

A temperature-driven model of phenological mismatch provides insights into the potential impacts of climate change on 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).

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

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

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

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

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 list our data sources and explain the fitting methods for the spruce budworm - balsam fir system.

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

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

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

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

138 A typical example for the accumulation rate function is

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

139 with parameters $b < 0$ and c (Chuine, 2000; Rebaudo & Rabhi, 2018). We illustrate the rate
140 function in Eq. 2 as well as the condition in Eq. 1 for two different species and two simplistic
141 temperature time series in Figure 1. As temperature patterns during the resting period change
142 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).

The rate accumulation function of a consumer and its resource will 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). We denote these by t_e^* (emergence time) for the insect (consumer) and by t_b^* (budburst time) for the host tree (resource). 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).

We use our theoretical model to predict general patterns of climate-change induced shifts in species phenologies and changes in the mismatch between interacting species. We use the spruce budworm and balsam fir system in eastern Canada to illustrate how estimated rate accumulation functions can be applied to different temperature scenarios to investigate how climate change may affect the phenological between these two species.

2.2 The spruce budworm – balsam fir system

2.2.1 Study system

The spruce budworm (SBW) (*Choristoneura fumiferana*) is the most destructive defoliator of North American boreal forests (Fleming, 2000). It feeds primarily on balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), white spruce (*Picea glauca*), and red spruce (*Picea rubens*). This univoltine insect has an 8-9 months winter resting period (diapause). The first stage ends in late winter and is followed by a quiescent period during which development

resumes at a rate dependent on outside temperatures. Diapause ends when second instar larvae emerge from their hibernacula (cocoon-like structure) in late April to late May. Larvae feed on expanding buds and developing needles as soon as they become available. Expanding needles from swelling buds are nutrient rich with a maximum concentration of nitrogen and mineral elements (Mattson & Scriber, 1987). Hence, the success of SBW populations in establishing 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 3.1.2 and Fig. 2).

2.2.2 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, &

187 Duval, 2012). Taking an earlier starting date would not affect the predicted date of emergence
 188 since temperatures are generally well below the 2.5°C development threshold prior to March 1st
 189 across the vast majority of SBW's geographical range. The heat accumulation rate during the
 190 quiescent stage is defined as (Régnière, St-Amant, & Duval, 2012)

$$R(x(t)) = \begin{cases} \beta_1 \left[\frac{1}{1 + \exp(\beta_2 - \beta_3)} - \exp(\tau - 1)/\beta_4 \right], & \text{if } x_b \leq x(t) \leq x_m \\ 0, & \text{otherwise} \end{cases} \quad \text{Eq. 3}$$

191 where

$$\tau = \frac{x(t) - x_b}{x_m - x_b} \quad \text{Eq. 4}$$

192 Accumulation occurs only when the temperature lies between a minimal (x_b) and a maximal
 193 value (x_m). Parameter values for SBW, estimated from laboratory experiments, are $\beta_1 = 0.194$
 194 , $\beta_2 = 3.0$, $\beta_3 = 5.94$, $\beta_4 = 0.034$, $x_b = 2.5$ °C, $x_m = 35$ °C and $F=1$ (Régnière, St-Amant, & Duval,
 195 2012). The accumulation rate function is increasing for temperatures up to 31°C, which is well
 196 above the temperatures observed during the quiescent stage.

197 2.2.3 Phenological model of balsam fir's budburst

198 Process-based tree phenology models describe the individual or interactive effects of
 199 environmental conditions (e.g., temperature or photoperiod) on bud development (Chuine &
 200 Régnière, 2017). We use the *Uniforc* model of Chuine (2000) to model balsam fir's budburst
 201 phenology. *Uniforc* predicts bud development as a function of temperature in the second stage of
 202 seasonal resting (i.e., ecodormancy). The heat accumulation rate is the same as in the theoretical
 203 example (see Eq. 2). Accumulation starts some time after January 1st (Desbiens, 2007), when

204 trees have accumulated enough cold to end bud dormancy. Budburst occurs when accumulation
205 reaches a threshold F^* .

206 We fitted the Uniforc model to budburst phenology data collected in the 1980s and 1990s
207 in Quebec and New Brunswick (Desbiens, 2007; Régnière pers. comm. 2020). Each year, bud
208 development was observed in different sites during the growing season at time intervals ranging
209 from two days to two weeks. Budburst occurs when buds develop from class I to II according to
210 the class scheme developed by Dorais & Kettela (1982). The budburst date was defined as the
211 date when 50% of the buds in the site have reached stage II.

212 We perform sensitivity analysis on both models using partial rank correlation
213 coefficients (Wu et al., 2013).

214 **2.3 Historical and future temperature regimes in eastern Canada**

215 We selected six locations on a latitudinal gradient across eastern Canada (Fig. 3) to explore the
216 effects of historical and future temperature regimes on the synchrony between SBW and balsam
217 fir phenology. The temperature data for these locations were calculated using BioSIM (Régnière,
218 Saint-Amant, Béchard, et al., 2014). BioSIM interpolates weather station historical data and
219 climate change scenarios across North America. We used data from 1996 to 2016 to explore
220 latitudinal trends of past insect emergence, tree budburst and their mismatch across years.

221 We used predicted temperatures under different warming scenarios to reveal expected
222 trends for emergence, budburst and mismatch. We selected three different scenarios, known as
223 RCP2.6, RCP4.5 and RCP8.5 (van Vuuren et al., 2011). For each scenario, we generated 1200
224 stochastic temperature time series over the 2001-2100 period.

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

3. Results

3.1 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.

3.1.1 Phenology shift of a single species

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

$$t_2^* = t_1^* - \frac{\Delta x}{R(x_1(t_1^*))} \int_{t_0}^{t_1^*} R'(x_1(t)) dt. \quad \text{Eq. 5}$$

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

$$t_2^* = t_1^* - \Delta x \Delta t \frac{R'(x_1(t_s))}{R(x_1(t_1^*))}. \tag{Eq. 6}$$

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

3.1.2 Effects on the mismatch

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 5 and 6 indicate that information about the current phenology ($R(x(t^*))$) and the sensitivity ($R'(x(t))$) are required to quantify the change in phenology in each species and therefore the change in mismatch.

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 and the rate functions at emergence time (the terms in the denominators in Eqs 5 and 6) could differ significantly. As a result, the effect of temperature increases depends on details of each scenario. We illustrate this dependence using the rate function $R_b(\cdot)$ for balsam fir (Eq. 2) and $R_e(\cdot)$ for SBW (Eq. 3) together with a simplified time series of daily mean temperatures as modelled by

$$x_1(t) = 6.9 + 15\cos\left(\frac{2\pi(t - 200)}{365}\right) \quad \text{Eq. 7}$$

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, we use Eq 5 to approximate the advance in phenology. In this simplified model, the end of the seasonal resting period for the resource (consumer) occurs on day 127 (131), the rate curve has its highest slope at 7.14 degrees (19.2 degrees), and the end of the resting period advances by about 3.75 (3.88) days per degree increase in mean temperature. The linear approximation in Eq. 5 captures the actual end of the resting period very well (Fig. 2A). Since the resting period of the resource at historical temperature regimes ends earlier, but advances more slowly with increasing mean temperature than that for the consumer, the mismatch decreases over time. However, the difference is small

(0.13 days per degree increase). With this simplified temperature time series, the tree emerges before the insect, whereas in reality the budworm usually emerges earlier. More realistic time series give us the empirically observed pattern (see Section 3.2).

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. 6) to each species. Then the mismatch changes according to

$$\underbrace{t_{e,2}^* - t_{b,2}^*}_{\text{mismatch2}} = \underbrace{t_{e,1}^* - t_{b,1}^*}_{\text{mismatch1}} - \Delta x \Delta t \left(\frac{R'_e(x_1(t_s))}{R_e(x_1(t_{e,1}^*))} - \frac{R'_b(x_1(t_s))}{R_b(x_1(t_{b,1}^*))} \right). \quad \text{Eq. 8}$$

Since the resource emerges roughly four days prior to the consumer under historical expectations in our simplified time series (see preceding scenario), mismatch 1 is positive. The sensitivity of the resource is a relatively narrow peak around the maximum at $x=c_l$, while the sensitivity of the consumer is much broader and peaks at much higher temperatures (higher, in fact, than usually arise before emergence) (Fig 2B). Hence, 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 $x=c_l$. In addition, the rate function at emergence (the denominators in Eq. 8) differs vastly between the two species. For our particular time series, the values are $R_b(x(t_{l,b}^*)) = 0.041$ and $R_e(x(t_{l,e}^*)) = 0.00198$, respectively. 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. 8 can still be negative because the denominator in the first term is much larger than in the second. Indeed, this is what happens with the simplified time series: the phenology of both species advances, and that of the consumer advances more, so

that the mismatch decreases, no matter when a warm spell happens. The situation with realistic time series that vary across latitude is more nuanced (see below).

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.

3.2 Case study: spruce budworm - balsam fir system

3.2.1 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. 4A). There is no obvious pattern for the residuals across latitude in the range of our study (Fig. 4B).

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, Neau, 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 accuracy of both models is satisfactory.

The budworm model is sensitive to most parameters (Fig. 4C). 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. 4D).

3.2.2 Spruce budworm – balsam fir system across latitude

Both emergence (Fig. 5A) and budburst (Fig. 5B) occur later at higher latitudes, although some discrepancies may occur due to altitude. However, insects and trees are not affected by temperatures in the same way. Hence, the mismatch between both species varies across latitude (Fig. 5C). At lower latitudes, emergence is expected to occur 5 to 10 days before budburst. Hence, the whole larval population may have time to emerge before budburst occurs, which allows larvae to benefit from an important source of nutrients. At higher latitudes, emergence may sometimes occur before budburst and sometimes after. In brief, insects seem more adapted to their host phenology at lower than at higher latitudes.

3.2.3 Predicted trends according to warming scenarios

Across all scenarios, emergence and budburst are expected to occur earlier when temperatures increase. 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 a 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. 5A). By contrast, emergence of SBW is expected to shift differently across latitude (about 15 days difference compared to 10 nowadays, see Fig. 5B).

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 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 3.1.2). 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. 5 and section 3.2.3).

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

The theoretical framework presented here can be applied to other consumer-resource systems. The concrete example of the spruce budworm - balsam fir system informs the required methodology. To estimate the mismatch, the two rate accumulation functions must be calibrated accurately. It appears that the model is sensitive to the temporal resolution of the temperature time series. There are two timescales at which temperatures affect the outcome of the model. The first one occurs at the daily scale. Average daily temperatures lead to different results than a four-

hour time interval for temperatures (used throughout the present study) since variations within a day may allow for development during a few hours, even when the average temperature over the whole day may not.

The second one occurs at a broader timescale (e.g., weekly). For the study system, temperature data modelled by BioSim (Régnière, Saint-Amant, Béchard, et al., 2014) lead to realistic emergence and budburst dates when compared to real data (see section 3.2) and to a phenological mismatch, i.e., budworm usually emerging before budburst, similar to field observations (Pureswaran, Neau, et al., 2019). More simplistic distributions that do not contain any warm spell can lead to the opposite pattern (i.e., budburst occurs first). Realistic temperatures show warm periods during days with low average temperatures (i.e., late winter - early spring), which advance the insect phenology compared to simplified (cosine) distributions. The tree is less sensitive to these short warm events.

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

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479 **Authors' contribution**

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

483 **Data Availability**

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

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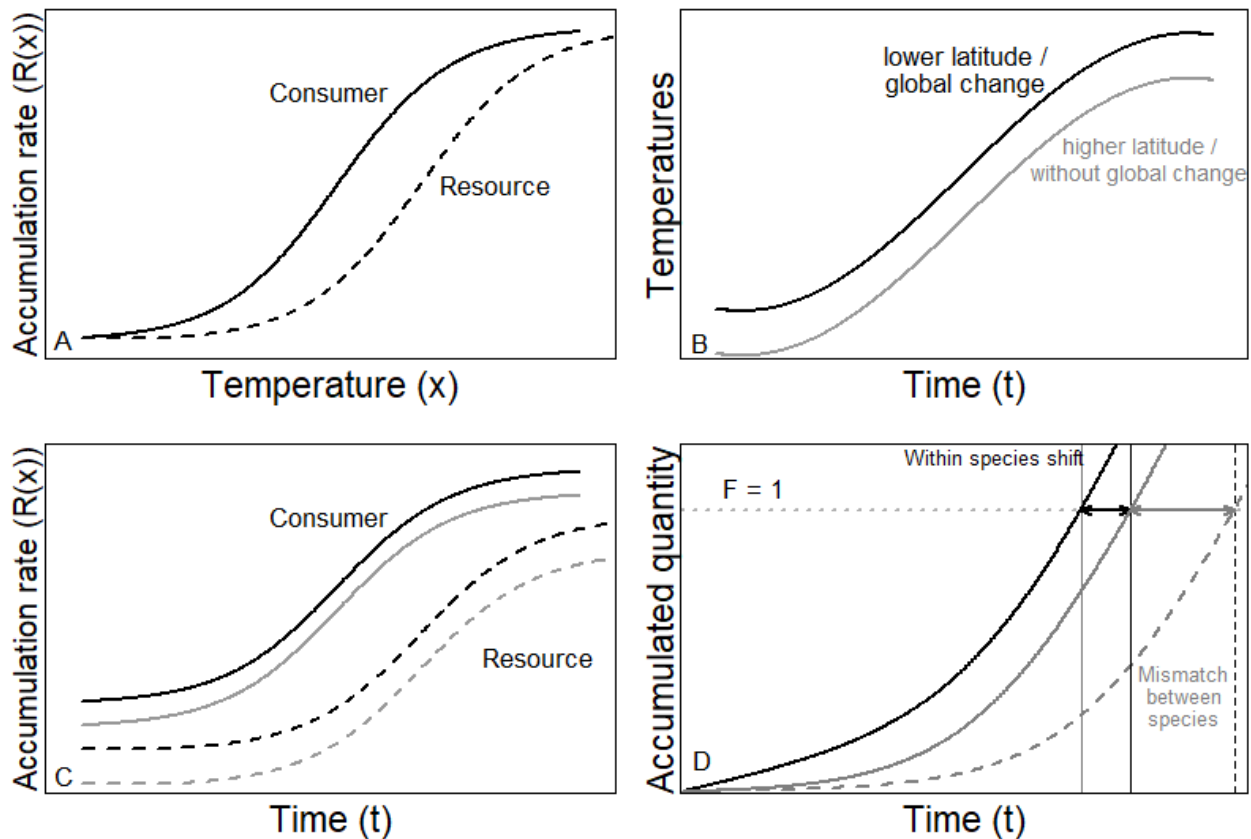
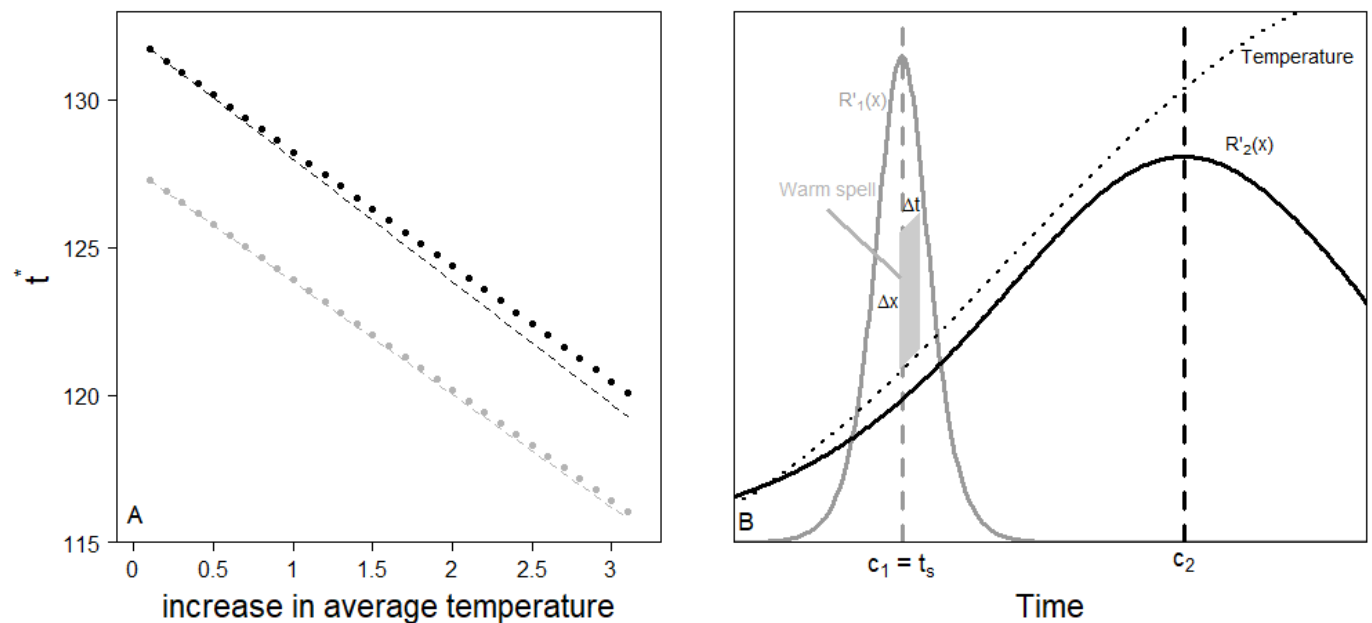


Figure 1: Illustration of theoretical development. (A) The rate accumulation function for two different species (solid line is consumer and dashed line is resource). (B) Two simplified temperature time series (black line is warmer and grey line is cooler). (C) Four combinations of rate accumulation; 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 (same location and same time).



663

664 **Figure 2:** Effects of (A) a constant temperature difference, and (B) a short warm spell, on species

665 phenology. For both panels, black is the consumer (SBW), and grey is the resource (balsam fir).

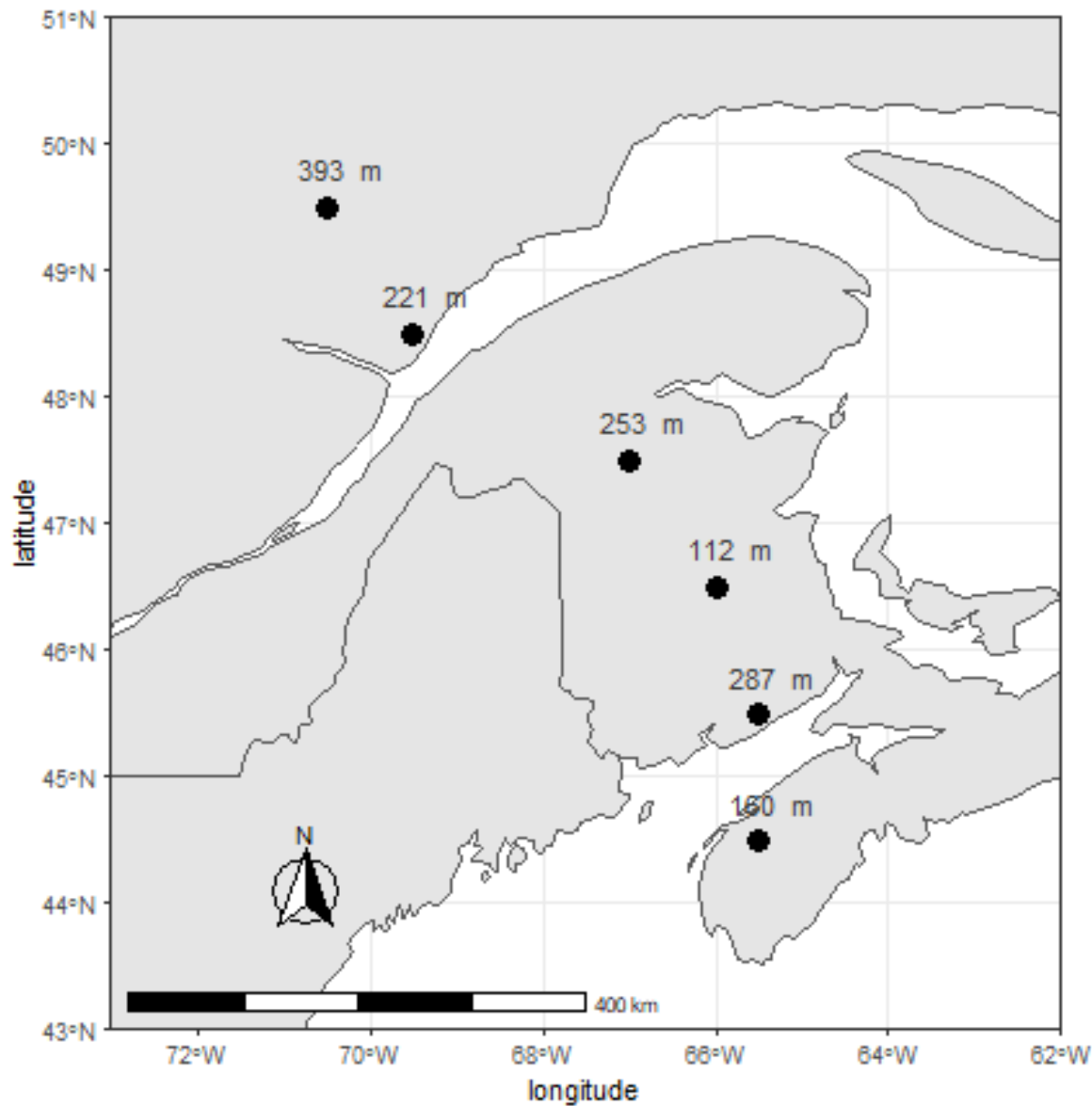
666 (A) A constant temperature difference advances species phenology. Solid is the predicted value,

667 dashed is the linear approximation from the model with simple time series. (B) The two species

668 have their R' that peaks at different temperatures. A short warm spell will mostly affect the

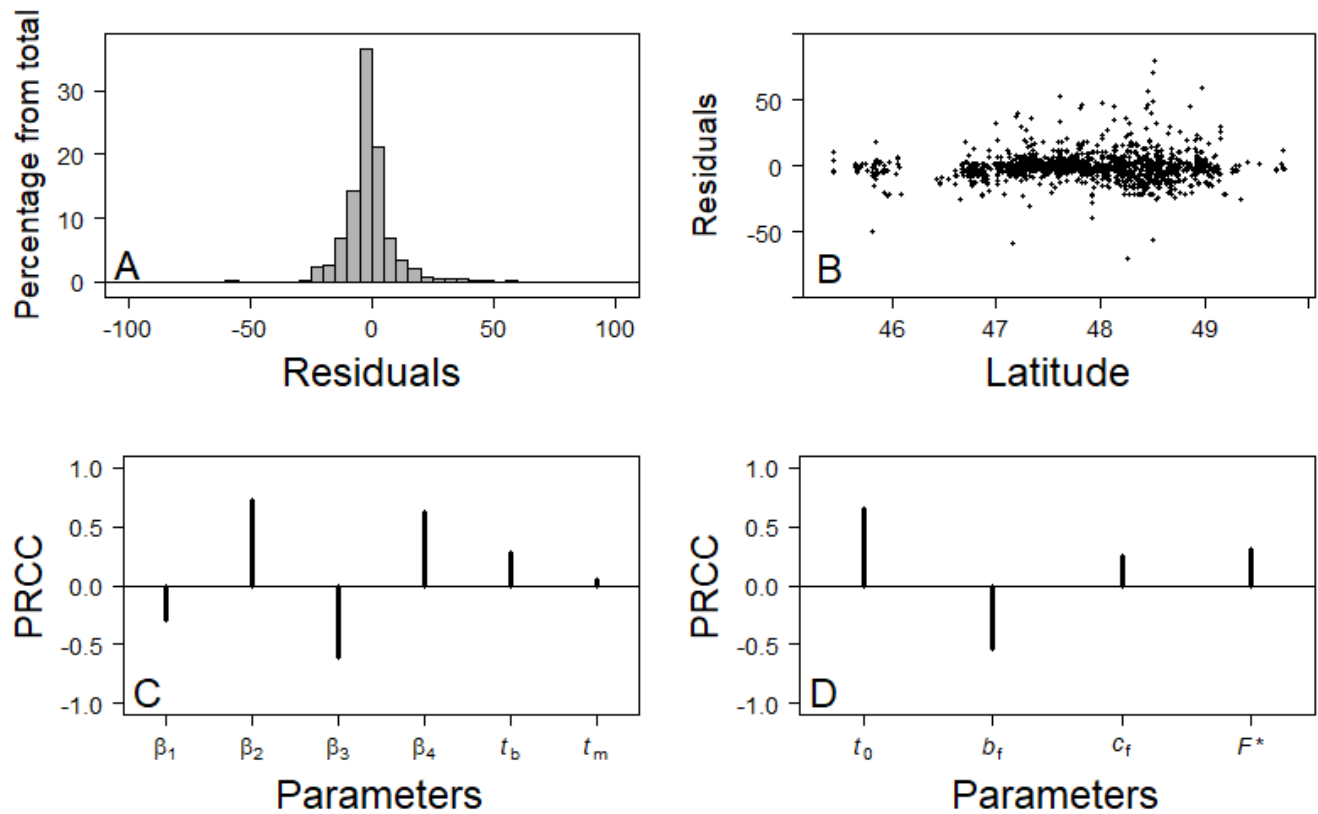
669 species for which R' is highest at that time (in this example, the tree is more sensitive than the

670 insect).



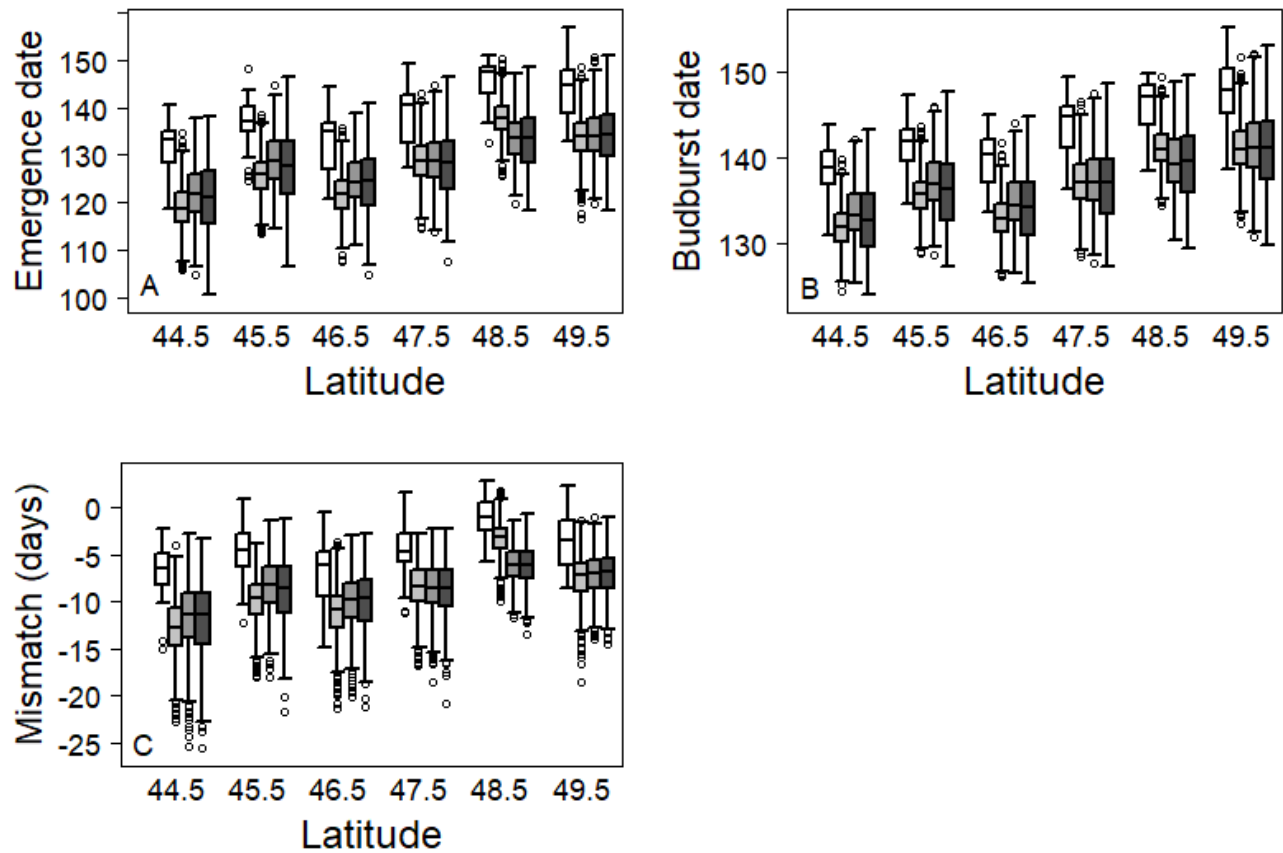
671

672 **Figure 3:** Location of the sample sites where temperature data were collected for past and future
673 trends. Points are located across a gradient of latitude in Nova-Scotia, New Brunswick, and
674 Quebec. Altitude is indicated above each point.



675

676 **Figure 4:** Fitting residuals of the balsam fir model and sensitivity analysis. (A) Residuals follow
 677 a Normal distribution centered on 0. (B) No obvious latitudinal patterns can be found on the
 678 residuals within the range of latitudes that is used throughout the rest of the study. (C) Partial
 679 Rank Correlation Coefficient (PRCC) shows that the SBW model is sensitive to most parameters
 680 especially β_2 , β_4 and x_b that delay emergence, and β_3 that advances phenology. (D) The tree
 681 model is mostly sensitive to b_f that hastens budburst, and t_0 that delays budburst.



682

683 **Figure 5:** Latitudinal distribution of (A) emergence date of SBW (Julian days), (B) budburst
684 date, and (C) mismatch between emergence and budburst date. For each latitude, the white box
685 (left one) represents the 1996-2016 period. Grey boxes represent expected outcomes according to
686 RCP 2.6 (light grey), RCP 4.5 (dark grey), and RCP 8.5 (black) scenarios over 2021 to
687 2100. Both emergence and budburst are expected to occur later at higher latitudes. Overall
688 warming scenarios, both events are expected to occur earlier in the year. Nowadays, emergence is
689 expected to occur 5 to 10 days before budburst at low latitudes, while at higher latitudes,
690 emergence may sometimes occur before budburst and sometimes after. For all warming
691 scenarios, an increase in mismatch is expected. At low latitudes, emergence may occur too early

692 some years, which may lead to low survival of SBW. At higher latitudes, emergence is expected
693 to systematically occur a few days before budburst, which would increase survival of SBW.

Supplementary information

A temperature-driven model of phenological mismatch provides insights into the potential impacts of climate change on consumer-resource interactions

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In this supplementary material, we give the details for the mathematical derivation of the two sensitivity formulas for the end time of the seasonal resting period of a species. The general equation that connects the start time t_0 , the rate curve $R(x)$ and the threshold F to the end time t^* of the resting period is

$$\int_{t_0}^{t^*} R(x(t))dt = F. \quad \text{Eq. S1}$$

General features

We want to determine how t^* changes when the temperature $x = x(t)$ changes by a small amount. More formally, we will derive a formula for the linear approximation

$$t^*(\epsilon) = t^*(0) + \epsilon \frac{dt^*}{d\epsilon} \quad \text{Eq. S2}$$

where ϵ measures the magnitude of the small change, $t^*(0)$ is the end time when there is no change in the temperature time series from historical data, and the derivative is the sensitivity of the end time with respect to small changes.

We write the change in temperature as $x(t) + \epsilon z(t)$, where $z(t)$ is the pattern in which the temperature differs from the expectation and ϵ is small. Since the end time now depends on ϵ , we write $t^* = t^*(\epsilon)$. The sensitivity of the end time with respect to ϵ is given by the derivative

$$\frac{dt^*}{d\epsilon} \text{ for } \epsilon = 0. \quad \text{Eq. S3}$$

This expression will depend on the pattern of temperature difference, $z(t)$. We will discuss two specific patterns below.

When we substitute these expressions into the defining equation for t^* above, ϵ appears twice: once in the upper limit of integration and once in the integrand. To emphasize these two occurrences, we write the left-hand side of the equation as a function of two variables, namely

$$I(t^*(\epsilon), R(x + \epsilon x)) = \int_{t_0}^{t^*(\epsilon)} R(x(t)) + \epsilon z(t) dt \quad \text{Eq. S4}$$

When we differentiate the equation that defines the end time, $I(t^*, R) = F$, with respect to ϵ , we

use the chain rule repeatedly and obtain

$$\frac{d}{d\epsilon} I(t^*(\epsilon), R(x + \epsilon x)) = \frac{\partial I}{\partial t^*} \frac{dt^*}{d\epsilon} + \frac{\partial I}{\partial R} \frac{dR}{dx} \frac{dx}{d\epsilon} = 0 \quad \text{Eq. S5}$$

The derivative of the integral in Eq. S4 with respect to the end time is simply the integrand evaluated at the end time. The derivative of the integral with respect to the integrand is the integral itself since this is linear. The derivative of the rate function with respect to x is the usual derivative and the derivative of x with respect to ϵ is z , by our definition above. Then we can solve the above equation for the quantity we are looking for and find

$$\frac{dt^*}{d\epsilon} = \frac{-\int_{t_0}^{t^*} R'(x(t))z(t)dt}{R(x(t^*))} \quad \text{Eq. S6}$$

Hence, the end time has the linear approximation

$$t^*(\epsilon) \approx t^*(0) + \epsilon \frac{dt^*}{d\epsilon} = t^*(0) + \epsilon \frac{-\int_{t_0}^{t^*} R'(x(t))z(t)dt}{R(x(t^*))} \quad \text{Eq. S7}$$

As expected, the pattern by which the temperature deviates, $z(t)$, appears in this formula. We look at two interesting special cases for this pattern.

Specific patterns

The first case is that the temperature change is constant throughout the period, independent of time.

In that case, we can set $\epsilon z(t) = \Delta x$ to be the constant temperature difference. Then the function

$z(t)$ drops out of the above integral and the end time is given by

$$t^*(\epsilon) \approx t^*(0) - \Delta x \frac{-\int_{t_0}^{t^*} R'(x(t))dt}{R(x(t^*))} \quad \text{Eq. S8}$$

Since $R'(x) > 0$ and $R(x) > 0$, the end time decreases if the temperature increases, i.e., the phenology advances. We knew this already from general consideration, but now we have an explicit expression for how much the advance is per degree increase.

The second case in which we can simplify the general formula is that there is a warm or cold spell of relatively short duration at a particular time during the resting phase. Then $\epsilon z(t) = \Delta x$ during the spell of duration Δt , starting at time t_s , and $z(t) = 0$ otherwise. The integral in the numerator of Eq. S6 can be approximated by

$$\epsilon \int_{t_0}^{t^*} R'(x(t))z(t)dt = \Delta x \int_{t_s}^{t_s+\Delta t} R'(x(t))dt \approx \Delta x \Delta t R'(x(t_s)) \quad \text{Eq. S9}$$

Hence, the expression for the end time is approximately

$$t^*(\epsilon) \approx t^*(0) - \Delta x \frac{\Delta t R'(x(t_s))}{R(x(t^*))} \quad \text{Eq. S10}$$

This means that the end time is most sensitive to a warm or cold spell when the derivative of the rate function is the highest, all other things being equal.

Derivative of the rate function

$$R(x) = \frac{1}{1 + \exp(b(x - c))}, \quad \text{Eq. S11}$$

we can explicitly calculate the derivative as

$$R'(x) = \frac{-b \exp(b(x - c))}{(1 + \exp(b(x - c)))^2}, \tag{Eq. S12}$$

which is positive since b is negative. To find the maximum of the derivative, we differentiate again and find

$$R''(x) = \frac{-b^2 \exp(b(x - c))(1 - \exp(b(x - c)))}{(1 + \exp(b(x - c)))^3} \tag{Eq. S13}$$

The maximum of R occurs where $R = 0$, which happens when $x = c$ (see Fig. 2B).