a small amount (see Supplementary Material). We use this formula to evaluate and discuss the impact of climate change on the phenology of a single species and the phenological mismatch between two species in two particular cases: a constant temperature difference throughout the resting period or a warm or cold spell during a short time period. Our results here apply to any general rate accumulation function.

165 2.2.1 Phenology shift of a single species

166 When temperatures differ by a constant (Δx), we write $x_2(t) = x_1(t) + \Delta x$. Then the
 167 corresponding end times t_2^* and t_1^* are related by

$$t_2^* = t_1^* - \frac{\Delta x}{R(x_1(t_1^*))} \int_{t_0}^{t_1^*} R'(x_1(t)) dt. \quad \text{Eq. 3}$$

168 When temperatures differ by warm or cold spell of short duration Δt at time t_s of temperature
 169 difference Δx (positive for a warm spell, negative for a cold spell), then the corresponding ends
 170 of the seasonal resting phases are related by

$$t_2^* = t_1^* - \Delta x \Delta t \frac{R'(x_1(t_s))}{R(x_1(t_1^*))}. \quad \text{Eq. 4}$$

171 Both formulas show the expected qualitative pattern that if time series x_2 is warmer than x_1 , i.e.,
 172 $\Delta x > 0$, then the phenology advances, i.e., end of the seasonal resting period t_2^* is before the
 173 corresponding t_1^* (since all the terms after the “—” sign are positive). More importantly, the
 174 formulas allow us to quantify the expected shift of the end time of the resting period. We observe
 175 that the shift depends on the *derivative* of the rate accumulation function. In particular, the impact
 176 of a short temperature spell is proportional to the derivative, $R'(x(t_s))$, at the time of the spell (t_s).
 177 Hence, the phenology is most sensitive to warm or cold spells where $R(\cdot)$ is at its maximal slope.
 178 For the rate function in Eq. 2, this occurs at temperature $x=c$.

2.2.2 Effects on the mismatch between two species

When heat accumulation occurs independently in each species, the mismatch between the two changes if they respond differently to changes in temperature. The mismatch increases if the phenology of the earlier emerging species advances more quickly and decreases if it advances more slowly. Equations 3 and 4 require information about the current phenology ($R(x_I(t_I^*))$) and the sensitivity ($R'(x_I(t_I))$) to quantify the change in phenology in each species and therefore the change in mismatch.

I don't like the prime symbol here; it is much better in the displayed equations, e.g., Eq 6

For a theoretical example, we consider the scenario that the resource emerges before the consumer and is more sensitive at lower temperatures. Then, if temperatures are higher than historical averages early in the season, the phenology of the resource is likely to advance more than that of the consumer, so that the mismatch increases. Vice versa, if temperatures exceed historical averages only late in the season, when the consumer is more sensitive, the phenology of the consumer is expected to advance more, so that the mismatch decreases. Hence, a change in mismatch is most likely if the two species are most sensitive at different temperatures, i.e., when the maximal slopes of their respective rate accumulation functions occur at very different temperatures.

In reality, the periods of high sensitivity of the two species may overlap more or less, and the rate functions at emergence time (the terms in the denominators in Eqs 3 and 4) could differ significantly. As a result, the effect of temperature increases depends on details of each scenario. We illustrate this dependence using a simplified time series of daily mean temperatures as modelled by

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$$x_i(t) = 6.9 + 15\cos\left(\frac{2\pi(t - 200)}{365}\right) \quad \text{Eq. 5}$$

where the mean, amplitude and offset have been chosen to match historical averages in Fredericton (NB, Canada). We denote the end times of the consumer for the time series $x_i(t)$ by $t_{e,i}^*$ (emergence time) and of the resource by $t_{b,i}^*$ (budburst time).

When future temperatures differ from historical expectation by a constant (Δx), we apply

Eq. 3 to each species. The resulting mismatch changes according to

We should mention that R_e is for insect and R_b for tree

could the prime and the index both be close to R at the same time?

$$\underbrace{t_{e,2}^* - t_{b,2}^*}_{\text{mismatch2}} = \underbrace{t_{e,1}^* - t_{b,1}^*}_{\text{mismatch1}} - \Delta x \left(\frac{\int_{t_0}^{t_{e,1}^*} R'_e(x_1(t)) dt}{R_e(x_1(t_{e,1}^*))} - \frac{\int_{t_0}^{t_{b,1}^*} R'_b(x_1(t)) dt}{R_b(x_1(t_{b,1}^*))} \right). \quad \text{Eq. 6}$$

The resulting linear approximation captures the actual end of the resting period very well (see supplementary Fig. S1). The derivative has to be integrated over the whole development period. Thus, it is difficult to estimate the resulting trend at first glance because it mostly depends on the amount of time that temperatures stay in the sensitive range of each species (that drives the numerator values), but it also depends on the value of the function at emergence time (denominator).

211

When future time series differ from historical expectation by a short spell of duration Δt and temperature difference Δx , we apply the corresponding formula (Eq. 4) to each species. Then the mismatch changes according to

see above

$$\underbrace{t_{e,2}^* - t_{b,2}^*}_{\text{mismatch2}} = \underbrace{t_{e,1}^* - t_{b,1}^*}_{\text{mismatch1}} - \Delta x \Delta t \left(\frac{\overbrace{R'_e(x_1(t_s))}^{\text{see above}}}{R_e(x_1(t_{e,1}^*))} - \frac{\overbrace{R'_b(x_1(t_s))}^{\text{see above}}}{R_b(x_1(t_{b,1}^*))} \right). \quad \text{Eq. 7}$$

In case of non-overlapping sensitivity periods, each species exhibits a sensitivity that is a relatively narrow peak around a maximum at $x=c_i$, and they peak at different temperatures. The phenology of one species will advance noticeably only when the spell occurs near its peak temperature. The other species is not affected (Fig. 2A).

In the case of two overlapping sensitivity periods, one species (e.g., the consumer) may exhibit a broader sensitivity that peaks at a different temperature than the other species (e.g., the resource). Hence, in this example, the phenology of the consumer will advance noticeably no matter when a warm spell occurs, whereas the phenology of the resource will advance noticeably only when it occurs near the temperature $x=c_I$ (Fig. 2B).

However, among all scenarios, the rate function at emergence (the denominators in Eq. 7) may differ vastly between the two species. Consequently, even if the resource is more sensitive than the consumer at the time of the spell ($R'_e > R'_b$), the difference in parentheses in Eq. 7 can still be negative if the denominator in the first term is much larger than in the second.

Despite their simplicity, these scenarios give us some important insights into the evolution of the mismatch. The advance of the phenology of each species is a nonlinear function of temperature increase and each species has a temperature regime during which its phenology is most sensitive to change, namely when the slope of the rate function is large. In this section, we used Eq. 1 to develop general theoretical insights. The model is agnostic about the specific R functions used. The model does not make any assumption on the consequences of a change in

234 synchrony between the two interacting species, in terms of survival, reproduction, or any life
235 history trait. These aspects are system-specific. In the following section, we apply the model
236 using realistic temperature time series in order to make predictions for a specific case study, at a
237 given place and time.

238 **3. A case study: the spruce budworm – balsam fir system**

239 We describe the spruce budworm – balsam fir system and provide the accumulation function for
240 both species. Then, we list our data sources and explain the fitting methods for the spruce
241 budworm - balsam fir system. Finally, we give the results for this case study. We use R (R core
242 team, 2020) to implement the model, analyze the results, and generate the figures. Past and future
243 temperature data were obtained using BioSIM ((Régnière, ~~Saint-Amant, Béchard~~, et al., 2014).

244 **3.1 Study system**

245 The spruce budworm (SBW) (*Choristoneura fumiferana*) is the most destructive defoliator of
246 North American boreal forests (Fleming, 2000). It feeds primarily on balsam fir (*Abies*
247 *balsamea*), black spruce (*Picea mariana*), white spruce (*Picea glauca*), and red spruce (*Picea*
248 *rubens*). This univoltine insect has an 8-9 months winter resting period (diapause). The first
249 stage ends in late winter and is followed by a quiescent period during which development
250 resumes at a rate dependent on outside temperatures. Diapause ends when second instar larvae
251 emerge from their hibernacula (cocoon-like structure) in late April to late May. Larvae feed on
252 expanding buds and developing needles as soon as they become available. Expanding needles
253 from swelling buds are nutrient rich with a maximum concentration of nitrogen and mineral
254 elements (Mattson & Scriber, 1987). Hence, the success of SBW populations in establishing
255 feeding sites in the spring depends on the synchrony of their development with that of their host

trees (Régnière & Nealis, 2008). Consequences for late-emerging SBW are severe: larval survival is depressed (from about 60% normal survival down to 10%), development is delayed, and average pupal mass decreases by about 50% (Lawrence et al., 1997). In the boreal forests of eastern Canada, the higher vulnerability of balsam fir to SBW defoliation compared to other host species has been attributed to its early budburst (Blais, 1957). The emergence of SBW generally precedes balsam fir budburst by several days. Balsam fir phenology appears to be related to forcing temperatures but not photoperiod (Osawa et al., 1983).

We assessed historical patterns and climate change predictions of synchrony between SBW's emergence from diapause and balsam fir's budburst using an existing model of budworm phenology and a general budburst model fitted to observations of budburst phenology in Canada. Each species has its own accumulation function which we used to illustrate the general theoretical case (see section 2.2.2 and Fig. 2).

3.2 Phenological models

3.2.1 Phenological model of spruce budworm's spring emergence

The first stage of SBW diapause is assumed to end in late winter, but the physiological processes and environmental factors that control this are still unknown (Bean, 1961). For modelling purposes, March 1st is generally taken as the start of the quiescent stage (Régnière, ~~St Amant, & Duval~~^{et al}, 2012). Taking an earlier starting date would not affect the predicted date of emergence since temperatures are generally well below the 2.5°C development threshold prior to March 1st across the vast majority of SBW's geographical range. The heat accumulation rate of the overwintering stage (L_{20}) of SBW is defined as (Régnière, ~~St Amant, & Duval~~^{et al}, 2012)

$$R(x(t)) = \begin{cases} \beta_1 \left[\frac{1}{1 + \exp(\beta_2 - \beta_3^T)} - \exp((\tau - 1)/\beta_4) \right], & \text{if } x_b \leq x(t) \leq x_m \\ 0, & \text{otherwise} \end{cases} \quad \text{Eq. 8}$$

277 where

$$\tau = \frac{x(t) - x_b}{x_m - x_b} \quad \text{Eq. 9}$$

278 Accumulation occurs only when the temperature lies between a minimal (x_b) and a maximal
 279 value (x_m). Parameter values for SBW, estimated by Régnière et al. (2012) from laboratory
 280 experiments, are $\beta_1 = 0.194$, $\beta_2 = 3.0$, $\beta_3 = 5.94$, $\beta_4 = 0.034$, $x_b = 2.5$ °C, $x_m = 35$ °C and $F=I$.
 281 The accumulation rate function is increasing for temperatures up to 31°C, which is well above the
 282 temperatures observed during the quiescent stage.

283 3.2.2 Phenological model of balsam fir's budburst

284 Process-based tree phenology models describe the individual or interactive effects of
 285 environmental conditions (e.g., temperature or photoperiod) on bud development (Chuine &
 286 Régnière, 2017). We use the *Uniforc* model of Chuine (2000) to model balsam fir's budburst
 287 phenology. *Uniforc* predicts bud development as a function of temperature in the second stage of
 288 seasonal resting (i.e., ecodormancy). The heat accumulation rate is the same as in the theoretical
 289 example (see Eq. 2). Accumulation starts some time after January 1st (Desbiens, 2007), when
 290 trees have accumulated enough cold to end bud dormancy. Budburst occurs when accumulation
 291 reaches a threshold F^* .

292 We fitted the *Uniforc* model to budburst phenology data collected in the 1980s and 1990s
 293 in Quebec and New Brunswick (Desbiens, 2007; Régnière pers. comm. 2020). Each year, bud
 294 development was observed in different sites during the growing season at time intervals ranging

295 from two days to two weeks. Budburst occurs when buds develop from class I to II according to
296 the class scheme developed by Dorais & Kettela (1982). The budburst date was defined as the
297 date when 50% of the buds in the site have reached stage II. We obtained temperature data at
298 each site for each year using BioSIM. We estimated parameter values of the Uniforc model using
299 simulated annealing in order to predict budburst date according to temperatures during
300 development period.

301 We performed sensitivity analysis on both models using partial rank correlation
302 coefficients (Wu et al., 2013).

303 **3.3 Historical and future temperature regimes in eastern Canada**

304 We selected six locations on a latitudinal gradient across eastern Canada (Fig. 4) to explore the
305 effects of historical and future temperature regimes on the synchrony between SBW and balsam
306 fir phenology. The temperature data for these locations were calculated using BioSIM (Régnière,
307 ~~Saint-Amant, Béchard~~, et al., 2014). BioSIM interpolates weather station historical data and
308 climate change scenarios across North America. We used data from 1996 to 2016 to explore
309 latitudinal trends of past insect emergence, tree budburst and their mismatch across years.

310 We used predicted temperatures under different warming scenarios to reveal expected
311 trends for emergence, budburst and mismatch. We selected three different scenarios, known as
312 RCP2.6 (moderate warming), RCP4.5 (intermediate) and RCP8.5 (strong) (van Vuuren et al.,
313 2011). For each scenario, we generated 1200 stochastic temperature time series over the 2001-
314 2100 period using BioSIM.

Both models used temperature data with a four-hour time interval, which allows for the capture of warm events within a day.

3.4. Mismatch in the spruce budworm - balsam fir system

3.4.1 Fitting and sensitivity

Fitting the *Uniforc* model to phenological data from Quebec and New Brunswick resulted in the parameter values: $b = -1.32$, $c = 7.14$ °C, $t_0 = 87$ (March 28th), and $F^* = 18.6$ (RMSE = 12.6). The residuals of this fitting follow a Normal distribution centred on 0 (Fig. 5A). There is no obvious pattern for the residuals across latitude in the range of our study (Fig. 5B).

In order to test the accuracy of both insect and tree models, we compared predicted budburst and emergence date with available data for two years (2013, 2014) in two sites in Quebec (Pureswaran, et al., 2019). Measured budburst occurred between May 16th and June 17th, in 2013, and between May 29th and June 15th, in 2014. The model predicts a median budburst on May 27th in 2013, and May 28th in 2014. For the insect, the emergence peak occurred on May 9th in 2013, and on May 23th in 2014. The model predicts a median emergence on May 20th in 2013, and May 21th in 2014. Hence, the model gives satisfactory results.

The budworm model is sensitive to most parameters (Fig. 5C). The only exception is x_m (the maximal temperature) since very high temperatures are rare during late winter and spring, and to a certain extent β_1 . Increasing parameters β_2 , β_4 , and x_b (minimal temperature) delays emergence, while increasing β_3 strongly advances phenology. The tree model is most sensitive to parameters t_0 (when the tree starts accumulating heat) and b (which drives the speed of

accumulation). An increase in t_0 postpones phenology, while an increase in b advances it (Fig. 5D).

3.4.2 Spruce budworm – balsam fir system across latitude

The model predicts median dates of emergence and budburst for each year. Results for past and future data were analyzed using a one-way analysis of variance (see supplementary material for full results).

Both emergence (Fig. 6A) and budburst (Fig. 6B) occur later at higher latitudes: $p < 0.05$ between sites 1, 2, 3 (South) and 4, 5, 6 (North), although some discrepancies may occur due to altitude (sites 2 and 4).

However, insects and trees are not affected by temperatures in the same way. Hence, the mismatch between both species varies across latitude ($p < 0.05$ between sites 1, 3 and 5, 6) (Fig. 6C). At lower latitudes, emergence is expected to occur 5 to 10 days before budburst. Hence, the majority of the larval population may have time to emerge before budburst occurs, which allows larvae to benefit from an important source of nutrients. Fuentealba, ~~Pureswaran, Bauce, & Despland~~ ^{et al} (2017) evaluated SBW performance on balsam fir according to their phenological mismatch. According to their study, we can infer SBW survival to be around 45% and reproductive output (fecundity * survival) to be 45%. At higher latitudes, emergence may sometimes occur before budburst and sometimes after, which would lead to 30% survival and 20% reproductive output. In brief, insects seem more adapted to their host phenology at lower than at higher latitudes.

3.4.3 Predicted trends according to warming scenarios

Across all scenarios, emergence and budburst are expected to occur earlier when temperatures increase. The differences in emergence, budburst and mismatch across latitude is highly significant ($p < 10^{-16}$ for almost all sites and for all scenarios). Warmer scenarios lead to an increase of variance, more than a real shift in date compared to less warm scenarios. Insects and trees react differently to temperature increase. Balsam fir shows an historical (1996-2016)

difference between northern and southern sites of 10 days on average. This difference stays approximately the same in case of warmer temperatures (i.e., budburst date is shifted similarly across latitude, see Fig. 6B). By contrast, emergence of SBW is expected to shift differently across latitude (about 15 days difference compared to 10 historically, see Fig. 6A).

Therefore, the mismatch is affected. Southern sites are expected to show emergence occurring before budburst most of the time. In case of a moderate warming scenario (RCP2.6), the waiting time is expected to be short, which would allow the larvae to have access to a rich source of nutrients. Thus, a moderate warming could be beneficial for the insect at low latitudes. In case of greater warming (RCP4.5, RCP8.5), variance may lead to emergence occurring too early some years, leading to larvae dying from starvation. Thus, a greater temperature increase may lead to stronger population variances among years.

In northern sites, all warming scenarios lead to an increased synchrony between the insect and its host. The overall pattern appears similar to what is currently expected in southern sites. However, the variance is expected to be greater with warmer scenarios, which may increase insect mortality from time to time, when emergence occurs too late.

4. Discussion

We propose a temperature-driven mechanistic model to determine the end of the seasonal resting period of species. We investigate the effects of temperature on species phenology, and its consequences on consumer-resource synchrony, across latitude and under future climate scenarios.

4.1 Expected impacts of climate change on phenological mismatch between consumer and resource

A growing body of literature shows phenological shifts of species due to climate change with different species shifting at different rates (Visser & Both, 2005; Donnelly et al., 2011; Kharouba et al., 2018). By linking development with temperature, our modelling approach predicts the expected phenological shift under various future climate scenarios for a species whose resting period is determined by temperature. More specifically, the change in phenology is determined by the interaction of the new temperature pattern and the slope of the rate accumulation function (R'); see Eq. 8 and Supplementary Material. For example, a warm spell occurring when the slope of development rate is very low may have little effect compared to the same warm spell occurring when development is more sensitive to temperature (i.e., when R' is high); see Fig. 2B. Consecutive spells will have additive effects: several warm spells will advance phenology several times, while a cold spell may cancel effects of a warm spell.

For a consumer to efficiently exploit a resource, some form of temporal synchrony is often required. Observations of consumer-resource systems show that, as an effect of climate change, their degree of synchrony can increase or decrease, but the mechanisms behind this difference are unclear (Kharouba et al., 2018). We focused on the duration of the seasonal resting period, which constitutes a significant stage in many species' life cycle. As different species react differently to temperature changes, we applied our model to each species separately to predict whether their degree of synchrony will increase or decrease as temperature patterns change.

A phenological shift of the consumer and its resource may affect their population dynamics and subsequently the larger food web in which they are embedded. For example, an

increase of the phenological mismatch may limit the consumer's food intake, which affects its biomass, its life cycle, and potentially even its ability to persist in the considered geographic zone (Simmonds et al., 2020). If a subsidiary resource is available, the consumer may switch resources (Stålhandske et al., 2016). A decrease of the phenological mismatch may lead to a stronger depletion of the resource. Both of these outcomes may cause ripple effects through the food web. Thus, a shift in relative phenology between the consumer and its resource can affect species demography in many ways (Miller-Rushing et al., 2010), as well as their geographic distribution. Our work, which is based on heat accumulation, improves our ability to predict the direction and the magnitude of the change in phenological synchrony, a research challenge identified by earlier studies (Kharouba et al. 2018).

4.2 The spruce budworm - balsam fir system and its general implications

We apply our general theory to predict the future mismatch between spruce budworm and balsam fir across latitude under different warming scenarios. According to the general theory, a warm spell occurring at any time during the heat accumulation period is likely to affect the insect because its $R'(\cdot)$ has a wide profile (see Fig. 2B, and section 2.2.2). The tree will react only if the warm spell occurs within its narrow sensitivity period. Therefore, under a change in temperature regime that would lead to several warm spells, the insect will advance its phenology more than the tree. Simulations with realistic temperature time series (showing several warm spells) confirm the theoretical results. Under an increase of temperatures, insect phenology would advance by 15 days on average, while the tree phenology would advance by 7 days on average. The expected overall mismatch increases by approximately 7 days on average (see Fig. 6 and section 3.4.2).

Budworms have to emerge within two weeks of budburst to have access to a rich source of nutrients. A shift in phenology increasing the likelihood of this pattern would in turn increase larval survival and population persistence in previously non-favourable regions. Under historical temperature regimes, budworm emergence date in northern sites is close to budburst date, which causes the budworm to emerge too late in some years, while emergence in southern sites occurs within 15 days before budburst. An increase of the mismatch benefits the insect in northern sites since it would emerge before budburst most of the time, while in southern sites, the budworm would emerge too early some years. A shift in phenology that leads to emergence occurring too early (or too late) would cause severe budworm mortality and prevent its persistence in some parts of its current distribution. Conversely, an increase in the persistence of the insect in other regions will increase damages to host trees. Since insect pests (especially SBW) are one of the main drivers of forest composition in the black spruce, white spruce and balsam fir zones (Harper et al., 2003), a change in phenological synchrony between these species may affect their future geographic distributions.

A change in mismatch between budworm and balsam fir would also affect other potential host species. It is known that black spruce is a suitable host, but its phenological mismatch with budworm protects the tree from a long-term budworm establishment (Pureswaran, ~~De Grandpré~~, et al., 2015). Moreover, in northern sites, black spruce seems to be somehow protected because the budworm cannot establish for a long period due to a high frequency of cold years (Pureswaran, ~~De Grandpré~~, et al., 2015). However, our model predicts that warming should lead to a better synchrony between the insect and balsam fir in these sites, therefore the budworm might be able to establish and generate outbreaks, which in turn would affect black spruce

populations. To test this hypothesis, we require *in situ* phenological data for a parameterization of the tree model (Eq. 2) for black spruce.

Our model assumes that neither the consumer nor the resource affects the phenology of the other species. Only temperature drives phenology. Recent observations of interactions between defoliation and host phenology suggest that severe defoliation by budworm may advance budburst phenology (Deslauriers et al., 2019). According to our model, an increase in temperature should increase the mismatch by advancing the budworm phenology more than that of the tree. If defoliation leads to an advance in phenology for the tree, then the resulting mismatch would stay close to the historical mismatch, which would reduce the benefit of this physiological response for the tree.

4.3 Future extensions

The present study provides novel insights towards a better understanding of the effects of an increase of temperatures on species phenology. Further studies may consider specific features that we do not include in the model. First, our study is limited to cases where the phenology is directly constrained by environmental variables (more specifically temperature). Organisms can also use temperature (or any other environmental variables) indirectly as cues for predicting an optimal time window to have access to resources or convenient environmental conditions (e.g., photoperiod, rainfall) (McNamara et al., 2011).

Second, we measure mismatch as the time lag between peaks of consumer demand and resource availability. Some authors have argued that more precise measurements should take into account the shape and location of the phenological distributions around these peaks (e.g., Lindén, 2018) while others showed that, in some cases, time lag between phenological peak dates was a

465 better predictor of resource availability than the overlap between phenological distributions
466 (Ramakers et al., 2020).

467 Third, a change in phenological synchrony will have an effect on the whole life cycle,
468 which would be beyond the scope of the present study. Rising temperatures are likely to affect
469 physiological processes at later life stages, by affecting metabolism for example (Brown,
470 ~~Gillooly, Allen, Savage, & West~~ ^{et al}, 2004). It is also clear that a change in the mismatch is likely to
471 affect the ecological and evolutionary dynamics of the consumer-resource system. These aspects
472 provide avenue for further studies.

473 The theoretical framework presented here can be applied to other consumer-resource
474 systems. The concrete example of the spruce budworm - balsam fir system informs the required
475 methodology. To estimate the mismatch, the two rate accumulation functions must be calibrated
476 accurately. It appears that the model is sensitive to the temporal resolution of the temperature
477 time series. There are two timescales at which temperatures affect the outcome of the model. The
478 first one occurs at the daily scale. Average daily temperatures lead to different results than a four-
479 hour time interval for temperatures (used throughout the present study) since variations within a
480 day may allow for development during a few hours, even when the average temperature over the
481 whole day may not.

482 The second one occurs at a broader timescale (e.g., weekly). For the study system,
483 temperature data modelled by BioSim (Régnière, ~~Saint-Amant, Béchard~~, et al., 2014) lead to
484 realistic emergence and budburst dates when compared to real data (see section 3.2) and to a
485 phenological mismatch, i.e., budworm usually emerging before budburst, similar to field
486 observations (Pureswaran, ~~Neau~~, et al., 2019). More simplistic distributions that do not contain

487 any warm spell can lead to the opposite pattern (i.e., budburst occurs first). Realistic temperatures
488 show warm periods during days with low average temperatures (i.e., late winter - early spring),
489 which advance the insect phenology compared to simplified (cosine) distributions. The tree is
490 less sensitive to these short warm events.

491 The modelling approach presented here allows for investigation of potential effects of
492 climate change on consumer-resource systems. Synchrony / mismatch between a consumer and
493 its resource is fundamental to predict future species distribution. Future studies may go further by
494 including more complex mechanistic approaches (e.g., energy budget models) in order to model
495 the whole life cycle of the consumer, which could lead to new insights on the dynamics of the
496 systems. Our model could be linked to models that explore the consequences of phenological
497 mismatch on the population dynamics of consumer – resource systems (e.g., Bewick et al., 2016).

498

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503 **Authors' contribution**

504 All authors conceptualized the study. FL and SP built the theoretical model. SP calibrated the tree
505 model, gathered the temperature data, and performed the simulations. SP, JNC and FL analyzed
506 the results, wrote and edited the manuscript.

507 **Data Availability**

508 Code will be stored on Zenodo public depository. Data on balsam fir phenology can be made available on
509 demand to Dr. J. Régnière (Natural Resources Canada).

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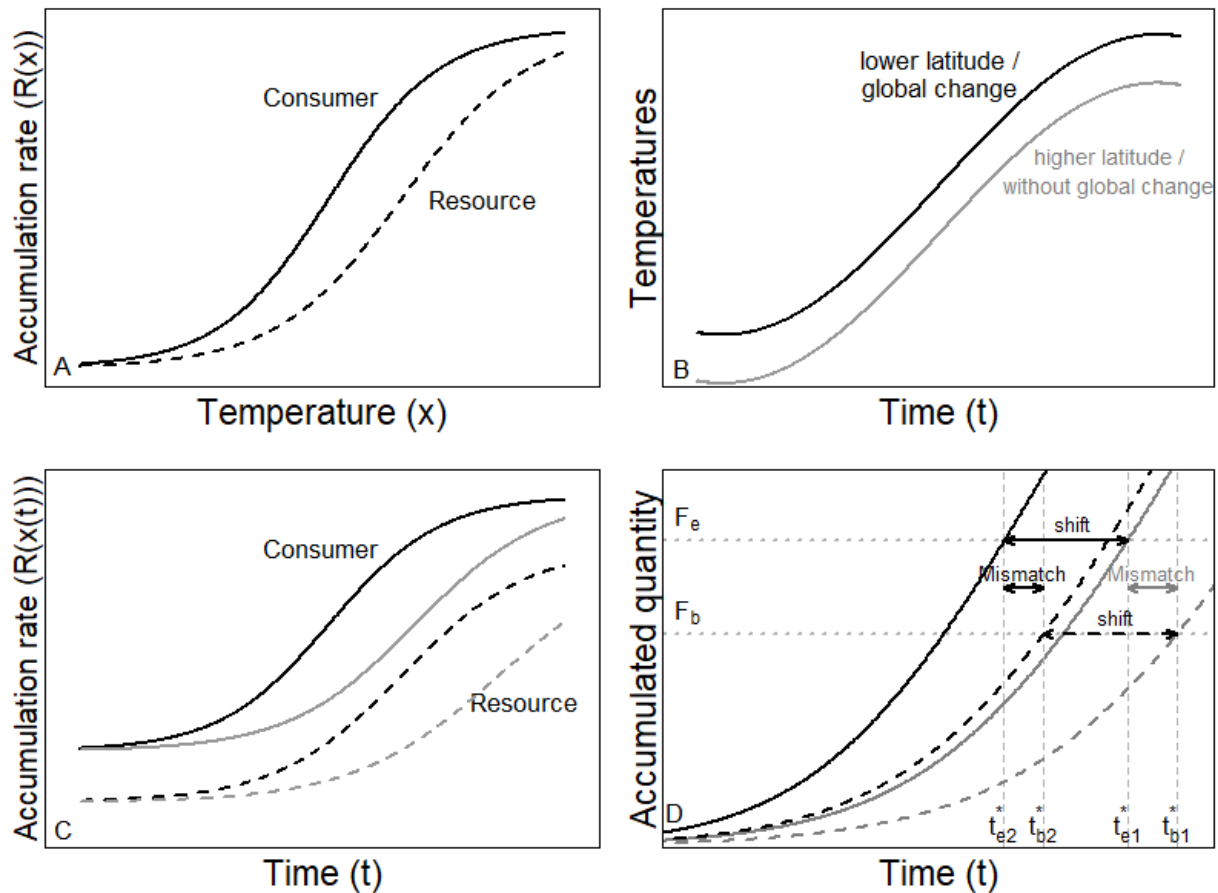
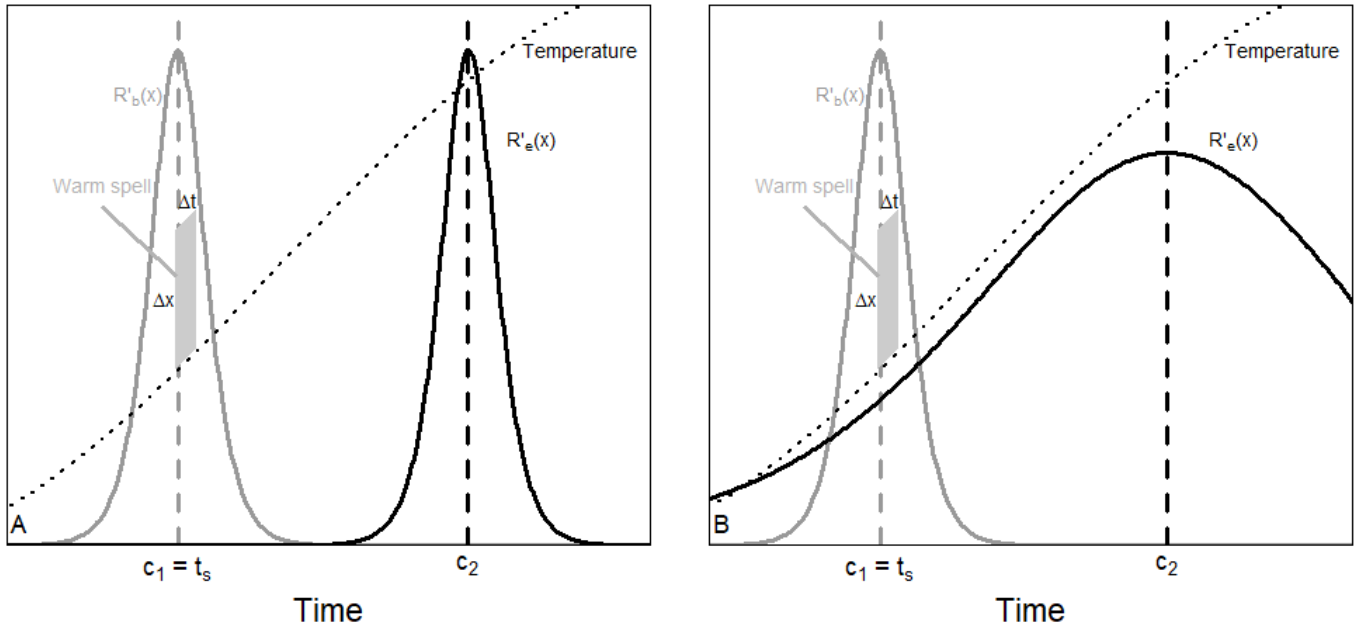


Figure 1: Illustration of theoretical development. (A) The rate accumulation function for two different species (solid line is consumer and dashed line is resource). (B) Two simplified temperature time series (black line is warmer and grey line is cooler). (C) Four combinations of rate accumulation; each species with two different temperature time series. (D) The resulting end of the resting phase for the consumer in cooler (grey solid line) and warmer (black solid line) temperatures and for the resource in cooler temperatures (black dashed line). The difference within species (grey vs. black line) indicates the shift in emergence in space (due to latitude or altitude) or time (due to global change). The difference between species (solid vs. dashed line) indicates the mismatch in the end of the seasonal resting phase for a fixed temperature regime

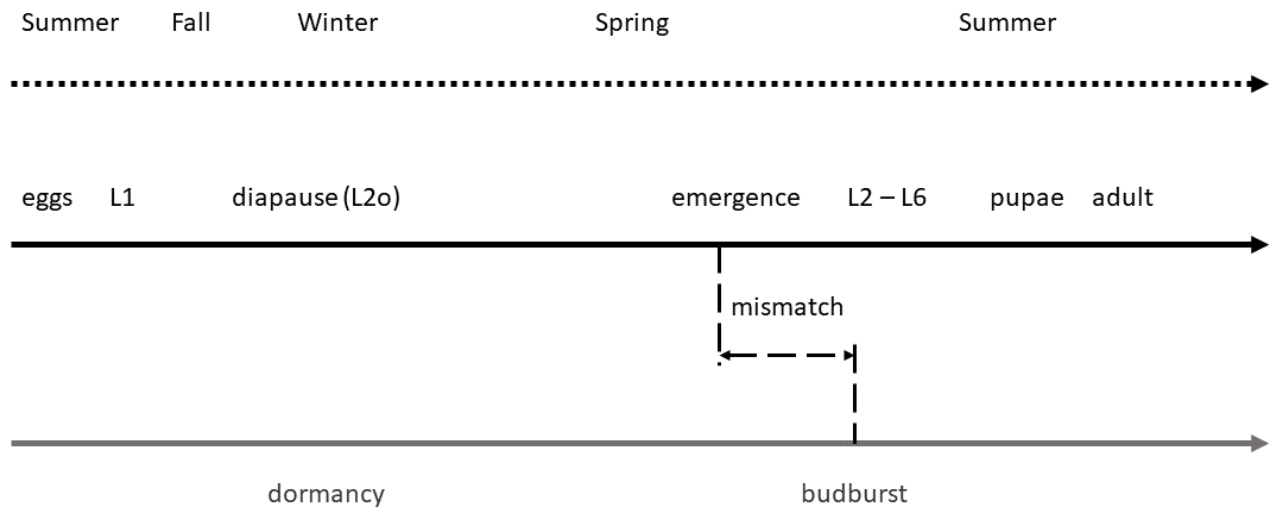
691 (same location and same time). Accumulation functions for both the consumer and the resource
692 use Eq. 2 with the following parameter values: $b_c = -1.32$, $c_c = 7.14$, $b_r = -1.16$, $c_r = 8.14$.



693

694 **Figure 2:** Sensitivity of resource accumulation functions, $R'(x(t))$, for two species when there is
 695 no (A) or some (B) overlap. In (A), the warm spell indicated will advance the phenology of
 696 species 1 (grey curve) but not alter that of species 2 (black curve). In (B), the same warm spell
 697 will advance both phenologies. For this illustration, we used the accumulation function in Eq 2
 698 for species 1 with parameter values for balsam fir (see section 3.4.1). We used the same function
 699 for species 2 in (A), but with $c = 15.2$. In (B), we used the accumulation function for spruce
 700 budworm in Eq. 8 with corresponding parameter values (see section 3.2.1). The temperature is
 701 chosen according to Eq. 5 (from January to June).

702



703

704 Figure 3: life cycles of balsam fir and spruce budworm. Black line represents SBW life cycle, and grey

705 line is balsam fir life cycle.

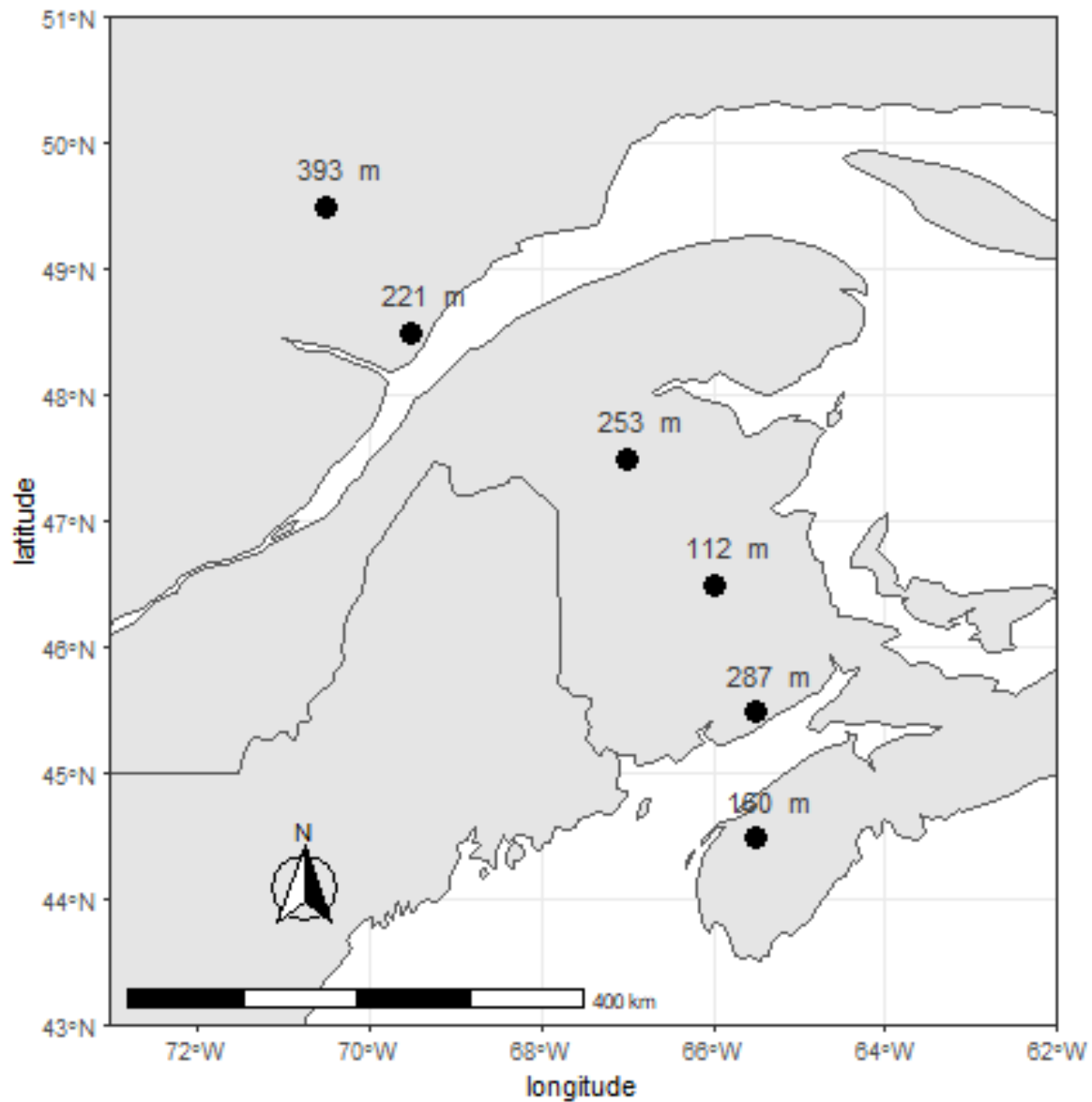
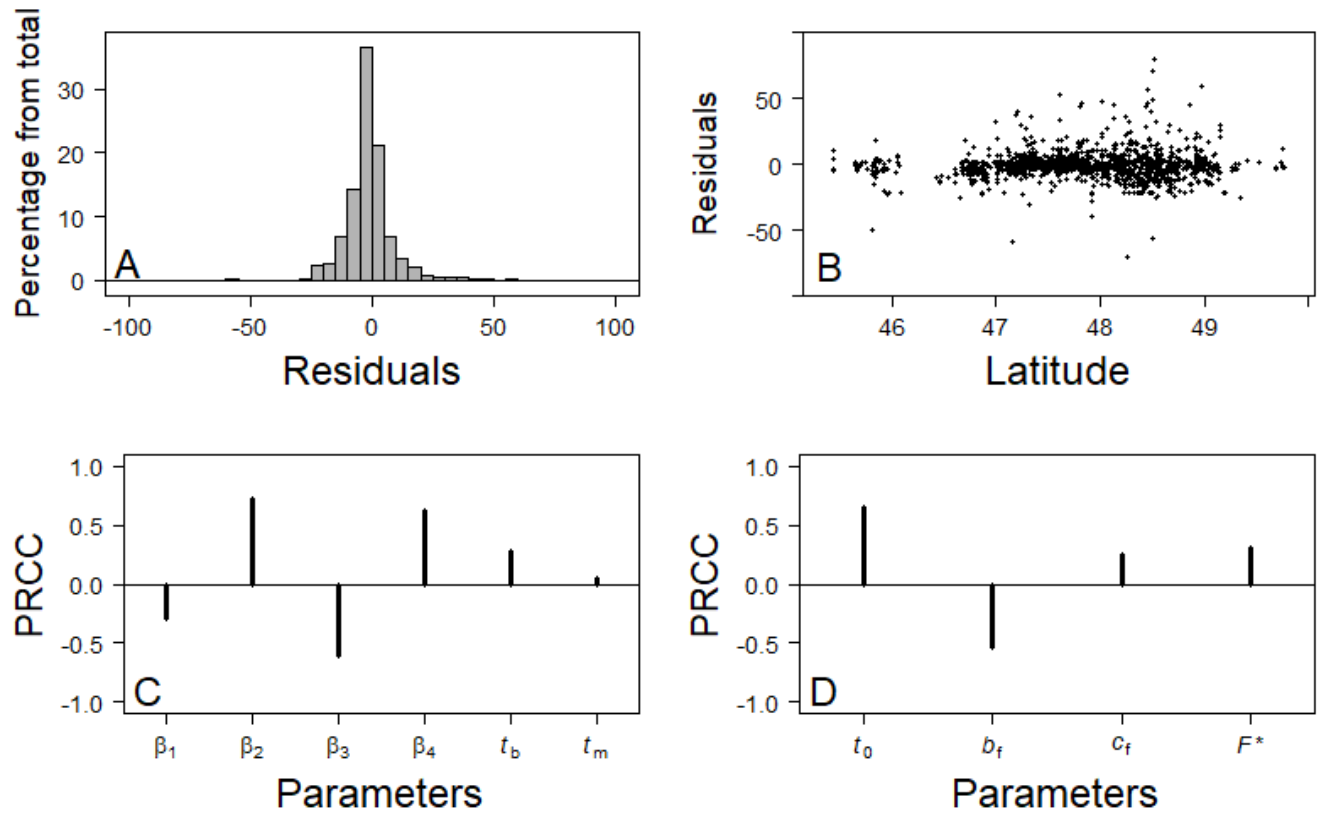
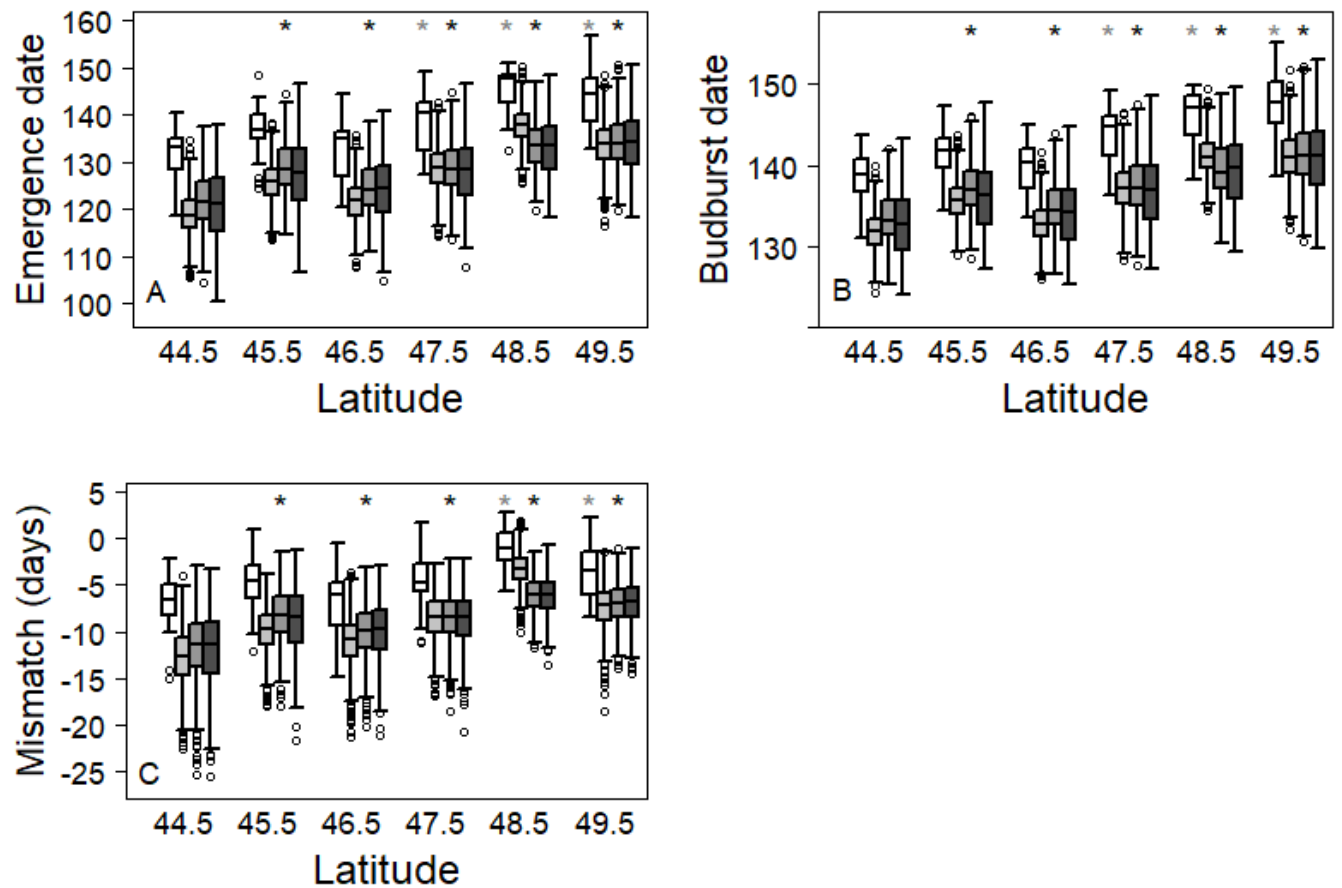


Figure 4: Location of the sample sites where temperature data were collected for past and future trends. Points are located across a gradient of latitude in Nova-Scotia, New Brunswick, and Quebec. Altitude is indicated above each point.



710

711 **Figure 5:** Fitting residuals of the balsam fir model and sensitivity analysis. (A) Residuals follow
712 a Normal distribution centered on 0. (B) No obvious latitudinal patterns can be found on the
713 residuals within the range of latitudes that is used throughout the rest of the study. (C) Partial
714 Rank Correlation Coefficient (PRCC) shows that the SBW model is sensitive to most parameters
715 especially β_2 , β_4 and x_b that delay emergence, and β_3 that advances phenology. (D) The tree
716 model is mostly sensitive to b_f that hastens budburst, and t_0 that delays budburst.



717

718 **Figure 6:** Latitudinal distribution of (A) median emergence date of SBW (Julian days), (B)
719 median budburst date, and (C) mismatch between emergence and budburst date. For each
720 latitude, the white box (left one) represents the 1996-2016 period. Grey boxes represent expected
721 outcomes according to RCP 2.6 (light grey), RCP 4.5 (dark grey), and RCP 8.5 (black) scenarios
722 over 2021 to 2100. A black (grey) star means that the corresponding site shows a significant
723 difference with the most southern site for present (future) predicted trait. Both emergence and
724 budburst are expected to occur later at higher latitudes. Overall warming scenarios, both events
725 are expected to occur earlier in the year. Nowadays, emergence is expected to occur 5 to 10 days
726 before budburst at low latitudes, while at higher latitudes, emergence may sometimes occur
727 before budburst and sometimes after. For all warming scenarios, an increase in mismatch is

728 expected. At low latitudes, emergence may occur too early some years, which may lead to low
729 survival of SBW. At higher latitudes, emergence is expected to systematically occur a few days
730 before budburst, which would increase survival of SBW.